Anim Cogn (2015) 18:1195–1206
DOI 10.1007/s10071-015-0897-6

REVIEW

What's inside your cat's head? A review of cat (*Felis silvestris catus*) cognition research past, present and future

Kristyn R. Vitale Shreve[1] · **Monique A. R. Udell**[1]

Received: 21 January 2015 / Revised: 2 June 2015 / Accepted: 28 June 2015 / Published online: 8 July 2015

Abstract The domestic cat (*Felis silvestris catus*) has shared an intertwined existence with humans for thousands of years, living on our city streets and in our homes. Yet, little scientific research has focused on the cognition of the domestic cat, especially in comparison with human's other companion, the domestic dog (*Canis lupus familiaris*). This review surveys the current status of several areas of cat cognition research including perception, object permanence, memory, physical causality, quantity and time discrimination, cats' sensitivity to human cues, vocal recognition and communication, attachment bonds, personality, and cognitive health. Although interest in cat cognition is growing, we still have a long way to go until we have an inclusive body of research on the subject. Therefore, this review also identifies areas where future research must be conducted. In addition to the scientific value of future work in this area, future research on cat cognition could have an important influence on the management and welfare of pet and free-roaming cats, leading to improved human–cat interactions.

Keywords Cat · Cognition · Social cognition · Human–cat communication · Human–cat bond · Domestication

✉ Kristyn R. Vitale Shreve
kristyn.shreve@oregonstate.edu

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

Introduction

At first glance, it may seem that any member of the family Felidae would make an unlikely human companion. Most members of Felidae lead solitary lives and only engage in social behaviors during mating or kitten rearing (Macdonald et al. 2000). The only members of Felidae that commonly live in social groups are lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), and the facultatively social domestic cat (*Felis silvestris catus*), which can display varying levels of non-obligatory social behavior depending on environment and upbringing (Leyhausen 1988; Mellen 1993; Bradshaw and Cameron-Beaumont 2000; Turner 2014). So, how did the domestic cat become one of the world's most popular pets, with over 600 million cats living among humans worldwide (Driscoll et al. 2009)?

We may have a long way to go before we know. While research on domestic cat behavior and cognition is growing, many questions remain unanswered. How the development of cat behavior and cognition is influenced by factors such as species-specific biological predispositions, domestication and lifetime experiences, including the human–cat bond, remains largely unexplored. In general, comparatively little research has been devoted to cat cognition, especially when compared to our other popular companion, the domestic dog (Udell et al. 2010; Merola et al. 2015). Nonetheless, research on cat cognition could have important theoretical value and management and welfare implications, including improved human–cat interactions (Bernstein 2014). Therefore, the purpose of this review is to survey the current status of several areas of cat cognition research, broadly defined as "all ways in which animals take in information through the senses, process, retain and decide to act on it" (see Shettleworth 2001, p. 277), that have received at least some scientific

attention and to identify areas where future research is needed to gain a better understanding of an animal with which many share their homes and almost all share their streets.

Perception

Cat sensation and perception have historically received more attention than other areas of cat cognition. The majority of this research has examined cat auditory perception (Gerken and Sandlin 1977; Costalupes 1983; Heffner and Heffner 1985; Rauschecker and Kniepert 1994; Cornwell et al. 1998; Malhotra et al. 2004; Witte and Kipke 2005), olfactory perception (Willey 1973; Verberne and de Boer 1976; Verberne 1976; Won et al. 1997; Mermet et al. 2007), visual perception (Blakemore and Cooper 1970, 1971; Peck and Blakemore 1975; Blakemore and Van Sluyters 1975; Blake and Hirsch 1975; Buisseret and Singer 1983; Cornwell et al. 1998), and cutaneous sensory mechanisms, including vibrissae, or whiskers, which aid in movement in low-light conditions (Bradshaw et al. 2012) and supplement for the cats lack of short-distance vision (Williams and Kramer 2010).

Research on cat perception has demonstrated how early sensory experiences influence brain development and perception (Blakemore and Cooper 1970; Blakemore and Van Sluyters 1975; Blake and Hirsch 1975; Korte and Rauschecker 1993; Burnat et al. 2002, 2005). One such classic experiment on vision by Blakemore and Cooper (1970) found kittens selectively reared in an apparatus covered with either vertical or horizontal lines could not detect the opposite line orientation to the one in which they were reared under, providing evidence for environment-dependent neural plasticity. Additionally, Blake and Hirsch (1975) found that monocularly deprived kittens had a reduced proportion of binocular cortical cells and impaired binocular depth perception, providing evidence that early experience is critical in developing cells used for binocular depth and stereopsis. Rearing environment also influences perception. Laboratory-reared cats have demonstrated an impairment in response and discrimination learning to visual stimuli (Żernicki 1993), an impairment of visual associative learning (Żernicki 1999), and delayed response to auditory cues (Wikmark and Warren 1972) as compared to free-roaming cats, indicating that poor rearing environment can influence perceptual ability later in life. Training has also been found to improve performance on visual perceptual tasks (Sasaki et al. 2010), such as an increased contrast sensitivity to specific frequencies of gratings accompanied by changes in the primary visual cortex (Hua et al. 2010).

While much of this research originated from scientific interest in the development of sensory systems and the effects of sensory deprivation on perceptual development more generally (including as a model for human sensation and perception), an understanding of the sensory development of cats can also provide insight into the umwelt of this species specifically (von Uexküll 1957). This is an important factor when designing research to study the behavior and cognition of cats. For example, olfaction appears to play an important role from birth, being especially important in the early days of the mother–kitten relationship (Ewer 1959; Mermet et al. 2007; Raihani et al. 2009; Arteaga et al. 2013). Olfactory cues remain important throughout a cat's life, providing social information about conspecifics (Verberne and de Boer 1976; Verberne 1976; Natoli 1985), defining home ranges (Feldman 1994), and influencing the human–cat relationship (Pageat and Gaultier 2003; Ellis and Wells 2010; Mills et al. 2011). Auditory and visual developments progress more slowly. Kittens begin to orient toward auditory stimuli between 11 and 16 days and visual stimuli between 16 and 21 days (Norton 1974). While many cognitive tests for cats have been visual in nature, a deeper understanding of the perceptual world of cats may allow for new approaches to the study of cognition that could capitalize on their other sensory abilities. For example, given the importance of olfaction in the social behavior of cats, studies of human–cat interaction or even individual recognition by cats should take olfaction into account. Social experiments based on olfaction specifically, or those comparing social recognition based on visual versus olfactory cues, could also be designed.

Object permanence and working memory

Object permanence, or the concept that when an object disappears from sight it continues to exist (Piaget 1936, 1937), is considered an important cognitive milestone for human infants. It can also be an important cognitive ability in animals, especially those that are adept hunters, such as cats. If prey disappears behind cover, obscuring the prey from view, cats would benefit from the ability to remember the location of the prey before its disappearance (Goulet et al. 1994). Visible displacement tests are one method of testing object permanence and involve the disappearance of an attractive object, such as food, behind an obstacle, such as a box. An individual is successful in the visual displacement test if they search for the object behind the obstacle where the object was last seen, suggesting the species is able to cognitively represent the object even when the object is not visible (Fiset and Doré 2006). Research indicates that cats are readily able to solve visible displacement tests (Triana and Pasnak 1981; Thinus-Blanc et al. 1982; Doré 1986; Goulet et al. 1994; Fiset and Doré

2006) rapidly acquiring this ability as they mature (Dumas and Doré 1989, 1991).

Object permanence can also be tested using an invisible displacement test. In this test, the attractive object is placed in a container and moved behind an obstacle, such as a screen, where the object is then removed. The container is then shown to the subject, this time with the object missing. In order to solve the invisible displacement test, the subject must recognize the object is no longer in the container, that it must have been removed behind the obstacle, and search for the object at this location (Miller et al. 2009). The majority of research has indicated that cats are unable to represent invisible displacement of an object (Doré 1986, 1990; Goulet et al. 1994, 1996) although Dumas (1992) found that cats successfully solved the invisible displacement test when a different, more species-relevant, methodology was used. In this version of the test, the cat was presented with an apparatus made of transparent and opaque screens, with a piece of food attached to a transparent string. The food was shown through a transparent portion of the screen and moved to attract the cat's attention. Once the cat began to approach the food and moved behind an opaque section of the screen so the food was out of sight, the food was moved behind a hiding screen using the strings. Thus, the food was invisibly displaced because the disappearance of the food behind the hiding screen was not perceived by the cat. On this version of the task, the 19 cats performed significantly above chance with a mean success rate of 8.57 trails out of ten attempted trails. Dumas concluded that this methodology was more ecologically relevant because, similar to a prey item, cats must anticipate the new position of the food. Additionally, the movement of the food on the string may have been more similar to the natural movement of prey and may have elicited more interest in the task than the containers typically used in invisible displacement tests.

Working memory is an important underlying mechanism for object permanence. To examine the duration of cats' working memory, many studies have implemented the delayed-response task, in which cats are delayed in searching for an attractive object, which has disappeared (Fiset and Doré 2006). Historically, studies employing the delayed-response task found cats had a shorter working memory given a task with more choices (Yarbrough 1917). Others found cats displayed a working memory of up to 30 s for a two-choice test (Cowan 1923); however, cats' performance rapidly declined between 1 and 16 s (Meyers et al. 1962).

More recently, Fiset and Doré (2006) performed a visual displacement test and retained cats for various intervals of time before allowing them to search for the object. They found that between 0 and 10 s, the cats' performance in finding the hidden object rapidly declined, continued to decline at 30 s and remained only slightly above chance at 60 s. Therefore, despite differences in methodology, these results align with those of prior studies (Yarbrough 1917; Cowan 1923; Meyers et al. 1962; Goulet et al. 1996), suggesting the domestic cats' working memory may last as long as a minute, but rapidly declines over the 30 s following the object's disappearance.

The long-term memory of cats appears to be highly developed, as demonstrated by use of delayed visual matching and non-matching to sample in which cats performed at criteria level (80 % in 100 consecutive trails) at delays up to 10 min (Okujava et al. 2005). Further research must be undertaken to disentangle additional factors, such as age, breed and lifetime experience, that may influence the working and long-term memory of cats.

Physical causality

The ability to understand cause and effect is of great adaptive advantage as the use of causal principles allows for the transfer of learning gained in one situation to a novel situation (Seed et al. 2006). Whitt et al. (2009) studied the extent to which cats understand physical causality through use of the string-pulling test. Cats were first trained to obtain a piece of food attached to a short string placed perpendicularly under a box, with only the tip of the string visible to the cat. They were then presented with different arrangements of strings including one long string, two parallel strings and two crossed strings. In arrangements with two strings, food was attached to only one string. Cats had ten attempts to retrieve the food successfully by pulling on the correct string. Although cats successfully pulled the *single* string to receive the food, they were unable to perform above chance when presented with either of the *two-string* arrangements. This finding suggests that the cats did not understand the function of the string in its means-end connection with the food reward. However, as this area of cognition has received sparse attention, more research must be conducted to fully examine the abilities of cats in this domain, especially to ensure confirmation or development of species appropriate methodology. For example, Whitt et al. (2009) suggested that the cats may have found string-pulling rewarding in itself, whether or not they received the food. As Whitt et al. (2009, p. 742) state, "It is therefore important to investigate cognitive abilities based on their importance for the differing ecological needs of species."

Quantity and time discrimination

Pisa and Agrillo (2009) undertook the first study to determine the cognitive ability of domestic cats to discriminate between quantities. The authors found that cats could be

trained to visually distinguish between groups of two and three dots. This ability was also seen in lions (*P. leo*), which were able to auditorily discriminate between the vocal recordings of an individual lion versus a group of three lions (McComb et al. 1994; Heinsohn 1997). Numerical competence in cats may provide an advantage in obtaining the largest quantities of food (Pisa and Agrillo 2009); however, more research must be undertaken to determine the mechanisms cats use for quantity discrimination and the evolutionary advantage of this ability.

Many owners believe their cat has a concept of time, stating their cat knows precisely when it is time for dinner or bed. This would be consistent with what is known about timing abilities in many animal species; however, to date, no research has thoroughly examined this behavior in domestic cats. There is, however, some empirical support for the idea that cats can discriminate varying time intervals. Rosenkilde and Divac (1976) found that cats were able to discriminate between confinement periods of 5 and 20 s, and most cats were able to discriminate between even shorter periods such as between 5 and 10 s or even between 5 and 8 s. The ability to discriminate time intervals may imply that cats have an internal clock that is responsible for assessing the duration of events (Bradshaw et al. 2012).

Social cognition

Many domestic cats live socially and rely on communication within and between species to thrive in a variety of environments; however, science is only in the beginning stages of understanding cat sociality and social communication (Bradshaw et al. 2012). In domestic cats, which display plasticity in whether or not they live socially, the formation of social groups is dependent on the availability of food, shelter and mates (Liberg et al. 2000; Macdonald et al. 2000; Turner 2014). Although many think of cats as solitary, research indicates free-roaming domestic cat social groups are not random aggregations around a food source (Macdonald et al. 2000; Denny et al. 2002), rather cats come into proximity and engage in social behaviors with preferred associates non-randomly (Curtis et al. 2003; see also unpublished thesis work by Wolfe 2001 and Shreve 2014). Additionally, cats display a wide array of affiliative, aggressive and investigatory behaviors toward conspecifics (Bradshaw and Cameron-Beaumont 2000; Curtis et al. 2003). Likewise, cats enter into a range of relationships with humans. Some live as companion animals in human homes, and others live as strays which navigate our urban spaces, often dependent on human caretakers for resources. Pet cats have countless social encounters with humans (as well as other household members), with varying levels of complexity and success, making this species an especially interesting subject for social cognition research. While more research is needed to determine whether parallels exist between human–cat relationships and cat–cat relationships, further exploration of cat social structure may be an important starting point.

For example, socialization is the process in which appropriate social behaviors are developed toward conspecifics (Serpell 1988; Bradshaw and Hall 1999; Turner 2000a); however, this is the same process by which cats may bond with other species, including humans. This typically first occurs during a sensitive period, which in cats appears to be between 2 and 7 weeks of life (Karsh and Turner 1988). Research indicates cats exposed to multiple humans (Collard 1967), with early and frequent handling, are friendlier and less fearful of humans than those that lack this experience (Collard 1967; McCune 1995; Turner 2000a; Lowe and Bradshaw 2002). In fact, kittens handled for 40 min a day were more amicable to later handling and approached humans more frequently than kittens handled for 15 min a day (Karsh and Turner 1988; Turner 2000a). Furthermore, Casey and Bradshaw (2008) found people who adopted additionally socialized kittens stated they received significantly more emotional support from their cats. These cats also displayed less fear toward humans, as supported by previous research (Collard 1967; McCune 1995). Thus, early experience with humans can influence the manner in which the human–cat relationship is formed.

Early handling by humans can also have a physiological influence on cats more generally. Meier (1961) found kittens handled for 10 min, twice a day, matured earlier than kittens that received no additional handling. Kittens handled by humans opened their eyes approximately 1 day earlier, left the nest box approximately 3 days earlier and showed more synchrony in their EEG patterns as compared to non-handled kittens. Kittens in the handled and non-handled groups even exhibited differences in coat coloration patterns. Therefore, early socialization and human handling can be a mechanism that influences a wide range of factors related to the early development of kittens. In addition to socialization, human gender, human martial status, housing conditions, number of cats and humans in the household (Mertens 1991; Turner 1991) and cat personality (see below) can influence the human–cat relationship.

Sensitivity to human cues

Research has begun to explore the human–cat relationship directly, delving into how cats respond to human interaction and communicate with humans. Sensitivity to human cues, such as the ability to follow human gestures, and the

use of social gazing are important mechanisms in human–animal communication. Miklósi et al. (2005) examined whether cats were able to follow human pointing cues that indicated the location of a hidden food reward and the extent to which cats gazed at humans for help on an unsolvable task. Cats successfully followed human gestures to obtain a reward. However, when unable to obtain the reward in the unsolvable task, cats persisted in trying to solve the task and often did not gaze at the human for assistance. The fact that cats infrequently gazed at humans prompted the researchers to suggest that cats do not utilize gazing as an attention-getting behavior. However, a recent study further examining cat–human gazing behavior suggests cats may engage in human-directed gazing more frequently than previously assumed (Merola et al. 2015).

Social referencing is the ability of an individual to use the emotional reactions of others to evaluate unfamiliar or difficult situations and adjust their behavior accordingly (Mumme et al. 1996). Merola et al. (2015) examined whether cats have the ability to evaluate the emotional state of humans via social referencing in the presence of an unfamiliar stimulus, a fan with streamers. Merola and colleagues only included cats that had a history of seeking human contact, were used to changes in their environment and were familiar with traveling in their carrier, to ensure cat participants would not be perturbed by the travel and experience of the new environment. After the cat investigated the testing room, cat–owner dyads experienced four test phases in one of two emotional conditions, positive (happy) or negative (fearful): (1) The fan was turned on and the human looked at the fan with a neutral facial expression, (2) the fan continued to run and the human talked in a happy or fearful manner, provided the matching facial expressions, and alternated their gaze between the fan and cat, (3) participants approached and interacted with the fan, talked in a happy voice or fearful voice, and both groups alternated their gaze between the fan and cat, (4) and finally the fan was turned off and participants continued to interact with the fan, talked in a happy or fearful voice, and both groups again alternated their gaze between the fan and cat. Merola et al. examined whether referential looking (looking to the owner immediately before or after looking at the fan) and behavioral regulation existed through five categories of behavior including gaze orientation (three consecutive looking behaviors toward owner, fan, etc.), action (static, interaction with owner or fan, etc.), body posture, stress signals (yawning, head shaking) and vocalizations.

Merola et al. (2015) found the majority of cats (79 %) looked referentially between their owner and the fan and that many cats (54 %) displayed gaze alternation when the owner stayed silent and still. This indicates cats look to their owner when presented with an unfamiliar stimulus, can discriminate between their owner's reactions and adjust their behavior in multiple ways. However, as stated above, Miklósi et al. (2005) found cats did not frequently gaze at humans for assistance on an unsolvable task. Merola and colleagues suggest these conflicting results may be due to the different incentives and social information gained in each of the experiments. It is possible cats do not use gazing when engaged in physical problem solving but reference humans when afraid or uncertain or when attempting to gain attention from humans in which they seek affiliative contact (Goodwin and Bradshaw 1998).

Further, research indicates cat behavior is influenced by human mood. Cats, within bouts of interaction, behaved sensitively to human depressive moods and engaged in more allorubbing of the head and flank (Rieger and Turner 1999), approached owners who described themselves as feeling numb less often, and approached owners who felt extroverted or agitated more frequently (Turner and Rieger 2001). Future research must build on these findings to gain a better understanding of how and when cats utilize human cues, social gazing behavior, and other methods of non-verbal communication such as emotional states. These mechanisms have allowed cats to obtain resources from humans including food, shelter and social attention, and development of these adaptations has significance in the evolution of interspecies social behavior and relationships.

Voice recognition and vocal communication

Studies have found evidence that cats can distinguish between individual humans. Saito and Shinozuka (2013) examined the abilities of pet cats to distinguish the voices of their owners from strangers. In this experiment, cats were played five human vocalizations, each calling the subject cat's name. The owner called the cat using the same inflection they would typically use when calling their cat. Four same-sex strangers also called the cat's name in the same style as the owner to keep phonological components constant between participants. Multiple behavioral responses were recorded in response to the vocal stimulus, including ear movement, head movement, pupil dilation, vocalization, tail movement, and displacement. The behavioral responses of the cats differed depending on the source of the vocalization (owner or strangers), with their response magnitude increasing when presented with their owner's voice. The results of this study suggest cats are able to recognize the vocalizations of individual humans, and that human vocalizations can prompt measurable changes in cat behavior. Additionally, Saito and Shinozuka (2013, p. 689) found cats "responded to human voices mainly through orienting behavior (ear movement and head movement), but not through communicative behavior

(vocalization and tail movement).” Further research is needed to determine how cats respond to different types of human vocalizations in different contexts (novel situations, feeding, play, etc.).

The purr is one of the most recognizable feline vocalizations, yet the biological function of the purr is still poorly understood (Bradshaw et al. 2012). Purring can occur in a variety of circumstances including social situations such as interaction with humans, interaction with conspecifics and interaction with kittens (Kiley-Worthington 1984). Research by McComb and colleagues (2009) indicates cats are able to subtly alter their purr to change the meaning of the vocalization. In this study, owners distinguished between purrs produced in food solicitation and non-solicitation contexts, such as resting, and found purr vocalizations in the food solicitation context to be more urgent and less pleasant than non-solicitation purrs. McComb et al. also found that when cats solicited food from their owners “a high-frequency voiced component” was embedded within the typical low-pitched purr (2014, p. 507). The high-frequency component of the purr may be akin to a human infant’s distress call, with the peak of this purr occurring at similar frequencies to that of an infant’s cry. McComb et al. infer there may be a mammalian propensity toward high-frequency cries to which the food solicitation purr may be appealing, and cats are able to use this purr to seek food from their owners. But, whether this high-frequency component is used specifically for communication with humans or whether it is used in other social situations, such as between mother and offspring, or between conspecifics, is still unknown. Additionally, whether the alteration of the purr between food solicitation and non-solicitation contexts is conscious or whether this purr frequently happens in other solicitation contexts, such as solicitation for affection, is also unknown. Because kittens are attributed with having at least nine different types of vocalizations and adult cats at least 16 different types of vocalizations (Moelk 1944), vocalization appears to be a key factor in cat communication. Additionally, research has found differences between vocalizations of socialized and feral cats, indicating human interaction influences vocal communication (Yeon et al. 2011). Further research must be conducted to better understand the vocal communication of cats in general, so we can discern the meaning and development of cat vocalizations for human communication, strengthening the human–cat bond.

Attachment

Attachment is an enduring affiliative social bond formed between an animal and a specific individual (Ainsworth and Bell 1970). In attachment, the animal behaves in ways that promote contact and proximity to the attachment figure (Bowlby 1958). However, secure attachments also allow individuals, be they humans or non-human animals, to feel comfortable in new settings and explore their environment (Ainsworth and Bell 1970). Edwards et al. (2007) used an adaptation of the Ainsworth Strange Situation Test (Ainsworth et al. 1978) to examine attachment between pet cats and their owners. In this test, the cat was exposed to seven events that alternated the presence and absence of an owner and stranger in the testing room, with two reunion events between the owner and cat: an introductory event to become familiar with the testing room, (1) an event between only the owner and cat, (2) an event between stranger, owner and cat where owner left at end of event, (3) an event with only stranger and cat, (4) an event when owner and cat are reunited with no stranger present, (5) an event with the cat alone in the testing room, (6) an event where the stranger re-entered the room and (7) a second reunion event between the owner and cat. Cats were observed during each event, and a number of attachment behaviors were scored including independent behaviors, such as locomotion/exploration, vigilance, inactivity and approaching the door, and interactive behaviors, including physical contact, allorubbing, playing and vocalizing with the owner or stranger.

Edwards et al. (2007) found there were significant differences in the cats’ behavior when cats were alone, with their owner or with a stranger. Cats spent significantly more time in contact with and allorubbing their owner compared with the stranger. Additionally, the cats only played with their owner and never with the stranger. Cats also engaged in more locomotion/exploration behaviors when their owner was present than when alone or with a stranger, and cats followed the owner but never the stranger. Cats spent the greatest amount of time near the door and displayed more alert behavior when the stranger was present or the cat was alone than when their owner was present. Cats were inactive longer and vocalized more when they were alone as compared to events when another person was in the testing room. Many of the aforementioned behaviors are considered attachment indicators under the Ainsworth Strange Situation Test (Ainsworth et al. 1978), indicating cats exhibit attachment behaviors and form attachment bonds with their owners (Edwards et al. 2007). Further research must be undertaken to determine what factors influence formation of attachment bonds and what attachment styles are displayed in the cat–human relationship.

If cats can form an attachment bond with their owners, it may be expected they can experience separation anxiety. Separation anxiety is a psychological condition related to attachment that occurs in many social species in which separation from an attachment figure initiates a set of

emotional, behavioral and physiological responses (Schwartz 2002). The degree of distress exhibited by the animal is directly related to how attached the animal is to the attachment figure. Schwartz (2002) examined 136 cats over a 9-year period to determine whether cats develop the clinical signs of separation anxiety characteristic of separation anxiety syndrome (SAS), and found that some cats do develop SAS and display clinical signs, such as inappropriate urination and defecation, excessive vocalization, destructiveness and psychogenic grooming.

While this body of research suggests that domestic cats have developed a range of mechanisms that facilitate their interaction with humans (Rieger and Turner 1999; Turner and Rieger 2001; Schwartz 2002; Miklósi et al. 2005; Edwards et al. 2007; McComb et al. 2009; Saito and Shinozuka 2013; Merola et al. 2015), popular articles have often presented current cat cognition research with a negative spin. For example, one popular article stated cats are "selfish" and "unfeeling" citing Saito and Shinozuka (2013) to support the idea cats "can hear you calling their name, but just don't really care" because they do not approach people in the same manner as dogs when called (Stromberg 2014). Another presented the McComb et al. (2009) research as cats "manipulating" their owners (Young 2009). This may reveal societal biases about cat behavior that have contributed to the paucity of scientific research on feline social cognition in the past. However, such interpretations demonstrate the importance of, and critical need for, more research investigating the human–cat relationship. Such biases not only shape our intellectual knowledge about cats but may also guide the behavior of cat owners, as well as others responsible for the care and welfare of millions of pet, stray or feral domestic cats. Given there are as many as 96 million cats living in human households in the USA alone (APPA 2014), outnumbering pet dogs by more than 10 million, and a large, unknown number of un-owned free-roaming cats living worldwide (Miller et al. 2014), more research in this area could have a dramatic and widespread impact.

Cat personality

Researchers across numerous disciplines have begun to explore individual differences in animal behavior, using various terms such as personality, individuality, temperament, distinctiveness, behavioral style or behavioral syndrome, (Gosling 2001, 2008; Raihani et al. 2014). While researchers have not always agreed on the correct terminology to describe the occurrence of individual differences within non-human animals, for consistency we will use the definitions provided by Gosling (2001) when referring to personality and temperament throughout. According to Gosling (2001) personality can be defined as "those characteristics of individuals that describe and account for consistent patterns of feeling, thinking and behaving" (p. 46); in other words, a prolonged state in which behavioral patterns are relatively consistent over time and various circumstances but can be influenced within the life of the animal. A closely associated idea is that of temperament, which Gosling describes as "inherited, early appearing tendencies that continue throughout life and serve as the foundation for personality" (p. 46). In this case, temperament can be used to describe the biological dispositions of the animal (Wynne and Udell 2013).

Cat owners and even researchers working with cats often indicate that they feel cats have definite personalities. For example, Feaver et al. (1986, p. 1016) stated "we felt that each animal in our laboratory colony had a distinct 'personality' in the sense that the sum total of its behaviour gave it an identifiable style." However, is this feeling supported by empirical science? Durr and Smith (1997) examined whether stable individual differences in cat temperament (a measure of personality as defined by Gosling) could be identified in testing situations. Study cats were first observed in their normal living conditions to provide an initial assessment of their behavior, including order of approach, latency, and attention span. Cats then experienced various conditions, including disruption of their social environment via confinement or overcrowding, to determine whether a stable environment is important in maintaining individual differences in cats. In additional tests, cats were presented with novel stimuli, including a moving stimulus that emitted moderate to loud noises (e.g., remote-controlled car with a motor), an unfamiliar animal (e.g., dog, rabbit), and an intense novel stimulus (e.g., vacuum cleaner that was turned on). Cats were also deprived of food and then presented with a highly desirable food item. Durr and Smith (1997) found that the behavioral responses of cats were consistent despite changes in their environment, indicating the stability of the social environment is not crucial in maintaining the stability of individual behavioral responses. The authors concluded "individuality is the expression of inherent temperament and not simply the release of responses created by a certain set of stable environmental variables" (Durr and Smith 1997, p. 416).

Other studies have also found evidence of stable personalities in cats. For example, Turner et al. (1986) found that the behavioral trait of "friendliness" was consistent in kittens aged 3–8 months. Lowe and Bradshaw (2001) found that four distinct personality styles were stable between 4 and 24 months of age (discussed further below). Additionally, Durr and Smith (1997) found that cat group structure is reliant on the individual characteristics of the cats in the group, indicating that individual differences

between cats can be influenced by conspecific social relationships and potential human relationships as well.

Studies have determined personality styles of cats utilizing various methodologies, such as human ranking of cat differences through direct observation of their behavior (Feaver et al. 1986; Turner et al. 1986; Raihani et al. 2014) or exposure to various conditions (novel stimuli, unfamiliar persons, increased socialization) with the cats' behavioral responses to these conditions recorded (Meier and Turner 1985; Mertens and Turner 1988; McCune 1995; Durr and Smith 1997). Combined, these studies have described many personality types within cats. Two traits commonly found include "boldness," which describe an individual who has actively approached novel stimuli in the past and would be expected to do the same in the future, or "shyness," which may describe an individual who has reluctantly or not approached novel stimuli in the past and would be expected to do the same in the future (Mendl and Harcourt 2000; Gosling 2001). Bradshaw et al. (2012) divided cat personality into three types, based on findings from previous research. The first personality type involves an individual with traits such as "sociable, confident, easy-going," "trusting," "bold" and initiates "friendly interactions" (Meier and Turner 1985; Feaver et al. 1986; Mertens and Turner 1988; McCune 1995). The second personality type involves an individual with traits such as "timid, nervous," "shy and unfriendly" (Meier and Turner 1985; Feaver et al. 1986; Mertens and Turner 1988), and the final personality type involves an individual with aggressive traits (Feaver et al. 1986). In addition, Lowe and Bradshaw (2001) described four distinct behavioral styles (a term they use interchangeably with personality) that exist in cats. These include the tendency to stay indoors, to rub (people or objects), to investigate and the tendency to boldness. But, other personality styles have also been described in cats (Mendl and Harcourt 1988, 2000; Bradshaw et al. 2012). More research may be needed to establish a consensus about which terminology, personality styles or traits have the most predictive value or whether some of these categories might be combined to establish a concise consistent categorization of feline behavior types.

Researchers have also questioned the point in development when differences in cat personalities arise. Raihani et al. (2014) found there were intra-litter differences in kitten behavior at as early as 5–6 days old, and kittens at 3–4 weeks old already display relatively stable behavioral differences. This indicates that differences in personality existing early in development maybe even from birth although this study did not examine kitten behavior prior to day 5, as to not disturb the early mother–kitten relationship. The researchers also noted they did not initially expect to find individual differences at such an early age. This finding may suggest there is a genetic component to personality. This is further supported by studies where fathers described as "friendly," typically sired "friendly" offspring, despite the fact the father and offspring never encountered one another (Turner et al. 1986; Reisner et al. 1994; McCune 1995) and by research indicating that littermates tend to behave more similarly than non-littermates (Lowe and Bradshaw 2001).

In addition to the genetic component of personality, proximate mechanisms appear to have an important influence as well. Lowe and Bradshaw (2001) examined the personality of the cat after the socialization period. As discussed previously, early socialization to humans can influence the friendliness of cats (Collard 1967; McCune 1995; Turner 2000a; Lowe and Bradshaw 2002), and Lowe and Bradshaw found additional support that early experiences, such as handling, also influenced the behavioral styles, or personality, of cats. Other factors have been correlated with cat personality traits including breed (Turner 2000b; Weinstein and Alexander 2010), coat color (Pontier et al. 1995; Ledger and O'Farrell 1996; Delgado et al. 2012) and social experience with conspecifics and environmental complexity (Mendl and Harcourt 2000).

There are multiple benefits to studying cat personality. By gaining a better understanding of the mechanisms underlying cat behavior, we can make more informed decisions about ways to improve the welfare of pet and shelter cats. As Gartner and Weiss (2013) point out, reliable measurements of personality can lead to an increase in cat welfare, health and well-being. For example, if we can evaluate the personality of cats using reliable methods (Feaver et al. 1986; Turner et al. 1986; Raihani et al. 2014), we can make better decisions about housing situations for shelter cats by matching up suitable personality types of cats to appropriate personality, lifestyle, and environmental factors of owners. This has been seen in an applied setting with the use of the ASPCA's Feline-ality and Meet Your Match assessments, where personality scores of adopters and cats are evaluated and matched. Shelters implementing the program have seen increased adoption rates, decreased return rates and decreased euthanasia rates of cats as a result (Weiss 2007). Therefore, understanding cat personality may lead to healthier human–cat relationships.

Cognitive functioning and aging

Cat cognitive function is another important aspect of cat welfare. Factors such as infection with the feline immunodeficiency virus (Steigerwald et al. 1999) and geriatric age (Gunn-Moore 2011) can alter and impair cognitive abilities. Cats today are living longer than ever before due to advancements in feline nutrition, veterinary medicine and owner awareness (Gunn-Moore 2011). As the geriatric

population increases so does the prevalence of age related cognitive decline due to the irreversible loss of brain cells and brain atrophy (Pan et al. 2013), known as cognitive dysfunction syndrome (CDS), which is difficult to both diagnose and treat (Gunn-Moore et al. 2007; Landsberg et al. 2010; Gunn-Moore 2011; Karagiannis and Mills 2014). In order to increase cat welfare, appropriate treatments that prevent, slow or improve CDS symptoms must be identified.

Araujo and colleagues (2012) found that the use of NOVIFIT tablets, an S-adenosylmethionine tosylate supplement, improved executive function in less impaired cats, but not more severely impaired cats, indicating NOVIFIT tablets are best used for cats during the early stages of CDS. Pan et al. (2013) found that supplementation of a nutritional blend, known as the "brain protection blend," containing antioxidants, arginine, B vitamins and fish oil significantly improved cat performance on three out of four cognition tests. This nutrient blend can be used to diminish or eliminate factors associated with age related cognitive decline by not only enhancing cognitive function but by potentially slowing brain aging. However, the authors do not indicate whether study cats were displaying symptoms of CDS; therefore, it is unknown how this supplement may influence cats that are already undergoing severe cognitive decline.

Although 28 % of cats aged 11–14 and 50 % of cats over age 15 develop at least one behavioral issue potentially related to CDS (Gunn-Moore 2011), not all geriatric cats undergo cognitive decline, with some demonstrating improved performance on cognitive learning tasks (Levine et al. 1987; McCune et al. 2008). Together, these results indicate treatment of CDS should begin early through use of dietary supplements to prevent and alleviate symptoms.

Conclusion

We still have a long way to go until we have an inclusive body of research on cat cognition. Many questions are still largely unexplored. To what extent do cats alter their social behaviors for communication with humans? Are there cognitive differences between various groups of cats (feral, shelter, pet)? How do lifetime experiences, such as training, influence cat cognition? Exploration of this research will contribute to our scientific understanding of how domestication, the human bond and adaptation from a solitary to social lifestyle influence cognition. This research could also have important applied applications; for example, free-roaming cat management is a topic of debate that may benefit from a greater understanding of how cats navigate and perceive human spaces. Additionally, cat cognition research may lead to improved human–cat relationships by providing insight into more beneficial ways for humans to enact their relationships with cats, thereby increasing cat welfare and reducing abandonment, surrender and euthanasia of cats. Although much remains to be done, the current literature has provided a solid foundation for future research. With consideration of species appropriate methodology and growing interest by the scientific community, we will likely learn much more about cat cognition in the years to come.

References

Ainsworth MDS, Bell SM (1970) Attachment, exploration, and separation: illustrated by the behavior of one-year-olds in a strange situation. Child Dev 41:49–67

Ainsworth MDS, Blehar MC, Waters E, Wall S (1978) Patterns of attachment: a psychological study of the strange situation. Lawrence Erlbaum Associates, Hillsdale

APPA (2014) National pet owners survey: industry statistics & trends. http://www.americanpetproducts.org/press_industrytrends.asp. Accessed 15 Oct 2014

Araujo JA, Faubert ML, Brooks ML et al (2012) NOVIFIT (R) (NoviSAMe (R) tablets improve executive function in aged dogs and cats: implications for treatment of cognitive dysfunction syndrome. Int J Appl Res Vet Med 10:90–98

Arteaga L, Bautista A, González D, Hudson R (2013) Smell, suck, survive: chemical signals and suckling in the rabbit, cat, and dog. In: East ML, Dehnhard M (eds) Chemical signals in vertebrates. Springer, New York, vol 12, pp 51–59

Bernstein PL (2014) Social behavior of domestic cats in the human home. In: Turner D, Bateson PPG (eds) The domestic cat: the biology of its behaviour, 3rd edn. Cambridge University Press, Cambridge, pp 71–80

Blake R, Hirsch HV (1975) Deficits in binocular depth perception in cats after alternating monocular deprivation. Science 190:1114–1116. doi:10.1126/science.1188391

Blakemore C, Cooper GF (1970) Development of the brain depends on the visual environment. Nature 228:477–478. doi:10.1038/228477a0

Blakemore C, Cooper GF (1971) Modification of the visual cortex by experience. Brain Res 31:366

Blakemore C, Van Sluyters RC (1975) Innate and environmental factors in the development of the kitten's visual cortex. J Physiol 248:663–716

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 DC, Bateson PPG (eds) The domestic cat: the biology of its behaviour, 2nd edn. Cambridge University Press, Cambridge, pp 67–93

Bradshaw JWS, Hall SL (1999) Affiliative behaviour of related and unrelated pairs of cats in catteries: a preliminary report. Appl Anim Behav Sci 63:251–255. doi:10.1016/S0168-1591(99)00007-6

Bradshaw JWS, Casey RA, Brown SL (2012) The behaviour of the domestic cat, 2nd edn. CABI, Wallingford

Buisseret P, Singer W (1983) Proprioceptive signals from extraocular muscles gate experience-dependent modifications of receptive fields in the kitten visual cortex. Exp Brain Res 51:443

Burnat K, Vandenbussche E, Żernicki B (2002) Global motion detection is impaired in cats deprived early of pattern vision.

Behav Brain Res 134:59–65. doi:10.1016/S0166-4328(01)00456-9
Burnat K, Stiers P, Lutgarde A et al (2005) Global form perception in cats early deprived of pattern vision. NeuroReport 16:751–754. doi:10.1097/00001756-200505120-00019
Casey RA, Bradshaw JWS (2008) The effects of additional socialisation for kittens in a rescue centre on their behaviour and suitability as a pet. Appl Anim Behav Sci 114:196–205. doi:10.1016/j.applanim.2008.01.003
Collard RR (1967) Fear of strangers and play behavior in kittens with varied social experience. Child Dev 38:877–891. doi:10.2307/1127265
Cornwell P, Nudo RJ, Straussfogel D et al (1998) Dissociation of visual and auditory pattern discrimination functions within the cat's temporal cortex. Behav Neurosci 112:800–811
Costalupes JA (1983) Temporal integration of pure tones in the cat. Hear Res 9:43–54
Cowan EA (1923) An experiment testing the ability of a cat to make delayed response and to maintain a given response toward a varying stimulus. J Comp Physiol Psychol 53:524–531
Curtis TM, Knowles RJ, Crowell-Davis SL (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
Delgado MM, Munera JD, Reevy GM (2012) Human perceptions of coat color as an indicator of domestic cat personality. Anthrozoos Multidiscip J Interact People Anim 25:427–440. doi:10.2752/175303712X13479798785779
Denny E, Yakovlevich P, Eldridge MDB, Dickman C (2002) Social and genetic analysis of a population of free-living cats (*Felis catus L.*) exploiting a resource-rich habitat. Wildl Res 29:405–413
Doré FY (1986) Object permanence in adult cats (*Felis catus*). J Comp Psychol 100:340–347
Doré FY (1990) Search behaviour of cats (*Felis catus*) in an invisible displacement test: cognition and experience. Can J Psychol 44:359–370
Driscoll CA, Clutton-Brock J, Kitchener AC, O'Brien SJ (2009) The taming of the cat. Sci Am 300:68–75
Dumas C (1992) Object permanence in cats *(Felis catus)*—an ecological approach to the study of invisible displacements. J Comp Psychol 106:404–410. doi:10.1037/0735-7036.106.4.404
Dumas C, Doré FY (1989) Cognitive-development in kittens (*Felis catus*)—a cross-sectional study of object permanence. J Comp Psychol 103:191–200. doi:10.1037//0735-7036.103.2.191
Dumas C, Doré FY (1991) Cognitive development in kittens (*Felis catus*): an observational study of object permanence and sensorimotor intelligence. J Comp Psychol 105:357–365. doi:10.1037/0735-7036.105.4.357
Durr R, Smith C (1997) Individual differences and their relation to social structure in domestic cats. J Comp Psychol 111:412–418
Edwards C, Heiblum M, Tejeda A, Galindo F (2007) Experimental evaluation of attachment behaviors in owned cats. J Vet Behav Clin Appl Res 2:119–125. doi:10.1016/j.jveb.2007.06.004
Ellis SLH, Wells DL (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 RF (1959) Suckling behaviour in kittens. Behaviour 15:146–162
Feaver J, Mendl M, Bateson P (1986) A method for rating the individual distinctiveness of domestic cats. Anim Behav 34:1016–1025
Feldman HN (1994) Methods of scent marking in the domestic cat. Can J Zool 72:1093–1099
Fiset S, Doré FY (2006) Duration of cats' (*Felis catus*) working memory for disappearing objects. Anim Cogn 9:62–70. doi:10.1007/s10071-005-0005-4
Gartner MC, Weiss A (2013) Personality in felids: a review. Appl Anim Behav Sci 144:1–13. doi:10.1016/j.applanim.2012.11.010
Gerken GM, Sandlin D (1977) Auditory reaction time and absolute threshold in cat. J Acoust Soc Am 61:602–606. doi:10.1121/1.381306
Goodwin D, Bradshaw JWS (1998) Regulation of interactions between cats and humans by gaze and mutual gaze. Int Soc Anthrozool 5, Abstract
Gosling SD (2001) From mice to men: what can we learn about personality from animal research? Psychol Bull 127:45–86. doi:10.1037//0033-2909.127.1.45
Gosling SD (2008) Personality in non-human animals. Soc Personal Psychol Compass 2:985–1001. doi:10.1111/j.1751-9004.2008.00087.x
Goulet S, Dore F, Rousseau R (1994) Object permanence and working-memory in cats (*Felis catus*). J Exp Psychol-Anim Behav Process 20:347–365. doi:10.1037/0097-7403.20.4.347
Goulet S, Dore FY, Lehotkay R (1996) Activation of locations in working memory in cats. Q J Exp Psychol Sect B-Comp Physiol Psychol 49:81–92
Gunn-Moore DA (2011) Cognitive dysfunction in cats: clinical assessment and management. Top Companion Anim Med 26:17–24. doi:10.1053/j.tcam.2011.01.005
Gunn-Moore D, Moffat K, Christie L-A, Head E (2007) Cognitive dysfunction and the neurobiology of ageing in cats. J Small Anim Pract 48:546–553. doi:10.1111/j.1748-5827.2007.00386.x
Heffner RS, Heffner HE (1985) Hearing range of the domestic cat. Hear Res 19:85–88
Heinsohn R (1997) Group territoriality in two populations of African lions. Anim Behav 53:1143–1147. doi:10.1006/anbe.1996.0316
Hua T, Bao P, Huang C-B et al (2010) Perceptual learning improves contrast sensitivity of V1 neurons in cats. Curr Biol 20:887–894. doi:10.1016/j.cub.2010.03.066
Karagiannis C, Mills D (2014) Feline cognitive dysfunction syndrome. Vet Focus 24:27–42
Karsh EB, Turner DC (1988) The human–cat relationship. In: Turner DC, Bateson PPG (eds) The domestic cat: the biology of its behaviour, 1st edn. Cambridge University Press, Cambridge, pp 157–177
Kiley-Worthington M (1984) Animal language? Vocal communication of some ungulates, canids and felids. Acta Zool Fenn 171:83–88
Korte M, Rauschecker J (1993) Auditory spatial tuning of cortical-neurons is sharpened in cats with early blindness. J Neurophysiol 70:1717–1721
Landsberg GM, Denenberg S, Araujo JA (2010) Cognitive dysfunction in cats: a syndrome we used to dismiss as "old age". J Feline Med Surg 12:837–848
Ledger R, O'Farrell V (1996) Factors influencing the reactions of cats to humans and novel objects. Proceedings of the 30th international congress of the international society for applied ethology, Guelph, University of Edinburgh p 112
Levine MS, Lloyd RL, Fisher RS et al (1987) Sensory, motor and cognitive alterations in aged cats. Neurobiol Aging 8:253–263. doi:10.1016/0197-4580(87)90010-8
Leyhausen P (1988) The tame and the wild: another just-so-story? In: Turner DC, Bateson PPG (eds) The domestic cat: the biology of its behaviour, 1st edn. Cambridge University Press, Cambridge, pp 57–66
Liberg O, Sandell M, Pontier D, Natoli E (2000) Density, space organisation and reproductive tactics in the domestic cat and other felids. In: Turner DC, Bateson PPG (eds) The domestic cat: the biology of its behaviour, 2nd edn. Cambridge University Press, Cambridge, pp 119–147
Lowe SE, Bradshaw JWS (2001) Ontogeny of individuality in the domestic cat in the home environment. Anim Behav 61:231–237. doi:10.1006/anbe.2000.1545

Lowe SE, Bradshaw JW (2002) Responses of pet cats to being held by an unfamiliar person, from weaning to three years of age. Anthrozoös 15:69–79

Macdonald DW, Yamaguchi N, Kerby G (2000) Group-living in the domestic cats: its sociobiology and epidemiology. In: Turner DC, Bateson PPG (eds) The domestic cat: the biology of its behaviour, 2nd edn. Cambridge University Press, Cambridge, pp 95–115

Malhotra S, Hall AJ, Lomber SG (2004) Cortical control of sound localization in the cat: unilateral cooling deactivation of 19 cerebral areas. J Neurophysiol 92:1625–1643. doi:10.1152/jn.01205.2003

McComb K, Packer C, Pusey A (1994) Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. Anim Behav 47:379–387. doi:10.1006/anbe.1994.1052

McComb K, Taylor AM, Wilson C, Charlton BD (2009) The cry embedded within the purr. Curr Biol 19:R507–R508. doi:10.1016/j.cub.2009.05.033

McCune S (1995) The impact of paternity and early socialization on the development of cats' behavior to people and novel objects. Appl Anim Behav Sci 45:109–124. doi:10.1016/0168-1591(95)00603-P

McCune S, Stevenson J, Fretwell L et al (2008) Ageing does not significantly affect performance in a spatial learning task in the domestic cat (*Felis silvestris catus*). Appl Anim Behav Sci 112:345–356. doi:10.1016/j.applanim.2007.08.013

Meier GW (1961) Infantile handling and development in Siamese kittens. J Comp Physiol Psychol 54:284–286

Meier M, Turner DC (1985) Reactions of house cats during encounters with a strange person: evidence for two personality types. J Delta Soc 2:45–53

Mellen JD (1993) A comparative analysis of scent-marking, social and reproductive behavior in 20 species of small cats (*Felis*). Am Zool 33:151–166. doi:10.1093/icb/33.2.151

Mendl M, Harcourt R (1988) Individuality in the domestic cat. In: Turner DC, Bateson PPG (eds) The domestic cat: the biology of its behaviour, 1st edn. Cambridge University Press, Cambridge, pp 41–54

Mendl M, Harcourt R (2000) Individuality in the domestic cat: origins, development and stability. In: Turner DC, Bateson P (eds) The domestic cat: the biology of its behaviour, 2nd edn. Cambridge University Press, Cambridge, pp 41–54

Mermet N, Coureaud G, McGrane S, Schaal B (2007) Odour-guided social behaviour in newborn and young cats: an analytical survey. Chemoecology 17:187–199. doi:10.1007/s00049-007-0384-x

Merola I, Lazzaroni M, Marshall-Pescini S, Prato-Previde E (2015) Social referencing and cat–human communication. Anim Cogn. 1–10. doi:10.1007/s10071-014-0832-2

Mertens C (1991) Human–cat interactions in the home setting. Anthrozoös 4:214–231

Mertens C, Turner DC (1988) Experimental analysis of human–cat interactions during first encounters. Anthrozoös 2:83–97

Meyers WJ, McQuiston MD, Miles RC (1962) Delayed-response and learning-set performance of cats. J Comp Physiol Psychol 55:515

Miklósi Á, Pongrácz P, Lakatos G et al (2005) A comparative study of the use of visual communicative signals in interactions between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and humans. J Comp Psychol 119:179–186. doi:10.1037/0735-7036.119.2.179

Miller HC, Gipson CD, Vaughan A et al (2009) Object permanence in dogs: invisible displacement in a rotation task. Psychon Bull Rev 16:150–155. doi:10.3758/PBR.16.1.150

Miller PS, Boone JD, Briggs JR et al (2014) Simulating free-roaming cat population management options in open demographic environments. PLoS ONE 9:e113553

Mills DS, Redgate SE, Landsberg GM (2011) A meta-analysis of studies of treatments for feline urine spraying. PLoS ONE 6:e18448. doi:10.1371/journal.pone.0018448

Moelk M (1944) Vocalizing in the house-cat: a phonetic and functional study. Am J Psychol 57:184. doi:10.2307/1416947

Mumme DL, Fernald A, Herrera C (1996) Infants' responses to facial and vocal emotional signals in a social referencing paradigm. Child Dev 67:3219–3237

Natoli E (1985) Behavioural responses of urban feral cats to different types of urine marks. Behaviour 94:234–243

Norton TT (1974) Receptive-field properties of superior colliculus cells and development of visual behavior in kittens. J Neurophysiol 37:674–690

Okujava V, Natishvili T, Mishkin M et al (2005) One-trial visual recognition in cats. Acta Neurobiol Exp 65:205–212

Pageat P, Gaultier E (2003) Current research in canine and feline pheromones. Vet Clin North Am Small Anim Pract 33:187–211

Pan Y, Araujo JA, Burrows J et al (2013) Cognitive enhancement in middle-aged and old cats with dietary supplementation with a nutrient blend containing fish oil, B vitamins, antioxidants and arginine. Br J Nutr 110:40–49. doi:10.1017/S0007114512004771

Peck C, Blakemore C (1975) Modification of single neurons in the kitten's visual cortex after brief periods of monocular visual experience. Exp Brain Res 22:57

Piaget J (1936) La naissance de I'intelligence chez I'enfant (The origin of intelligence in children). Delachaux and Niestle, Neuchatel

Piaget J (1937) La constructiondu reel chez I'enfant (The construction of reality in children). Delachaux and Niestle, Neuchatel

Pisa PE, Agrillo C (2009) Quantity discrimination in felines: a preliminary investigation of the domestic cat (*Felis silvestris catus*). J Ethol 27:289–293. doi:10.1007/s10164-008-0121-0

Pontier D, Rioux N, Heizmann A (1995) Evidence of selection on the orange allele in the domestic cat *Felis catus*: the role of social structure. Oikos 73:299–308. doi:10.2307/3545954

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

Raihani G, Rodríguez A, Saldaña A et al (2014) A proposal for assessing individual differences in behaviour during early development in the domestic cat. Appl Anim Behav Sci 154:48–56. doi:10.1016/j.applanim.2014.01.013

Rauschecker JP, Kniepert U (1994) Auditory localization behaviour in visually deprived cats. Eur J Neurosci 6:149–160. doi:10.1111/j.1460-9568.1994.tb00256.x

Reisner I, Houpt K, Erb H, Quimby F (1994) Friendliness to humans and defensive aggression in cats: the influence of handling and paternity. Physiol Behav 55:1119–1124. doi:10.1016/0031-9384(94)90396-4

Rieger G, Turner DC (1999) How depressive moods affect the behavior of singly living persons toward their cats. Anthrozoos 12:224–233. doi:10.2752/089279399787000066

Rosenkilde CE, Divac I (1976) Discrimination of time intervals in cats. Acta Neurobiol Exp (Warsz) 36:311–317

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

Sasaki Y, Gold J, Watanabe T (2010) Perceptual learning: cortical changes when cats learn a new trick. Curr Biol 20:R557–R558

Schwartz S (2002) Separation anxiety syndrome in cats: 136 cases (1991–2000). J Am Vet Med Assoc 220:1028–1033

Seed AM, Tebbich S, Emery NJ, Clayton NS (2006) Investigating physical cognition in rooks, *Corvus frugilegus*. Curr Biol 16:697–701. doi:10.1016/j.cub.2006.02.066

Serpell JA (1988) The domestication and history of the cat. In: Turner DC, Bateson P (eds) The domestic cat: the biology of its

behaviour, 1st edn. Cambridge University Press, Cambridge, pp 151–158
Shreve KR (2014) The influence of food distribution and relatedness on the social behaviours and proximities of free-roaming cats (*Felis silvestris catus*). M.En. thesis, Miami University, Oxford, OH
Shettleworth SJ (2001) Animal cognition and animal behaviour. Anim Behav 61:277–286. doi:10.1006/anbe.2000.1606
Steigerwald ES, Sarter M, March P, Podell M (1999) Effects of feline immunodeficiency virus on cognition and behavioral function in cats. J Acquir Immune Defic Syndr Hum Retrovirol 20:411–419. doi:10.1097/00042560-199904150-00001
Stromberg J (2014) What research says about cats: they're selfish, unfeeling, environmentally harmful creatures. In: Vox. http://www.vox.com/2014/10/16/6982177/the-case-against-owning-cats. Accessed 16 Jan 2015
Thinus-Blanc C, Poucet B, Chapuis N (1982) Object permanence in cats: analysis in locomotor space. Behav Processes 7:81–86
Triana E, Pasnak R (1981) Object permanence in cats and dogs. Anim Learn Behav 9:135–139. doi:10.3758/BF03212035
Turner D (1991) The ethology of the human–cat relationship. Schweiz Arch Tierheilkd 133:63–70
Turner DC (2000a) The human–cat relationship. In: Turner D, Bateson PPG (eds) The domestic cat: the biology of its behaviour, 2nd edn. Cambridge University Press, Cambridge, pp 195–208
Turner DC (2000b) Human–cat interactions: relationships with, and breed differences between, non-pedigree, Persian and Siamese cats. In: Podberscek AL, Paul ES, Serpell JA (eds) Companion animals and us: exploring the relationships between people and pets. Cambridge University Press, Cambridge, pp 257–274
Turner DC (2014) Social organisation and behavioural ecology of free-ranging domestic cats. In: Turner DC, Bateson PPG (eds) The domestic cat: the biology of its behaviour, 3rd edn. Cambridge University Press, Cambridge, pp 63–80
Turner DC, Rieger G (2001) Singly living people and their cats: a study of human mood and subsequent behavior. Anthrozoos Multidiscip J Interact People Anim 14:38–46
Turner DC, Feaver J, Mendl M, Bateson P (1986) Variation in domestic cat behaviour towards humans: a paternal effect. Anim Behav 34:1890–1892
Udell MAR, Dorey NR, Wynne CDL (2010) What did domestication do to dogs? A new account of dogs' sensitivity to human actions. Biol Rev 85:327–345. doi:10.1111/j.1469-185X.2009.00104.x
Verberne G (1976) Chemocommunication among domestic cats, mediated by the olfactory and vomeronasal senses. II. The relation between the function of Jacobson's organ (vomeronasal organ) and Flehmen behaviour). Z Für Tierpsychol 42:113–128
Verberne G, de Boer J (1976) Chemocommunication among domestic cats, mediated by the olfactory and vomeronasal senses. Z Für Tierpsychol 42:86–109. doi:10.1111/j.1439-0310.1976.tb00958.x
von Uexküll J (1957) A stroll through the worlds of animals and men: a picture book of invisible worlds. In: Schiller CH (ed) Instinctive behavior. International Universities Press, Madison, CT, pp 5–80 (trans: Schiller CH)
Weinstein L, Alexander R (2010) College students and their cats. Coll Stud J 44:626
Weiss E (2007) New research helps adopters meet their feline soul mates. In: Animal sheltering. Humane Society of the United States, pp 61–63
Whitt E, Douglas M, Osthaus B, Hocking I (2009) Domestic cats (*Felis catus*) do not show causal understanding in a string-pulling task. Anim Cogn 12:739–743. doi:10.1007/s10071-009-0228-x
Wikmark G, Warren JM (1972) Delayed response learning by cage-reared normal and prefrontal cats. Psychon Sci 26:243–245
Willey TJ (1973) The ultrastructure of the cat olfactory bulb. J Comp Neurol 152:211–232. doi:10.1002/cne.901520302
Williams CM, Kramer EM (2010) The advantages of a tapered whisker. PLoS ONE 5:e8806. doi:10.1371/journal.pone.0008806
Witte RS, Kipke DR (2005) Enhanced contrast sensitivity in auditory cortex as cats learn to discriminate sound frequencies. Cogn Brain Res 23:171–184. doi:10.1016/j.cogbrainres.2004.10.018
Wolfe RC (2001) The social organization of the free ranging domestic cat (*Felis catus*). PhD dissertation, University of Georgia, Athens, GA
Won M-H, Wie M-B, Lee J-C et al (1997) Distribution and characteristics of cholecystokinin-like immunoreactivity in the olfactory bulb of the cat. Neurosci Lett 225:105–108
Wynne CDL, Udell MAR (2013) Animal cognition, 2nd edn. Palgrave Macmillan, New York
Yarbrough JU (1917) The delayed reaction with sound and light in cats. J Anim Behav 7:87–110
Yeon SC, Kim YK, Park SJ et al (2011) Differences between vocalization evoked by social stimuli in feral cats and house cats. Behav Process 87:183–189. doi:10.1016/j.beproc.2011.03.003
Young E (2009) Cats manipulate their owners with a cry embedded in a purr. In: Exactly Rocket Sci. http://scienceblogs.com/notrocketscience/2009/07/13/cats-manipulate-their-owners-with-a-cry-embedded-in-a-purr/. Accessed 7 Jan 2015
Żernicki B (1993) Learning deficits in lab-reared cats. Acta Neurobiol Exp (Warsz) 53:231–236
Żernicki B (1999) Visual discrimination learning under switching procedure in visually deprived cats. Behav Brain Res 100:237–244