Stress, Security, and Scent: The influence of chemical signals on the social lives of domestic cats and implications for applied settings

Kristyn R. Vitale Shreve, Monique A. R. Udell

Department of Animal and Rangeland Sciences, Oregon State University 112 Withycombe Hall, 2921 Southwest Campus Way, Corvallis, OR 97331, USA

Corresponding author- Kristyn Vitale Shreve, Email: kristyn.shreve@oregonstate.edu Phone: (541) 737-3431, Fax (541) 737-4174

Abstract

Although millions of cats live among humans worldwide the scientific community knows relatively little about cat behavior and cognition. Olfaction is an important perceptual sense for many members of Carnivora, however the role of chemical signals in cat social relationships is not fully understood. Research indicates chemical signals play an important role in many areas of cat behavior including mother-offspring and conspecific interactions and exploration of their environment. Chemical cues appear to play a role in stress and anxiety reduction, allowing cats to feel secure in their environment. A better understanding of cat chemical signals, especially as it relates to within and between species communication, may lead to an increase in cat wellbeing as humans can utilize this knowledge in applied settings. Therefore, the purpose of this review is to investigate how cats process and use chemical signals in social contexts and identify ways this information can be applied to address cat behavioral issues, such as inappropriate litter box and scratching behavior, and improve cat welfare, including species-appropriate ways of reinforcing the human-cat bond.

Keywords

Cat, *Felis sylvestris catus*, Olfactory Communication, Chemical Signals, Social Cognition, Human-Cat Bond

1. Introduction

Chemical signals, which include pheromones and “signature mixtures”, are an important component of communication for members of the order Carnivora and are often used to facilitate or promote species-typical behaviors (Crowell-Davis et al., 2004; Gorman and Trowbridge, 1989; Pageat and Gaultier, 2003; Wyatt, 2010). Wyatt (2015) defines pheromones as a molecule or set of chemical compounds that have evolved for communication within a species. One individual emits the pheromone, which elicits a stereotyped behavior or response in the conspecific receiving the pheromone. Animals also produce signature mixtures, which are signals with a unique chemical profile that may be used to distinguish individuals or members of a specific group. All signature mixtures, and almost all pheromones, are detected by olfactory processes in the main olfactory system or vomeronasal organ (Wyatt, 2010).

Although millions of cats, *Felis sylvestris catus*, coexist with humans worldwide, the scientific community is only beginning to understand the cognition and behavior of cats (for a review see Vitale Shreve and Udell, 2015). Chemical communication is essential for solitary cats which establish large home ranges and do not commonly encounter conspecifics face-to-face (Bradshaw and Cameron-Beaumont, 2000). These signals provide a scent history of the spatial movements, behavior, health and sexual status of conspecifics, allowing cats to gain this information without physically contacting the other individual (Gorman and Trowbridge, 1989; Leyhausen, 1965). Socially living cats engage in non-random associations with “preferred associates” (Curtis et al., 2003) and may use signature mixtures to distinguish between familiar and unfamiliar individuals (Nakabayashi et al., 2012; Natoli, 1985a) in order to engage in affiliative or agonistic interactions with these conspecifics (Bradshaw and Cameron-Beaumont, 2000; Crowell-Davis et al., 2004).

Although the production of chemical signals, their perception through olfactory processes, and the behavioral response to these signals plays a central role in domesticated cat communication and behavior (especially social behavior), the function, scope and importance of these abilities are often not

given the same level of attention dedicated to other domesticated species (e.g. dogs or pigs), which may lead some to erroneously underestimate the significance of this communication modality in cats. Importantly, a better understanding of cat chemical signals has critical applied implications, as scent (and marking) plays an important role in many species-typical cat behaviors, problem behaviors, and can also serve as enrichment if properly understood and applied. Therefore the purpose of this review is to investigate how cats process and use chemical signals in social contexts, and identify ways this information can be used to improve cat welfare, including additional species-appropriate ways of reinforcing the human-cat bond.

2. Perception, Production & Behavioral Response to Chemical Signals

2.1. Processing chemical signals

The perception of chemical cues occurs via a number of olfactory mechanisms that allow the cat to process signals they receive from other individuals. One pathway to olfactory perception occurs when a scent enters the cat's nasal pathways through their nostrils. The cat's nasal cavity is lined by the mucociliary blanket, which contains nerves, blood vessels, and cilia. The cilia aid in keeping bacteria and foreign objects out of the nasal cavity (Eldredge et al., 2008). In order to detect odor, the scent molecules must travel through the surface of the olfactory epithelium, which contains a layer of mucus, produced by the Bowman's glands and protects it from direct contact with air. After traveling through the mucus, the odor molecules reach the scent receptors, which are located on the dendrites of the first-order olfactory neurons (Bradshaw et al., 2012). Finally, signals are sent from the olfactory bulb to areas of the brain associated with the chemical structure of the odorant.

Currently, there is limited knowledge about what parts of the brain are activated in response to specific, or categories, of scents in domestic cats, although this may now be possible for future research to address given greater accessibility to brain scan technology. For example, the caudate is one region of the brain associated with processing odorants. In other species including humans, dogs, monkeys and rats (see Berns et al., 2015), a wealth of knowledge indicate activation of the caudate is associated with rewards and positive experiences. Berns and colleagues (2015) examined the influence of scent stimuli on

the activation of brain activity in un-sedated dogs. Dogs were trained to remain still in an fMRI machine while experimenters presented scents from familiar and unfamiliar humans and conspecifics. Berns and colleagues found that although the olfactory bulb/peduncle was activated by all scents, the caudate region was maximally activated by the scent of the familiar human. This indicates dogs can discriminate the scent of individuals and they have the highest positive association with the familiar human's scent. Even though no such study has yet been conducted with cats, we propose a similar response might be seen in the caudate region of cats, which are known to discriminate between individual humans (Collard, 1967; Saito and Shinozuka, 2013; Slingerland et al., 2008), something that could be put to empirical test in the future.

The second important pathway to the perception of chemical signals in cats occurs through the mouth and involves the vomeronasal organ; a specialized olfactory organ containing neurons that detect chemical stimuli. Research on the function of the vomeronasal organ indicates it receives information from chemical stimuli, including but not limited to, sexual pheromones (Verberne and de Boer, 1976). Structurally, the vomeronasal organ is located at the roof of the mouth and is connected to the nasal and oral cavities via the nasopalatine canal (Bradshaw et al., 2012). The organ is comprised of two fluid-filled sacs that run backward from the nasopalatine canal and connect to the nasal cavity (Bradshaw et al., 2012; Eldredge et al., 2008). To process chemical cues with the vomeronasal organ, cats engage in a behavior called flehmen in which they slightly open their mouth into a grimace, allowing the ducts to open and scent molecules to pass into the vomeronasal receptors. This behavior is involved in chemosensory analysis and transports fluid-borne materials from the oral cavity to the vomeronasal organ which allows the cat to "taste" chemical stimuli (Hart and Leedy, 1987). Males engage in the flehmen behavior when identifying sexually receptive females as mates (Verberne and de Boer, 1976) and both males and females display flehmen behavior when presented with urine markings (Bradshaw et al., 2012; Hart and Leedy, 1987).

There are three families of receptor proteins within the mammalian vomeronasal organ: V1Rs, V2Rs and FPRs. Thus far, only V1Rs have been studied in domestic cats; therefore, not much is known

about the functionality of the V2R and FPR receptors (Bradshaw et al., 2012; Young et al., 2010). One hypothesis is the number of V1R receptor gene variants is correlated with the ability to discriminate between chemical stimuli. Research indicates tigers have 21 gene variants (Brahmachary and Poddar-Sarkar, 2015) and domestic cats have 30 gene variants (Young et al., 2010) indicating that some felids are able to discriminate between a great variety of chemical stimuli.

Although additional behavioral research is needed to determine the extent to which cats can discriminate between scents, this research would suggest that understanding cat olfaction is just as central to ensuring optimal cat welfare as it has been considered for dogs, and could have important implications for cat enrichment. It also raises the question about whether cats could be utilized in scent based working roles in environments where dogs are less appropriate. Like other species, cats are able to discriminate between various cues, including olfactory, auditory, and visual stimuli (Burnat et al., 2005; Mayes et al., 2015; Mumma and Warren, 1968; Pisa and Agrillo, 2009; Wilkinson and Dodwell, 1980). Therefore, it may be possible to train cats for search and rescue or other scent detection applications in settings where a cat's physical agility or size would make them a superior choice (ability to climb, fit in small spaces, balance, lighter weight). More research in this area is needed for cats specifically, however similar considerations including size, weight and agility have already resulted in a broader spectrum of species being considered for use in these working roles in recent years, including the giant African pouched rat (*Cricetomys gambianus*) which has been successfully used for scent detection of landmines, tuberculosis (Poling et al., 2011; Weetjens et al., 2009) and may also prove to be a viable option for human search and rescue (La Londe et al., 2015) with additional research. Given that more cats are kept as pets in the United States than dogs, domestic cats may also prove to be appropriate alternatives for medical scent detection or olfactory assistance animals for patients who are uncomfortable with dogs or rats.

2.2. Production and use of chemical signals

Domesticated cats, like many of their wild counterparts, have a number of mechanisms to produce chemical signals. Scent glands exist throughout a cat's body, however the location and function of these glands are still debated (Spotte, 2014) Sebaceous glands are located on the head, between the

digits, and in the perianal area. Temporal glands are located on each side of the forehead. The submental gland exists under the chin. The circumoral glands exist at the corners of a cat's lips (Bradshaw and Cameron-Beaumont, 2000; Crowell-Davis et al., 2004). As cats rub these glands against objects or other individuals, it is thought a secretion is left behind and the individual's scent is deposited (Crowell-Davis et al., 2004). Allorubbing, in which a cat rubs their body (often forehead, cheeks, flank or tail) against another individual, is seen as an affiliative behavior that indicates a social relationship between the individuals involved (Bradshaw et al. 2012; Crowell-Davis et al., 2004). During this "mutual rubbing" both tactile and olfactory signals are exchanged resulting in sharing of the cats' scents (Bradshaw et al., 2012).

Five types of facial pheromones have been identified from the sebaceous secretions of cat cheeks (Pageat and Gaultier, 2003). The function of all five pheromones it is not yet well understood, however it appears the various pheromones are secreted in different contexts, with the F2, F3, and F4 pheromones known to be involved in marking behavior (Pageat and Gaultier, 2003). The F2 pheromone is used predominately in a sexual context as males display for a mate. Tomcats will rub their faces on objects near a sexually active female, depositing the F2 pheromone, and potentially improving the effectiveness of a male's sexual display. The F3 pheromone is often deposited when rubbing on objects and may be used by the cat to orient themselves spatially, marking "known" and commonly used areas in their home range. Finally, the F4 pheromone is used for allomarking of other individuals. The F4 pheromone is deposited in social situations where cats allorub conspecifics, humans, or other species. This promotes affiliative behavior that signals the decreased likelihood of aggressive behavior with the individual (Bradshaw et al., 2012). The F4 pheromone may also play a role in communication with familiar conspecifics specifically, as cats appear to commonly engage in this marking behavior in the presence of a familiar individual (Pageat and Gaultier, 2003). Although the function of the F1 and F5 pheromones remain unknown, the chemical compounds comprising all 5 pheromones is known (for a list of chemical composition see Pageat and Gaultier, 2003). Future research should examine the behavioral response of cats to presentation of the F1 and F5 pheromones. Additionally, the mechanisms that influence the release

of each specific pheromone are unknown. Evidence indicates the secretions produced by the ear gland of dogs are influenced by the social status of the dog, with some secretions only being produced by more assertive dogs (Pageat and Gaultier, 2003). Future research should examine the circumstances under which each facial pheromone in cats is produced, to what extent cats have voluntary control over pheromone production, and the function(s) of this response. This knowledge could have important implications for understanding cat social behavior and may prove useful in applied settings, as synthetic cat pheromones become more commonplace.

The first pheromone to be produced synthetically was the F3 pheromone, which is known commercially as Feliway™. As stated, in its natural context the F3 pheromone is associated with chin and neck rubbing on objects or object marking. In its commercial form, this compound has been shown to reduce negative behaviors (e.g., urine marking, scratching), stereotypic behaviors (e.g., excessive grooming), and anxiety and improve feeding, activity, and play behavior. Overall, Feliway™ appears to have a calming influence on cats, prevents stress, and exhibits an overall emotionally stabilizing function (Pageat and Gaultier, 2003). This may support the idea this kind of scent marking, even if the scent is left by other cats or placed artificially on objects within a home range, may facilitate stress reduction. Additionally, the presence of natural or artificial cat odors applied to a previously cat-free environment (e.g., a new home, a shelter room or enclosure) might aid a new cat's transition into this space, facilitating exploration and reducing stress. Furthermore, it would also suggest cleaning procedures that remove too much cat scent from an area where cats are housed might result in increased stress and reduced welfare.

The F4 synthetic pheromone, known as Felifriend™, is used for increasing amicability for unfamiliar intra- and inter-specific interactions. Cats exposed to Felifriend™ in the presence of an unfamiliar conspecific or human seem to react to the individual as though he/she is familiar and therefore more amicable and less aggressive encounters occur (Pageat and Gaultier, 2003). This is similar to the function of the naturally produced F4 pheromone. Typically Felifriend™ is used when introducing cats to new people or conspecifics or under other stressful situations, such as when cats are taken to the veterinarian (Pageat, 1997; Pageat and Tessier, 1997). However with additional research other

possibilities could exist, for example it is possible that natural or artificial applications of the pheromone could facilitate socialization to other species (for example dogs).

In addition to gland secretions and pheromones, cats use scratching, saliva, urine, and feces, as marking signals in chemical communication. Saliva, can be deposited during allorubbing (Feldman, 1994; Verberne and de Boer, 1976) and may also be used as a communication signal to newborn kittens, as discussed below (Arteaga et al, 2013). Object scratching can serve as a chemical signal as scent is deposited from the plantar pad glands onto the object (Mengoli et al., 2013). This scent may accumulate as scratching events on the object occur more frequently (Feldman, 1994) and may serve as an olfactory reference point for the individual (Mengoli et al., 2013). With scratching a normal behavior for cats to engage in, it is not surprising many owners consult professionals about inappropriate scratching or choose to declaw their cats (Landsberg, 1991). However, a survey of Italian cat owners found when a scratching post is present in a cat's environment, the cat will typically use the post (Mengoli et al., 2013). Therefore, many inappropriate scratching events may be addressed by merely providing the cat with an appropriate scratching surface, placing that surface in an area of the home the cat frequents, and using behavioral modification to positively reinforce use of the surface.

Another method of scent marking, use of urine and feces, can cause distress for owners. Litter box issues lead as the most common reason owners take their cat to the veterinarian (Kuhne, 2015) and inappropriate use of the litter box is a leading reason for surrendering cats to shelters (Miller et al., 1996). It is thought urine communicates specific information on the sexual status, location, or emotional state of another individual (e.g., conspecific is aroused) (Crowell-Davis et al., 2004). Urine spraying can be categorized as occurring in sexual (reproductive function) or reactional (threats to resources/insecurity) conditions or may be a response to a health issue (Mills et al., 2011). Both sexes display the behavior, however males seem to engage in the behavior at a higher rate (Feldman, 1994).

Although less common, inappropriate defecation can also be an issue for cat owners. In domestic cats and some smaller felids, including bobcats (*Lynx rufus*), feces are typically buried, especially when in close proximity to kitten denning sites as seen with the black-footed cat (*Felis nigripes*) (Bailey, 1974;

Molteno et al., 1998). This behavior makes adaptive sense, as the odor of the feces may signal to predators the availability of potential prey (Molteno et al., 1998). However, feces are not always buried but sometimes left uncovered to communicate with conspecifics (Bailey, 1974; Feldman, 1994; Ishida and Shimizu, 1998). In domestic cats, factors such as hygiene, scent marking, territorial defense, animal sex, animal weight and social rank of the individual have been proposed as influences over whether feces are covered or uncovered, with evidence supporting the various roles of each of these factors (Feldman, 1994; Ishida and Shimizu, 1998). Similar to marking with urine, domestic cats also mark areas with feces. Although less common than urine marking, feces marking may serve to communicate to unfamiliar cats the marked territory is off-limits and claimed by the cat that produced the marking (Crowell-Davis et al., 2004).

Both defecation and urination outside the litter box can stem from a medical or behavioral cause—such as marking, aversion to litter box or litter box substrate, or anxiety (Herron, 2010; Siracusa, 2013). The placement of litter boxes in frequently used areas and the preservation of the cat’s scent in the box may facilitate use of the litter box and covering of feces. As stated above, cats tend to scent mark “known” areas, cats tend to have reduced anxiety in response to objects with familiar scent (Pageat and Gaultier, 2003), and felids typically cover their feces near denning sites (Bailey, 1974; Molteno et al., 1998). Finally, use of the synthetic F3 pheromone, Feliway™, has been shown to reduce inappropriate urination and may therefore be useful in cases where inappropriate litter box use is due to anxiety (Herron, 2010).

2.3. Behavioral responses to chemical stimuli

In addition to naturally produced chemical signals, other biologically relevant olfactory stimuli appear to elicit a behavioral response in cats. Researchers have studied and developed applied uses for olfactory stimuli to increase the welfare of domestic and wild cats in captive settings. Ellis and Wells (2010) exposed domestic cats to one of five olfactory stimuli conditions. Conditions included a control, in which no additional olfactory stimulus was presented, a cloth infused with no scent, a cloth infused with lavender scent (a biologically non-relevant odor known to have a calming influence), a cloth infused with

catnip (a stimulant known to evoke a response in cats), and a cloth containing the scent of a prey item (a biologically relevant odor). Researchers observed cat behavior in the different conditions to determine if olfactory enrichment benefited the cats. Ellis and Wells found cats exposed to catnip spent an average of 11.4% of their time interacting with the stimulus, significantly more than any of the other conditions. This would suggest cats have a preference for this stimulus, and may indicate catnip can serve as olfactory enrichment for domestic cats by increasing activity level, exploration, and possibly other species typical behaviors.

A similar experiment was conducted by Wells and Egli (2004) with captive black-footed cats (*Felis nigripes*), a member of the same genus as the domestic cat. Black-footed cats were exposed to a control condition, a cloth infused with nutmeg, a cloth infused with catnip, and finally a cloth infused with the body odor of a prey animal. The black-footed cats' behavior was significantly influenced by all of the experimental odors. Cats spent more time moving around their pen, grooming, exploring the cloth and exploring the pen as compared to when no scent was present. Cats also spent less time exhibiting sedentary behaviors such as sitting and resting in response to the experimental odors. Together, this indicates olfactory enrichment can positively influence active behaviors and reduce the overall duration of sedentary behaviors and potentially stereotypic behaviors, leading to a viable enrichment alternative for domesticated pet, and wild captive, cats. However, in both studies, researchers found a decreased response to the odor stimuli as time progressed, indicating habituation to the stimuli across both hours and days (Ellis and Wells, 2010; Wells and Egli, 2004). Consequently, Wells and Egli (2004) propose the type of scent utilized may be less important than ensuring the rotation of different odors when scents are to be used as enrichment tools, to help prevent habituation (Ellis and Wells, 2010).

Although the production, processing and behavioral response to chemical signals are important aspects of cat behavior, many cats today live in multi-cat and even multi-species households. Therefore, it is vital to examine how cats utilize these chemical signals while in engaging in social behaviors. This knowledge can better inform human-cat and cat-cat interactions as well as aid in the security of cats within the home.

3. Influence of Chemical Signals on Cat Social Behaviors

3.1. Mother-kitten relationship

Kittens are altricial, however, unlike vision and hearing, tactile and olfactory functions are operational from birth highlighting the importance of these senses for early development (Bradshaw et al., 2012; Larson and Stein, 1984; Villablanca and Olmstead, 1979). For the first two weeks of life, a kitten's communication with its littermates and mother is guided primarily through thermo-tactile and olfactory inputs (for review see Mermet et al., 2007). In the first days, interactions revolve around nursing- as milk is the only source of sustenance for young kittens. By 1-2 days old kittens begin to display a preference for specific nipples (i.e. "teat constancy"), consistently using the same nipple to nurse (Mermet et al., 2007; Rosenblatt, 1972, 1971). This influence is so strong that kittens nursing on a non-preferred nipple will display weak sucking behavior and sometimes even release the nipple completely (Arteaga et al., 2013; Raihani et al., 2009; Rosenblatt, 1972). Kittens continue to nurse solely from their mother and display teat constancy until about 32 days old when kittens become more independent and mobile (Ewer, 1961). Following this time, kittens will nurse from unfamiliar females in addition to their mother. This suggests the reactivity to chemosensory cues that influence teat constancy decreases over time, allowing kittens to become more independent from their mother and utilize new sources of food- an important adaptation for growing kittens (Ewer, 1961; Mermet et al., 2007).

The mechanism for nipple recognition is chemical, not locational- a finding that has been shown experimentally. Kittens aged 2-6 days, rendered anosmic through removal of the olfactory bulb, were unable to locate a nipple, even after 96 hours. Therefore removal of olfactory capabilities left kittens unable to locate and respond to their mother's nipple, however it did not impair the kittens ability to suck from a bottle (Kovach and Kling, 1967; Mermet et al., 2007). Researchers believe the kitten's saliva may leave a chemical signature or that each nipple may have a different chemical profile that allows kittens to distinguish between nipples (Arteaga et al., 2013). In either case, a kitten's ability to detect olfactory cues appears to be critical to their early survival outside of human intervention.

Other early mother-kitten social interactions are mediated through chemical signals as well.

Mother cats mark the nest area through use of the secretions released from glands on their body (Mermet et al., 2007) and the kitten's scent (and that of its littermates) is also added as hair, urine and saliva are deposited in the nest area (Rosenblatt et al., 1969). The nest becomes an olfactory reference point and allows the kittens to spatially orient themselves as they become more mobile (Mermet et al., 2007). In tests where kittens have been displaced from their nest, anosmic kittens have a lower nest return rate than non-anosmic kittens. Anosmic kittens can still use auditory cues, such as cries from littermates or mother, to orient themselves, but it takes them longer to return to the nest when compared with kittens that can detect odor (Luschekin and Shuleikina, 1989; Mermet et al., 2007).

In addition to providing a spatial reference for kittens, the nest odor may facilitate kitten wellbeing, serving to reduce stress when in proximity of this stimulus. With other stimuli experimentally controlled for, kittens displaced further from the home region of their nest emit more maximum intensity distress vocalizations than those displaced closer to their nest region. Additionally, when the home region of their nest was washed, kittens did not approach their home nest and instead backed away and emitted vocalizations (Freeman and Rosenblatt, 1978a). Together, this indicates kittens are able to discriminate their surroundings based on olfactory cues and suggests the odor of the nest may exert a calming effect on kittens by indicating they are in a safe location (Freeman and Rosenblatt, 1978a; Mermet et al., 2007; Rosenblatt, 1971). Bowlby suggested a similar concept, the secure base effect, in which human infants use parents as a point from which to explore and learn about their environment. Infants can retreat to their parents when frightened to receive reassurance and comfort (Bowlby, 1958). Similarly, the nest, or scent of the mother, may serve as a secure base that promotes exploration and learning about their environment while providing a comforting area to retreat to if a frightening situation is encountered.

Additionally, it appears experience with the olfactory stimulus is important in forming this calming response. Kittens that have been isolated from birth from their mother and littermates are unable to orient to the home region of their family's nest and being placed in the nest region did not exert a calming influence on the kittens, unlike their normally reared littermates (Rosenblatt, 1971). Considering

this, it is not surprising kittens placed in an unfamiliar nest with an unfamiliar mother emit more distress vocalizations than with their own mother and also have trouble orienting to the nest region in the unfamiliar cage (Freeman and Rosenblatt, 1978b). Together, this indicates experience with family odors is necessary to respond to the olfactory cues, and those kittens that do gain this experience can readily distinguish between their family scent and an unfamiliar scent.

Many applied benefits could be discovered in this area with additional research. For example, the calming influence of the nest might be further explored using the principles of the secure base effect to examine if the presentation of the nest's scent encourages exploration in unfamiliar locations. If this is the case, this has far reaching implications for socialization of kittens and cats outside of the home. Researchers and animal trainers have commented on the difficulty of working with cats outside the home (Grimm, 2014) and with cat behavior research lagging behind dog research, the scientific and animal training community would benefit in finding ways to comfort cats outside the home. Olfactory reference points, such as cat towers where the cat's scent is deposited, could serve a function similar to a kitten's nest site, and may provide comfort to cats when outside of the home, allowing them to explore unfamiliar locations. Additionally, as seen by Freeman and Rosenblatt (1971), kittens emit distress vocalizations and fail to approach washed areas of their home nest. Taken together the current literature appears to suggest that the use of cleaning products near areas of rest, scratching posts, and litter boxes should be used sparingly. Cleaning products that cover the cat's scent or wash the scent away may cause anxiety or failure to approach the cleaned areas, leading the cat to engage in these behaviors in alternative, unwanted areas. Preserving the cat's scent should be an important consideration when dealing with behavioral issues such as inappropriate scratching and elimination.

3.2. Social relationships between conspecifics

Chemical cues continue to be important throughout a cat's life by aiding in discrimination of conspecifics. Cats presented with the feces of conspecifics spent significantly more time sniffing the feces of the unfamiliar individual over the familiar individual (Nakabayashi et al., 2012). A similar result was seen with urine, with cats investigating urine marks of unfamiliar conspecifics for longer periods of time

than the marks of familiar individuals (Natoli, 1985b; Passanisi and Macdonald, 1990). These results indicate cats collect social information about conspecifics via chemical characteristics of biological substrates (e.g. nesting material, urine, faces). No study has yet examined if cats can discriminate individuals by directly sniffing the body of another conspecific. However, in a study observing social behaviors between free-roaming colony cats, the single most common behavior exhibited between conspecifics was sniffs (one cat smells the body of another cat). Out of 22 social behaviors observed, sniffs alone made up 30.85% of total behaviors (unpublished thesis by Shreve, 2014). Additionally, cats were often observed to first sniff one another and then engage in further social interactions, suggesting this form of chemical communication may facilitate or guide subsequent social responses to conspecifics (Shreve, personal observation, 2014).

A similar result was seen by Verberne and de Boer (1976) who found sniffs often proceeded other behaviors such as rubbing on or displaying a flehmen toward a conspecific's scent. Verberne and de Boer collected ~1,200 observations of cat responses to various chemical stimuli. When placed in a room with the conspecific's scent (either with wood pegs rubbed by another cat or urine) the cats spent the initial 5 minutes of observation engaging in investigatory behaviors related to the processing of chemical signals, such as sniffing and displaying a flehmen. As time progressed, cats displayed less investigatory behaviors and more grooming and resting behaviors with rubbing and rolling staying constant throughout the observation session. This finding demonstrates that, as cats investigate the odors of their surroundings, they become more comfortable within the room, which leads to an increase in grooming and resting behaviors. Interestingly, this seems to be true independent of the type of marking present. As cats investigate conspecific odors and deposit their own scent in the room, the space may become an olfactory reference point for the cat, similar to the nest scent used by kittens, allowing cats to become more comfortable and settled within the room.

Additionally, Verberne and de Boer (1976) observed sex differences in the cat's response to the urine and glandular scents. Although both males and females extensively explored the scent marks of conspecifics by sniffing, rubbing and rolling on the various scents, males engaged in more frequent urine

spraying and flehmen behavior than females. Males may have engaged in the flehmen behavior disproportionately to collect sexual information about conspecifics (e.g., is the conspecific in heat?) and spraying to mark the area with their scent (discussed more below). Compared to males, females showed more interest in skin secretions than in urine marks; suggesting females may be investigating glandular secretions to gain social information about conspecifics (i.e. is this individual familiar?). This research suggests the chemical cues produced through urine and gland secretions are important signals in both sexual and social contexts- however the function of and behavioral response to such signals appear to be sexually dimorphic.

Given chemical communication is a key element of species typical cat social behavior, it may be especially valuable for future applied research to study the influence of added conspecific scent on the behavior and welfare of pet and captive felids. As mentioned, cats have been found to frequently sniff, explore, rub and roll on scent marks of conspecifics (Verberne and de Boer, 1976) suggesting conspecific scent may serve as effective enrichment. Given the biological relevance of this enrichment item, it is also possible cats would take longer to habituate to such stimuli or may have additional biologically relevant responses when compared with artificial olfactory enrichment items. Although it is important to note that habituation effects have been reported for cats' response to unfamiliar conspecific feces (Nakabayashi et al., 2012) and urine (Verberne and de Boer, 1976), and therefore even biologically relevant olfactory enrichment may require rotation to be optimally effective. Additionally, scent swapping could be an effective way of reducing stress during introduction of unfamiliar conspecifics or humans. Scent swapping would allow the cat to become familiar with the other individual's scent prior to physically meeting. This would be similar to how free-roaming cats would naturally encounter one another initially, first by scent and then by sight.

3.3. Home range marking

Within the scientific community there is disagreement as to whether cats hold a territory or patrol a looser home range that may overlap with the ranges of other cats (Feldman, 1994). Cats are often thought of as territorial, implying they should be found to defend specific geographic areas and resources

within them. Those that have reported on such behavior have predicted cats use chemical signals to define the extent of their territory (Crowell-Davis et al., 2004). However another possibility is cats may utilize scent marking within their home range, not specifically as a deterrent to other cats, but possibly akin to the way kittens rely on the scent of their home nests. Feldman (1994) observed cat scent marking behavior within an outdoor enclosure to determine if markings were being used territorially or to define a home range. Scent marking behaviors included urine spraying, deposition of feces, tree scratching, and object rubbing. Feces were buried and not left exposed and trees were scratched along movement paths rather than along the perimeter of the area. Similar to Verberne and de Boer (1976), Feldman found behavioral differences between males and females. Males sprayed urine more frequently than females, with males often spraying visible objects, such as tree stumps. Both sexes rubbed on objects within their enclosure, with males rubbing more frequently than females.

Overall, Feldman (1994) found no indication of cats using chemical signals specifically as a mechanism for territorial marking. Feldman concluded, if cats were marking a territory the majority of scent marking behavior would occur along the perimeter of the enclosure and would indicate the area belonged to a specific group of cats and unknown conspecifics should avoid the territory. Instead, scent markers were found more often within the enclosure, along areas commonly used by the cats within the group, which may again point to the use of olfactory cues as spatial reference points. The only exception was feces, which were located outside of the core feeding area, along the perimeter of the enclosure. Researchers have noted feces are often deposited away from core feeding areas, potentially for hygienic regions (Bateson et al., 1988; Ishida and Shimizu, 1998) and Feldman notes the limited space in the enclosures may have influenced placement of feces along the perimeter rather than feces being placed as a territorial marker. Feldman notes, cats were rarely seen avoiding or leaving an area after investigating scent marks, indicating they were not used as an active method of deterrence. However, Feldman does not discuss how the addition of an unfamiliar individual (not a member of the social group) into the enclosure may change this result. Because only conspecifics that lived in the enclosure investigated the scent marks, the social relationships within the group may have influenced how conspecifics reacted to the feces (e.g.

the feces are from a familiar, preferred associate and therefore would not serve as a deterrent). Future research should explore these topics more in-depth to determine if social relationships influence how scent markers are used.

Finally, it may be possible cats display flexibility in whether they patrol a home range or defend a territory. The formation of domestic cat social groups are influenced by the distribution of food, shelter and mate resources (Liberg et al., 2000; Macdonald et al., 2000) and this may influence the style in which they form ranges. The availability of resources is known to influence bobcat behavior. When resources (denning and prey) are available, bobcats have more dispersed ranges than when resources are scarce and bobcats have greater overlap in their home ranges (Bailey, 1974). Therefore, future research should examine how the availability and distribution of resources influence chemical signals and range formation in cats. Such research would have an applied benefit relating to aggression and litter box use. Knowledge of the extent to which environmental conditions produce territorial behavior and the potential manipulation of these conditions may prove useful in multi-cat homes where urine spraying or fighting may be an issue.

4. Conclusion

An animal's welfare can be "determined by whether, and how closely, it is able to perform behaviours that are 'natural'" (Casey and Bradshaw, 2005). Therefore, in order to increase the welfare and wellbeing of cats, we must understand what behaviors are vital to the mental health of the cat. The research covered in this review has demonstrated that the exchange of chemical signals are vital to the social lives of domestic cats. As more people keep exclusively indoor cats, often for safety or environmental reasons, cats lose the opportunity to encounter a wide range of changing scents as well as the opportunity to deposit their scent outdoors or in areas shared with cats outside the family unit. The loss of this natural opportunity should prompt questions and empirical investigations into what this means for pet cat welfare in the absence of recommended alternatives. In addition to the provisioning of rotating scents, other options such as outdoor catteries (enclosures where cats can spend part of their time safely outdoors) or leash walking should be considered where cats can not only encounter new scents but rub

their scent along commonly used areas. Although many hold the false belief that cats are untrainable, both empirical and applied evidence has demonstrated that cats can be trained- including the skill of walking on lead- especially when started early in life (Vitale Shreve and Udell, 2015).

Additionally, cats seem to be naturally comforted by the scent of themselves or conspecifics (Rosenblatt, 1971; Verberne and de Boer, 1976), therefore, owners should consider the importance of scent as a 'spatial reference tool' when placing litter boxes around the home and allowing for 'cat spaces', such as scratching posts, where cats can deposit their scent along areas of their home they commonly use (as seen by Feldman 1994). Along this same idea, research in this area may inform understanding and treatment of undesirable or ill-placed (e.g. in owner's bed) urination, defecation, spraying and scratching behavior in cats. Although more research needs to be done in this area, existing research may suggest that some of this behavior could be related to nest marking or serve a calming function (Freeman and Rosenblatt, 1978a,b; Mermet et al., 2007; Rosenblatt, 1971), as opposed to a territorial function. Consequently, in some cases, a cat urinating and defecating within the home (especially in areas of rest/nesting) may be a sign of anxiety, not territoriality. If this is the case, then the common recommendation of thoroughly removing this scent to prevent re-marking may actually produce the opposite effect, further increasing anxiety.

Behavioral issues, including scratching and litter box issues, are a leading reason for surrender of cats at shelters (Miller et al., 1996) and feral and stray populations continue to increase due largely to the abandonment of unneutered pets outdoors. Although odorants have been utilized in the management of free-roaming cats, (i.e. use of odor to attract cats to management devices) little is known about how chemical signals influence the behavior of free-roaming cat populations (Fisher et al., 2015). Additionally, the role human intervention (early weaning, use of artificial odorants, neutering) plays in the use and response to chemical signals remains relatively unstudied in cats. In dogs, sexual status (i.e. neutered or intact) influences the amount of time another dog investigates urine from that individual, with urine from intact dogs eliciting longer investigation than urine from neutered individuals (Lisberg and Snowdon, 2009). A better understanding of cat chemical signals, especially as it relates to within and

between species communication and individual wellbeing, may lead to a decrease of cats surrendered to shelters or abandoned outdoors. As we learn more about the domestic cat, humans may also find ways to utilize cats' natural communicative style and sensitivity to scent to help this species feel even more secure in the human home.

Acknowledgements

KVS was supported by the Oregon State University Provost's Distinguished Graduate Fellowship Program and the National Science Foundation Graduate Research Fellowship Program under Grant No. (1314109-DGE). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation. Thank you to Dr. Samantha O'Hanlon of the Oregon State University School of Psychological Science for her comments on an early version of this manuscript.

References

- Arteaga, L., Bautista, A., González, D., Hudson, R., 2013. Smell, suck, survive: chemical signals and suckling in the rabbit, cat, and dog, in: East, M.L., Dehnhard, M. (Eds.), *Chemical Signals in Vertebrates 12*. Springer, New York, NY, pp. 51–59.
- Bailey, T.N., 1974. Social Organization in a Bobcat Population. *J. Wildl. Manag.* 38, 435–446. doi:10.2307/3800874
- Bateson, P., Turner, D.C., Bateson, P., 1988. Questions about cats, in: Turner, D.C. (Ed.), *The Domestic Cat: The Biology of Its Behaviour*. Cambridge University Press, Cambridge, UK, pp. 193–201.
- Berns, G.S., Brooks, A.M., Spivak, M., 2015. Scent of the familiar: An fMRI study of canine brain responses to familiar and unfamiliar human and dog odors. *Behav. Processes, New Directions in Canine Behavior* 110, 37–46. doi:10.1016/j.beproc.2014.02.011
- Bowlby, J., 1958. The nature of the child's tie to his mother. *Int. J. Psychoanal.* 39, 350–373.
- Bradshaw, J., Cameron-Beaumont, C., 2000. The signaling repertoire of the domestic cat and its undomesticated relatives., in: Turner, D.C., Bateson, P.P.G. (Eds.), *The Domestic Cat: The Biology of Its Behaviour*. Cambridge University Press, Cambridge, UK, pp. 67–93.
- Bradshaw, J.W.S., Casey, R.A., Brown, S.L., 2012. *The Behaviour of the Domestic Cat*, 2 edition. ed. CABI, Wallingford, Oxfordshire, UK ; Boston, MA.
- Brahmachary, R.L., Poddar-Sarkar, M., 2015. Fifty years of tiger pheromone research. *Curr. Sci.* 108, 2178.

- Burnat, K., Stiers, P., Lutgarde, A., Vandenbussche, E., Zernicki, B., 2005. Global form perception in cats early deprived of pattern vision. *NeuroReport* 16, 751–4. doi:10.1097/00001756-200505120-00019
- Casey, R., Bradshaw, J.W., 2005. The Assessment of Welfare., in: Rochlitz, I. (Ed.), *The Welfare of Cats*. Springer New York, New York, NY, pp. 23–45.
- Collard, R.R., 1967. Fear of strangers and play behavior in kittens with varied social experience. *Child Dev.* 38, 877–891. doi:10.2307/1127265
- Crowell-Davis, S.L., Curtis, T.M., Knowles, R.J., 2004. Social organization in the cat: a modern understanding. *J. Feline Med. Surg.* 6, 19–28. doi:10.1016/j.jfms.2003.09.013
- Curtis, T.M., Knowles, R.J., Crowell-Davis, S.L., 2003. Influence of familiarity and relatedness on proximity and allogrooming in domestic cats (*Felis catus*). *Am. J. Vet. Res.* 64, 1151–1154. doi:10.2460/ajvr.2003.64.1151
- Eldredge, D., Carlson, D.G., Carlson, L.D., Griffin, J., 2008. *Cat Owner's Home Veterinary Handbook, Fully Revised and Updated, 3 edition*. ed. Wiley Publishing, Hoboken, New Jersey.
- Ellis, S.L.H., Wells, D.L., 2010. The influence of olfactory stimulation on the behaviour of cats housed in a rescue shelter. *Appl. Anim. Behav. Sci.* 123, 56–62. doi:10.1016/j.applanim.2009.12.011
- Ewer, R.F., 1961. Further Observations On Suckling Behaviour in Kittens, Together With Some General Considerations of the Interrelations of Innate and Acquired Responses. *Behaviour* 17, 247–260. doi:10.1163/156853961X00060
- Feldman, H.N., 1994. Methods of scent marking in the domestic cat. *Can. J. Zool.* 72, 1093–1099.
- Fisher, P., Algar, D., Murphy, E., Johnston, M., Eason, C., 2015. How does cat behaviour influence the development and implementation of monitoring techniques and lethal control methods for feral cats? *Appl. Anim. Behav. Sci.* 173, 88–96. doi:10.1016/j.applanim.2014.09.010
- Freeman, N.C.G., Rosenblatt, J.S., 1978a. The interrelationship between thermal and olfactory stimulation in the development of home orientation in newborn kittens. *Dev. Psychobiol.* 11, 437–457. doi:10.1002/dev.420110508
- Freeman, N., Rosenblatt, J., 1978b. Specificity of Litter Odors in the Control of Home Orientation Among Kittens. *Dev. Psychobiol.* 11, 459–468. doi:10.1002/dev.420110509
- Gorman, M.L., Trowbridge, B.J., 1989. The role of odor in the social lives of carnivores, in: Glittleman, J.L. (Ed.), *Carnivore Behaviour, Ecology and Evolution*. Chapman and Hall, London, UK, pp. 57–88.
- Grimm, D., 2014. What Are Cats Thinking? *Slate*.
- Hart, B.L., Leedy, M.G., 1987. Stimulus and hormonal determinants of flehmen behavior in cats. *Horm. Behav.* 21, 44–52. doi:10.1016/0018-506X(87)90029-8

518 Herron, M.E., 2010. Advances in Understanding and Treatment of Feline Inappropriate Elimination. *Top.*
 519 *Companion Anim. Med.* 25, 195–202. doi:10.1053/j.tcam.2010.09.005
 520 Ishida, Y., Shimizu, M., 1998. Influence of social rank on defecating behaviors in feral cats. *J. Ethol.* 16,
 521 15–21. doi:10.1007/BF02896349
 522 Kovach, J.K., Kling, A., 1967. Mechanisms of neonate sucking behaviour in the kitten. *Anim. Behav.* 15,
 523 91–101. doi:10.1016/S0003-3472(67)80017-4
 524 Kuhne, F., 2015. Causes, diagnosis, and animal behavioural therapy of feline house soiling. *Tieraerztliche*
 525 *Prax. Ausg. Kleintiere Heimtiere* 43, 50–57.
 526 La Londe, K.B., Mahoney, A., Edwards, T.L., Cox, C., Weetjens, B., Durgin, A., Poling, A., 2015.
 527 Training pouched rats to find people. *J. Appl. Behav. Anal.* 48, 1–10. doi:10.1002/jaba.181
 528 Landsberg, G.M., 1991. Feline scratching and destruction and the effects of declawing. *Vet. Clin. North*
 529 *Am. Small Anim. Pract.* 21, 265–279.
 530 Larson, M.A., Stein, B.E., 1984. The use of tactile and olfactory cues in neonatal orientation and
 531 localization of the nipple. *Dev. Psychobiol.* 17, 423–436. doi:10.1002/dev.420170408
 532 Leyhausen, P., 1965. The communal organization of solitary mammals. Presented at the Symposium of
 533 Zoological Society, London, UK, pp. 249–263.
 534 Liberg, O., Sandell, M., Pontier, D., Natoli, E., 2000. Density, space organisation and reproductive tactics
 535 in the domestic cat and other felids., in: Turner, D.C., Bateson, P.P.G. (Eds.), *The Domestic Cat:*
 536 *The Biology of Its Behaviour.* Cambridge University Press, Cambridge, pp. 119–147.
 537 Lisberg, A.E., Snowden, C.T., 2009. The effects of sex, gonadectomy and status on investigation patterns
 538 of unfamiliar conspecific urine in domestic dogs, *Canis familiaris*. *Anim. Behav.* 77, 1147–1154.
 539 doi:10.1016/j.anbehav.2008.12.033
 540 Lushekin, V.S., Shuleikina, K.V., 1989. Some sensory determinants of home orientation in kittens. *Dev.*
 541 *Psychobiol.* 22, 601–616. doi:10.1002/dev.420220606
 542 Macdonald, D.W., Yamaguchi, N., Kerby, G., 2000. Group-living in the domestic cats: its sociobiology
 543 and epidemiology, in: Turner, D.C., Bateson, P.P.G. (Eds.), *The Domestic Cat: The Biology of Its*
 544 *Behaviour.* Cambridge University Press., Cambridge, pp. 95–115.
 545 Mayes, E.-R.E., Wilkinson, A., Pike, T.W., Mills, D.S., 2015. Individual differences in visual and
 546 olfactory cue preference and use by cats (*Felis catus*). *Appl. Anim. Behav. Sci.*
 547 doi:10.1016/j.applanim.2015.01.003
 548 Mengoli, M., Mariti, C., Cozzi, A., Cestarollo, E., Lafont-Lecuelle, C., Pageat, P., Gazzano, A., 2013.
 549 Scratching behaviour and its features: a questionnaire-based study in an Italian sample of
 550 domestic cats. *J. Feline Med. Surg.* 15, 886–892.

551 Mermet, N., Coureaud, G., McGrane, S., Schaal, B., 2007. Odour-guided social behaviour in newborn
 552 and young cats: an analytical survey. *Chemoecology* 17, 187–199. doi:10.1007/s00049-007-
 553 0384-x
 554 Miller, D.D., Staats, S.R., Partlo, C., Rada, K., 1996. Factors associated with the decision to surrender a
 555 pet to an animal shelter. *J. Am. Vet. Med. Assoc.* 209, 738–742.
 556 Mills, D.S., Redgate, S.E., Landsberg, G.M., 2011. A meta-analysis of studies of treatments for feline
 557 urine spraying. *PLoS ONE* 6, e18448. doi:10.1371/journal.pone.0018448
 558 Molteno, A.J., Sliwa, A., Richardson, P.R.K., 1998. The role of scent marking in a free-ranging, female
 559 black-footed cat (*Felis nigripes*). *J. Zool.* 245, 35–41. doi:10.1111/j.1469-7998.1998.tb00069.x
 560 Mumma, R., Warren, J.M., 1968. Two-cue discrimination learning by cats. *J. Comp. Physiol. Psychol.* 66,
 561 116–121. doi:10.1037/h0025987
 562 Nakabayashi, M., Yamaoka, R., Nakashima, Y., 2012. Do faecal odours enable domestic cats (*Felis catus*)
 563 to distinguish familiarity of the donors? *J. Ethol.* 30, 325–329. doi:10.1007/s10164-011-0321-x
 564 Natoli, E., 1985a. Spacing pattern in a colony of urban stray cats (*Felis catus* L.) in the historic centre of
 565 Rome. *Appl. Anim. Behav. Sci.* 14, 289–304. doi:10.1016/0168-1591(85)90009-7
 566 Natoli, E., 1985b. Behavioural responses of urban feral cats to different types of urine marks. *Behaviour*
 567 94, 234–243.
 568 Pageat, P., 1997. The F3 facial pheromone (FELIWAY): a means to inhibit sexually stimulated urine
 569 marking in cats. Presented at the Congress of the European Association of Veterinary
 570 Pharmacology and Toxicology, Madrid.
 571 Pageat, P., Gaultier, E., 2003. Current research in canine and feline pheromones. *Vet. Clin. North Am.*
 572 *Small Anim. Pract.* 33, 187–211.
 573 Pageat, P., Tessier, Y., 1997. Usefulness of the F3 synthetic pheromone FELIWAY in preventing
 574 behaviour problems in cats during holidays. Presented at the Proceedings of the first International
 575 Conference on Veterinary behavioural Medicine, Birmingham, p. 231.
 576 Passanisi, W.C., Macdonald, D.W., 1990. Group discrimination on the basis of urine in a farm cat
 577 colony., in: Macdonald, D.W., Muller-Schwarze, D., Natzynczuk, S.E. (Eds.), *Chemical Signals*
 578 *in Vertebrates* 5. Oxford University Press, Oxford, pp. 337–345.
 579 Pisa, P.E., Agrillo, C., 2009. Quantity discrimination in felines: a preliminary investigation of the
 580 domestic cat (*Felis silvestris catus*). *J. Ethol.* 27, 289–293. doi:10.1007/s10164-008-0121-0
 581 Poling, A., Weetjens, B., Cox, C., Beyene, N.W., Bach, H., Sully, A., 2011. Using Trained Pouched Rats
 582 to Detect Land Mines: Another Victory for Operant Conditioning. *J. Appl. Behav. Anal.* 44, 351–
 583 355. doi:10.1901/jaba.2011.44-351

584 Raihani, G., González, D., Arteaga, L., Hudson, R., 2009. Olfactory guidance of nipple attachment and
585 suckling in kittens of the domestic cat: Inborn and learned responses. *Dev. Psychobiol.* 51, 662–
586 671. doi:10.1002/dev.20401

587 Rosenblatt, J., 1972. Learning in Newborn Kittens. *Sci. Am.* 227, 18–25.

588 Rosenblatt, J., Turkewitz, G., Schneirla, T.C., 1969. Development of Home Orientation in Newly Born
589 Kittens. *Trans. N. Y. Acad. Sci.* 31, 231–250.

590 Rosenblatt, J.S., 1971. Suckling and Home Orientation in the Kitten: A Comparative Developmental
591 Study., in: Tobach, E., Aronson, L., Shaw, E. (Eds.), *The Biopsychology of Development*.
592 Academic Press, New York, NY, pp. 345–410.

593 Saito, A., Shinozuka, K., 2013. Vocal recognition of owners by domestic cats (*Felis catus*). *Anim. Cogn.*
594 16, 685–690. doi:10.1007/s10071-013-0620-4

595 Siracusa, C., 2013. Animal Behavior Case of the Month. *J. Am. Vet. Med. Assoc.* 243, 213–215.
596 doi:10.2460/javma.243.2.213

597 Slingerland, L.I., Robben, J.H., Schaafsma, I., Kooistra, H.S., 2008. Response of cats to familiar and
598 unfamiliar human contact using continuous direct arterial blood pressure measurement. *Res. Vet.*
599 *Sci.* 85, 575–582. doi:10.1016/j.rvsc.2007.12.008

600 Verberne, G., de Boer, J., 1976. Chemocommunication among domestic cats, mediated by the olfactory
601 and vomeronasal senses. *Z. Für Tierpsychol.* 42, 86–109. doi:10.1111/j.1439-
602 0310.1976.tb00958.x

603 Villablanca, J.R., Olmstead, C.E., 1979. Neurological development of kittens. *Dev. Psychobiol.* 12, 101–
604 127. doi:10.1002/dev.420120204

605 Vitale Shreve, K.R., Udell, M.A.R., 2015. What’s inside your cat’s head? A review of cat (*Felis silvestris*
606 *catus*) cognition research past, present and future. *Anim. Cogn.* 1–12. doi:10.1007/s10071-015-
607 0897-6

608 Weetjens, B.J., Mgode, G.F., Machang’u, R.S., Kazwala, R., Mfinanga, G., Lwilla, F., Cox, C., Jubitana,
609 M., Kanyagha, H., Mtandu, R., Kahwa, A., Mwessongo, J., Makingi, G., Mfaume, S., Van
610 Steenberge, J., Beyene, N.W., Billet, M., Verhagen, R., 2009. African pouched rats for the
611 detection of pulmonary tuberculosis in sputum samples. *Int. J. Tuberc. Lung Dis.* 13, 737–743.

612 Wells, D.L., Egli, J.M., 2004. The influence of olfactory enrichment on the behaviour of captive black-
613 footed cats, *Felis nigripes*. *Appl. Anim. Behav. Sci.* 85, 107–119.
614 doi:10.1016/j.applanim.2003.08.013

615 Wilkinson, F., Dodwell, P.C., 1980. Young kittens can learn complex visual pattern discriminations.
616 *Nature* 284, 258–259. doi:10.1038/284258a0

617 Wyatt, T.D., 2015. How Animals Communicate Via Pheromones. *Am. Sci.* 103, 114–121.

618 Wyatt, T.D., 2010. Pheromones and signature mixtures: defining species-wide signals and variable cues
619 for identity in both invertebrates and vertebrates. *J. Comp. Physiol. A* 196, 685–700.
620 doi:10.1007/s00359-010-0564-y
621 Young, J., Massa, H.F., Hsu, L., Trask, B.J., 2010. Extreme variability among mammalian V1R gene
622 families. *Genome Res.* 20, 10–18. doi:10.1101/gr.098913.109
623