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The quality of being sociable: The influence of human attentional state, population, and human familiarity on domestic cat sociability



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ABSTRACT

Two experiments were conducted to assess the influence of human attentional state, population, and human familiarity on domestic cat sociability. Sociability behaviors included duration of time in proximity and contact with the human and the frequency of meow vocalizations. Human attentional state influenced cat behavior, with cats spending significantly more time in proximity with the attentive human in both the pet (U(22) = 389, Z = -2.72, P = 0.007) and shelter groups (F(44) = 15.34, P = 0.0003). Cat population influenced sociability and shelter cats spent more time in proximity with the inattentive unfamiliar human as compared to pet cats (U(44) = 91, Z = 3.8, P = 0.0001) Additionally compared to pet cats, more individuals in the shelter cat group meowed at least once during the unfamiliar human inattentive phase (Fisher's exact test, P = 0.02). Human familiarity did not significantly influence pet cat sociability behaviors. Overall, a wide range of sociability scores was seen, indicating individual variation is an important consideration in cat social behavior. Future research in this area will predict conditions under which strong cat-human bonds form and establish a more comprehensive scientific understanding of cat behavior.

1. Introduction

Despite the popularity of the domestic cat, surprisingly little is known about cat social behavior or factors influencing the human-cat relationship (Vitale Shreve and Udell, 2015). The lack of research in this field may be due in part to a common misconception that cats are not a social species (Spotte, 2014). Although many think of cats as solitary, domestic cats are facultatively social and can live either socially or solitarily, depending on their environment and upbringing (Leyhausen, 1988; Bradshaw and Cameron-Beaumont, 2000; Turner, 2014). Domestic cats display a wide array of social behaviors with conspecifics and interact non-randomly with "preferred associates" (Wolfe, 2001; Curtis et al., 2003; Crowell-Davis et al., 2004) and with humans (Edwards et al., 2007; Vitale Shreve and Udell, 2015).

Sociability is often considered an important dimension of an animal's personality (Gosling and John, 1999) and can be defined as the tendency of an individual to interact with others (Capitanio, 2002). Sociability is characterized by seeking and maintaining proximity and contact with other individuals (Gosling and John, 1999; Barrera et al., 2010). Sociability is a trait of extraversion, a larger personality dimension described by factors such as sociable and outgoing behavior, boldness, and high activity levels (Gosling and John, 1999). In domestic cats, outgoing, sociable, and active personality traits have been

identified (Gosling and John, 1999; Vitale Shreve and Udell, 2015). Although sociability has been studied in many mammalian species (for a review see Gosling and John, 1999), the majority of this research has examined sociability between conspecifics. Interspecies sociability has been less studied, with most of the research that does exist focusing on the domestic dog-human relationship (Udell et al., 2010). Research has examined some aspects of cat behavior that may impact sociability including socialization, personality, and sensitivity to cues (for review see Vitale Shreve and Udell, 2015), however further research on cat social behavior, specifically cat sociability, may prove to be equally important to understanding cats' success in human homes and other human-controlled environments.

Several factors may be important in shaping animal sociability, or the creation of a new behavior through gradual reinforcement of behaviors under various social contexts (Powell et al., 2012). Lifetime factors which may be important in shaping cat social behavior include the attentional state of the individual the cat is interacting with, the animal's population, and the cat's familiarity to the individual. For example, several species including the domestic dog (Udell et al., 2010; Barrera et al., 2010), the domestic pig (Nawroth et al., 2013), jackdaws (von Bayern and Emery, 2009), and several species of nonhuman primates (Poss et al., 2006; Maille et al., 2012; Defolie et al., 2015) have been shown to discriminate between human attentional states

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(attentive vs. inattentive) and modify their behavior in response. In some cases, attentional state has been found to have a direct impact on sociability. Barrera et al. (2010) found dogs spent significantly more time in proximity to an attentive human, who actively sought their attention, over an inactive human. Ito et al. (2016) found that cats approach and engage in begging behavior significantly more toward an attentive human that provided both visual and auditory cues. Additionally, a study with socially living laboratory colony cats found cats displayed more social behaviors such as head rubbing and play behavior to the unfamiliar interactive human over an unfamiliar passive human (Mertens and Turner, 1988).

Individuals in different populations may have distinctive life experiences, which can influence their behavior in sociability tests. For example, Barrera et al. (2010) conducted sociability tests with pet and shelter dogs. The researchers found, on average, shelter dogs spent significantly more time in proximity to an unfamiliar passive human than did pet dogs, suggesting different social tendencies across these two populations. This is consistent with other research suggesting that reduced opportunity to interact with humans, or the absence of a bonded attachment figure, may result in greater generalized proximity-seeking or sociability towards humans, including unfamiliar individuals (Gácsi et al., 2001). Research with cats has found that groups of cats with varying levels of socialization display different social behavior toward humans (Collard, 1967). However, to date no research has examined how human directed sociability differs between cats living in different populations.

Research with mammals, including cats, has also indicated that familiarity between conspecifics influences social interactions, with more familiar individuals typically displaying more affiliative and proximityseeking behaviors and less aggressive behaviors towards one another (Barry and Crowell-Davis, 1999; Curtis et al., 2003; Færevik et al., 2007; Ancillotto and Russo, 2014). Research exploring interspecies interactions indicates that some mammals (Davis et al., 1997; Boivin et al., 1998; Győri et al., 2010; Cunningham and Ramos, 2014), including cats (Collard, 1967; Edwards et al., 2007; Galvan and Vonk, 2016), can discriminate familiar from unfamiliar humans and often display a preference for the familiar human, however not all studies have found evidence of preferential behavior toward a familiar human (Podberscek et al., 1991; Potter and Mills, 2015). Research has found that when presented with a stranger's voice and the owner's voice, cats display a significantly higher orienting response (movement of ears and head) to their owner's voice (Saito and Shinozuka, 2013). Similar to humans (Baun et al., 1984) and dogs (Astrup et al., 1979), one study found the blood pressure of cats increased significantly when presented with a bonded individual, potentially indicating excitement for interaction or expectation for further rewards due to past reinforcement (Slingerland et al., 2008).

The aims of the present study were to characterize average and individual patterns of sociability displayed by both pet cats and those living in an animal shelter, and to evaluate factors (environment, human attentional state, and familiarity) that might influence social behavior towards humans. Two experiments were undertaken to evaluate three specific factors that were predicted to influence cat sociability. Experiment 1 utilized methodology similar to that of Barrera et al. (2010) to examine the influence of human attentional state (inattentive or attentive) and cat population (pet vs. shelter) on proximity-seeking and contact behavior as well as meow vocalizations toward an unfamiliar experimenter. Experiment 2 evaluated the influence of human familiarity on pet cat sociability by presenting pet cats with a familiar human in addition to a stranger, as done in Experiment 1.

It was predicted that if cats are sensitive to human cues, cats would show greater sociability and engage in more meow vocalizations in the attentive phase as compared with the inattentive phase (Mertens and Turner, 1988). Additionally, as in research conducted with dogs (Barrera et al., 2010), shelter cats were expected to display a greater amount of sociable behaviors towards the unfamiliar human than pet

cats. Finally, consistent with literature indicating familiar individuals display increased proximity-seeking behavior, pet cats were expected to display more sociable behaviors (greater proximity-seeking and contact) towards their owner over an unfamiliar individual.

2. Methods

2.1. Subjects

Pet cats included individuals living with a primary caretaker in a human home. Twenty-three mixed-breed adult pet cats were tested in a small familiar room of the owner's home. Pet cats ranged in age from 2 to 16.5 years old (mean = 6.2, SD = 3.7) and were mixed sex, with 13 males and 10 females all neutered. Pet cats lived both singly and in multi-cat households. Pet cats were found via recruitment materials (online, fliers) and via word of mouth. Shelter cats included individuals that had no primary caregiver (or had recently lost their owner), undergone the shelter's intake procedure (veterinary assessment), and were currently living in the shelter environment. Experience in the shelter environment may include more constant exposure to unfamiliar stimuli (people, toys, bedding, examination rooms, cages, etc.) compared to pet cats. Twenty-three mixed-breed adult shelter cats were tested in a small unfamiliar room at the Heartland Humane Society, in Corvallis, OR. Shelter cats ranged in age from 1 to 12 years old (mean = 5.6, SD = 3.5) and were mixed sex, with 12 males and 11 females all neutered. At the time of testing, the length of stay for shelter cats ranged from 3 days to 455 days (mean = 100.09 days, SD = 109.52). Shelter cats were pseudo-randomly chosen from cages with only the sex and age of the cat considered for consistency with the pet population. Shelter cats lived both singly and in multi-cat cages. Of the shelter cats tested, 34.8% (8/23) were strays, 30.4% (7/23) were surrendered by their owner to the shelter, 30.4% (7/23) were adopted from the shelter and returned, and 4.4% (1/23) came from a hoarding situation.

2.2. Room setup

Each testing room had a 1 m radius circle marking of tape with an X in the center. Although the size of the testing room varied, all rooms were big enough so the cat had space to explore and sit outside of the circle away from the human. A video camera (Sony Handycam, HDR-CX405) was attached to a tripod and set in the corner of the room to videotape interactions.

2.3. Petting protocol

Two petting protocols were utilized to reflect differing levels of human attentional state. For the inattentive phase, a limited petting protocol was utilized (similar to Barrera et al., 2010) and for the attentive phase, a free interaction petting protocol was used to help match the cat's normal expectation for attentive interactions (Ellis et al., 2015). The human was either a stranger to the cat (Experiment 1) or the familiar owner of the cat (Experiment 2).

2.3.1. Inattentive phase

After the cat was placed in the room, the human entered, sat on the floor in the center of the circle and remained quiet, ignoring the cat and looking at the floor. If the cat came within the circle (at least two paws inside the circle), the person could pet the subject twice but could never vocalize to the cat and always had to look at the floor. If the cat left the circle and came back the human could again pet twice, but no other interaction was allowed.

2.3.2. Attentive phase

The human could now interact freely with the cat by calling the cat by name and trying to make contact with it (keep cat's attention and

keep cat within the circle to be pet without restraining the cat) for as much of the 2 min as possible. If the cat moved out of reach, the person could continue to attract the cat's attention but the person could never get up or leave the middle of the circle.

2.4. Experiment 1 procedure

Cats were transported to the testing room and placed outside of the circle. Shelter cats were allowed 1-min of habituation time since their testing room was unfamiliar. All cats were only tested with the procedure once. The sex of the unfamiliar human was held constant and was always a female aged between 20–30 years old.

2.5. Experiment 2 procedure

Immediately following Experiment 1, pet cats underwent two additional phases with their owner. Shelter cats did not participate in Experiment 2 due to the lack of a primary owner/caretaker.

2.6. Data analysis

Behaviors were coded from video using the program JWatcher, 1.0 (Blumstein et al., 2000). We coded the proportion of time the cat spent in proximity to the human (inside the circle/within 1 m), the proportion of time the human and cat were in physical contact with one another, and the frequency of meow vocalizations. Meow vocalizations were characterized by an initial nasal sound and a long "a" vowel series ("aou" as in Father, as described by Moelk 1944). To calculate interobserver reliability, 85% of videos were double-coded. An 8% range of tolerance was applied for the time spent in proximity and contact with the human. An inter-observer reliability score of was 95% was calculated for time spent in proximity, a score of 89% was calculated for time spent in human-cat contact, and an agreement score of 89% was calculated for the frequency of meows.

All data were non-normal (Shapiro-Wilk all P < 0.05) except the shelter cat data on proximity to the unfamiliar human (Shapiro-Wilk P = 0.11). Normal data were analyzed using a one-way ANOVA in R (Hartmann, 1977; R Development Core Team, 2013). Non-normal data were analyzed with a two-tailed Mann-Whitney U test in the Vassar-Stats program. In addition to looking at average differences with Mann-Whitney tests, differences between individuals were also examined for the proximity data and vocalization data using a two-tailed Fisher's exact test. For the Fisher's test, 2×2 contingency tables were analyzed by grouping cats by percent of time spent in the circle with the human (0-49%, 50-100%) for the proximity data and by whether or not the cat meowed at least once during the 2-min session (0,1) for the meow data. All statistical tests had an alpha level of (P < 0.05).

3. Results

3.1. Experiment 1: sociability towards an unfamiliar human

3.1.1. Attentional state

The influence of human attentional state in both pet and shelter cats was examined. For pet cats, attentional state influenced the average time spent in proximity to the unfamiliar human, as seen in Fig. 1. As determined by the Mann-Whitney U test, pet cats spent more time in proximity to the unfamiliar human when they were attentive to the cat, U(22) = 389, Z = -2.72, P = 0.007. This finding was supported by the individual data, with more individual pet cats spending at least 50% of the time in proximity to the attentive unfamiliar human (Fisher's Exact Test, P = 0.001) when compared to cats in the inattentive phase. Attentional state also influenced the average time spent in contact between the pet cat and unfamiliar human. Pet cat-human dyads spent more time in contact in the attentive phase, U(22) = 394, Z = -2.83, P = 0.005. However, as seen in Fig. 2, human attentional state did not

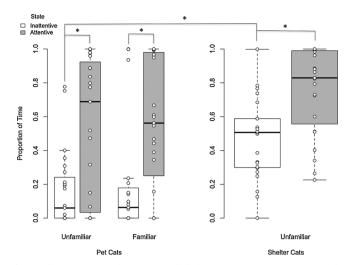


Fig. 1. The proportion of time pet and shelter cats spent in proximity to the human in the inattentive (white bars) and attentive (gray bars) phases. Each dot represents an individual cat. * P < 0.05.

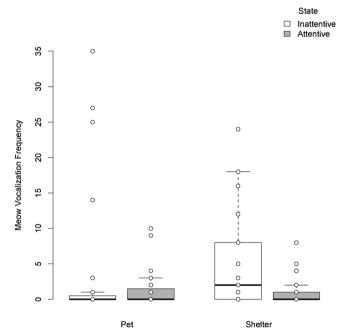


Fig. 2. The frequency of meow vocalizations pet and shelter cats produced in the unfamiliar human inattentive (white bars) and attentive (gray bars) phases. Each dot represents an individual cat.

influence the average frequency of pet cat meow vocalizations to the unfamiliar human, U(22) = 284, Z = -0.42, P = 0.68. There was also no influence of attentional state on whether pet cats meowed at least once during the session to the unfamiliar human (Fisher's Exact Test, P = 0.54).

Attentional state also significantly influenced shelter cat behavior. As determined by one-way ANOVA, shelter cats spent significantly more time on average in proximity to the attentive unfamiliar human as compared to the inattentive human, F(44) = 15.34, P = 0.0003. The same held true for shelter cat-human contact, with dyads in contact significantly more in the attentive phase, F(44) = 25.18, P = 0.000009. Similar to pet cats, attentional state did not significantly influence whether individual shelter cats meowed at least once to the unfamiliar human (Fisher's Exact Test, P = 0.24). Additionally, on average shelter cats displayed a trend toward meowing more to the unfamiliar human during the inattentive phase as compared to the attentive phase, U

(22) = 176, Z = 1.93, P = 0.05.

3.1.2. Population comparison

To explore the influence of lifetime experience, two populations of cats, pet and shelter cats, were compared to one another in their behavior with the unfamiliar human. There were significant differences between the pet and shelter cats in the time spent in proximity to the unfamiliar human. Shelter cats spent significantly more time on average than pet cats in proximity to the inattentive human, U(44) = 91, Z = 3.8, P = 0.0001. However, there was no significant difference in the average time shelter and pet cats spent in proximity to the unfamiliar attentive human, U(44) = 181, Z = 1.82, P = 0.07. Again, these findings are mirrored in the individual data. More shelter cats spent at least 50% of the time in proximity to the inattentive human as compared to pet cats in this condition (Fisher's exact test, P = 0.003), however there was no significant difference between shelter and pet cats in the attentive phase (Fisher's exact test, P = 0.1075).

Shelter cats spent significantly more time than pet cats in contact with the inattentive human, U(44) = 106, Z = 3.47, P = 0.0005 but again there was no difference in the attentive phase, U(44) = 208.5, Z = 1.22, P = 0.22. Finally, there was no between-subject difference in average meow frequency between the pet and shelter cats for either the inattentive, U(44) = 189, Z = 1.65, P = 0.09 or attentive human U(44) = 268.5, Z = -0.08, P = 0.94. However, compared to pet cats, more individuals in the shelter cat group meowed at least once during the inattentive phase (Fisher's exact test, P = 0.02), however there was no difference in the attentive phase (Fisher's exact test, P = 1).

Shelter cat data were also analyzed to examine if length of time living in the shelter environment was correlated with the proportion of time spent in proximity to the human or the frequency of meow vocalizations produced. Because data were skewed toward shorter lengths of stay at the shelter, one outlying individual was removed from analysis (length of stay 455 days) leaving 22 individuals. As seen in Table 1, there was no strong correlation between length of stay on proximity-seeking behavior in either phase or vocalization in the attentive phase. However, meow vocalizations in the inattentive phase were moderately correlated with length of stay (0.52), with more meows produced the longer a cat has been in the shelter.

3.2. Experiment 2: pet cat sociability towards a familiar human

3.2.1. Attentional state of owner

Similar to the findings with the unfamiliar human and as seen in Fig. 1, attentional state influenced the average time spent in proximity to the owner. Pet cats spent more time in proximity to familiar human when the owner was attentive to the cat, U(22) = 377, Z = -2.46, P = 0.01. This was supported by the individual data, with more individual cats spending at least 50% of the time in proximity to the attentive owner (Fisher's Exact Test, P = 0.01) when compared to pet cats in the inattentive phase.

3.2.2. Influence of familiarity

Human familiarity did not significantly influence the proportion of time pet cats spent in proximity to the human. There were no average differences between the unfamiliar and familiar groups in either the

Table 1 Factor analysis examining correlation of length of time living in shelter with time spent in proximity to the human and the frequency of meow vocalizations in each Phase. N=22.

Behavior	Phase	Pearson Correlation
Proximity Seeking	UI	0.05
	UA	0.01
Meow Vocalization	UI	0.52
	UA	-0.11

inattentive (U(22) = 263, Z = 0.02, P = 0.98) or attentive phase (U (22) = 281, Z = -0.35, P = 0.73). This was mirrored by the individual data, with no difference in the number of individual cats spending at least 50% of time in proximity to the unfamiliar or familiar human in either the inattentive (Fisher's Exact Test, P = 0.67) or attentive phase (Fisher's Exact Test, P = 0.67). There was also no influence of human familiarity on the proportion of time pet cats and humans spent in contact with one another. There were no significant average differences between the unfamiliar and familiar groups in either the inattentive (U (22) = 284, Z = -0.42, P = 0.68) or attentive phase (U(22) = 276.5, Z= -0.25, P = 0.80). Finally, human familiarity did not significantly influence the frequency of meows. There were no average differences between the frequency of meows for unfamiliar and familiar groups in either the inattentive (U(22) = 267.5, Z = -0.05, P = 0.96) or attentive phase (U(22) = 256, Z = 0.18, P = 0.86) and no significant difference between individuals as to whether or not the cat meowed at least once during the session in the inattentive (Fisher's Exact Test, P =1) or attentive phase (Fisher's Exact Test, P = 0.76).

4. Discussion

4.1. Attentional state

As predicted, attentional state influenced the social behavior of cats. Pet and shelter cats spent significantly more time in proximity and contact to the human during the attentive phase. These findings are aligned with research in other species including pigs, birds, primates and canines, where social behavior (such as proximity-seeking, approach behavior, and communicative behaviors) increased in response to the human's attentive state (Poss et al., 2006; von Bayern and Emery, 2009; Udell et al., 2010; Barrera et al., 2010; Maille et al., 2012; Nawroth et al., 2013; Defolie et al., 2015). This finding is also supported by the work of Ito et al. (2016) that found cats approach and beg from humans providing attentive visual and auditory cues and that of Mertens and Turner (1988) who found colony cats exposed to an unfamiliar human, who was either reading a book and ignoring the cat or interacting freely, displayed more head rubbing and play behavior during the attentive phase. These findings indicate that like other species, cats have the ability discriminate human attentional state and modify their behavior in response.

It is not surprising cats modify their behavior in response to human attentional state since research indicates cats are sensitive to many human cues (for a review see Vitale Shreve and Udell, 2015) including pointing gestures (Miklósi et al., 2005), human emotions (Merola et al., 2015), human mood (Rieger and Turner, 1999; Turner and Rieger, 2001), and human vocalizations (Saito and Shinozuka, 2013). There also seems to be an interactive effect on the ability of cats to pick up on human cues. Galvan and Vonk (2016) found that although cats were only modestly sensitive to emotional cues, they responded most to their owner's happy emotional cues over an unfamiliar human's happy cues and cats spent significantly more time in contact with their owner in the positive condition but not with the unfamiliar human, indicating familiarity and attentional state may be related. Overall, the ability to follow human cues has likely contributed to the cat's success in human homes, as seen with the domestic dog (Udell et al., 2010). Future research should continue to examine the influence of human attentional state on other aspects of the human-cat relationship, including engaging in forbidden behaviors in the presence of an inattentive or attentive human, as has been conducted with the domestic dog (Udell et al., 2010).

4.2. Population

As predicted, pet and shelter cats differed in their degree of sociability towards an unfamiliar human. Shelter cats spent more time in proximity to the unfamiliar human in the inattentive phase as

compared to pet cats, both on average and at the individual level. However, a significant difference was not detected during the attentive phase. These findings match those reported by Barrera et al. (2010) who found shelter dogs remained near an unfamiliar passive human for longer periods of time than pet dogs. Just as in the current study, no difference between shelter and pet dogs were found when the unfamiliar human was attentive. These results may indicate that both shelter dogs and shelter cats have greater motivation to seek social proximity with any human, even if the human is inattentive and the animal does not have an attachment bond with the human. Alternatively, shelter animals may be exposed more frequently to unfamiliar humans than pet animals and may therefore have a richer reinforcement history of interacting with unfamiliar humans, making them more likely to spend time near novel humans as compared to pet animals.

In an applied sense, the results on population differences are particularly relevant to animal shelters. Compared to pet cats, more individuals in the shelter group meowed at least once during the inattentive phase and shelter cats also displayed a trend of meowing more frequently on average when the human was inattentive to them. Although meows were considered a sociable behavior and were predicted to increase in the attentive state, meows may actually serve as an attention-getting behavior. Therefore, meows could serve as a signal to shelter workers that the cat may be soliciting for human attention. These data, coupled with prior research that indicated cats surrendered by owners are more stressed than stray cats (Dybdall et al., 2007), might be used to inform interaction protocols for shelter cats. For example, more opportunities for cat-shelter volunteer interaction could potentially increase cat sociability and decrease stress (Coppola et al., 2006). Future research should be conducted to evaluate these factors and how they might influence adoption success.

It is possible differences in the testing environment itself may have influenced performance on sociability tests. The two populations of cats were tested in locations differing in familiarity to each subject. Pet cats were tested in their home while shelter cats were tested in an unfamiliar room in the shelter. Because cats living in shelters are often confined to cages, testing in a familiar room was not possible for this population. However, these data suggest the habituation time to the unfamiliar room was sufficient since shelter cats displayed a similar sensitivity to cues of attention and inattention as pet cats and that shelter cats also display high levels of sociability. However, future research should further explore how the testing environment influences sociability behaviors in different populations of cats.

4.3. Familiarity

Although we predicted pet cats would display more sociable behaviors towards their owner over an unfamiliar individual, pet cats did not spend significantly more time in proximity to or in contact with their owners. There was also no difference in the use of meow vocalizations when in the presence of the owner vs. stranger. These findings are aligned with previous research by Ellis et al. (2015) who found no significant difference in the display of affiliative behaviors by cats toward a familiar or unfamiliar human. Interestingly, Ellis et al. found an increase in negative behavioral responses toward the familiar handler. However, unlike the present study, Ellis et al. standardized the petting protocol in terms of location of petting on the cat's body, duration of petting, and petting style. Ellis et al. suggest this standardized petting may differ from the owner's typical petting style, which may not match the cat's normal expectation for interactions with the owner. This may have led to an increase in negative behaviors related to frustration towards the owner (Falk, 1971; Heath, 2009; Ellis et al., 2015). Therefore, the present study allowed both the stranger and owner to freely interact in the attentive state (petting and vocalizing), thereby meeting the cat's expectations for typical interactions with their owner. However, this methodology also presents a potential issue since the strength or frequency of attentive behaviors may differ between people. For example,

some of the strangers may have called the cat more loudly and more frequently than the owner, which could have led to individual differences that were a product of the dyad and not the cat alone. Future research should consider the potential benefits and disadvantages of employing different interaction protocols depending on the aim of the study. Research can also examine if the direction of the behavior influences the cat's behavior. For example, employing a condition in which a human is not attentive to the cat but is still vocalizing (such as talking on a cell phone) would provide more information on the conditions under which cat social behavior is modified.

On average sociable behaviors displayed by cats did not appear to significantly differ between the unfamiliar human or owner. On the surface this finding may appear to suggest cats do not display preferential behavior toward their owners over strangers. However, a careful look at the individual data would suggest that it is instead more likely some cats have a strong preference for their owners (Edwards et al., 2007), while others display less of a preference or no preference at all (Potter and Mills, 2015). In other words, as seen in Fig. 1, there is a significant amount of individual variability in preference for the stranger or owner among cats. Another important consideration is the current study only examined one facet of pet cat attachment behavior, proximity-seeking behavior. It should be noted that, even in humans, preferential proximity-seeking towards a primary attachment figure typically does not extend into adulthood. In human children exclusive preference for a parent typically occurs for a short period of time sometime prior to 18 months of age, however the formation of ongoing attachments to new people are common after this time (Schaffer and Emerson, 1964). Therefore, other behavioral patterns related to cathuman attachment need further exploration. In fact, pioneers of attachment theory, Ainsworth and Bowlby (1991) state in response to attachment in human infants, "Indications that an attachment had clearly been formed were distress and following when separation occurred or threatened, and forms of greeting when mother returned from an absence". It appears that distress during separation and the existence of the secure base effect are clear indicators of attachment alone (Bowlby, 1973). Future research should examine the existence of secure base behaviors (balance of proximity-seeking and exploration behaviors following a potentially distressing experience) and different attachment styles in response to their owner compared to a stranger (Ainsworth and Bell, 1970). In all, the observed social diversity in pet cats may be related to the facultative quality of cats' social repertoire (Turner, 2014) or may relate more generally to the malleable nature of attachment

Additionally, novel situations or objects can also influence an animal's behavior, with some animals being more likely to approach and investigate novel objects, such as the unfamiliar human (Waiblinger et al., 2003), as seen in prior research with colony cats (Podberscek et al., 1991). In the present study, the order of humans (unfamiliar first, familiar second) was held constant to compare pet and shelter groups to one another, something that may have also been a factor. Future research should build off these findings and counterbalance the order of humans to determine if the novelty of presenting the stranger first influences cat social behavior. Additionally, further research can compare the sociability of cats toward their owner and a less novel individual, such as a familiar human that is not their owner. The blood pressure rates of cats are significantly higher when presented with a bonded human (Slingerland et al., 2008), as seen with dogs and humans (Astrup et al., 1979; Baun et al., 1984). Therefore, although there was no observable difference in the social behaviors displayed to either the unfamiliar or familiar human, a physiological influence may occur, such changes in cortisol (Coppola et al., 2006; Handlin et al., 2011) or oxytocin levels (Handlin et al., 2011; Thielke and Udell, 2015). Finally, as Saito and Shinozuka (2013) found, cats typically respond to their owner's voice with an orienting response instead of an approach response, therefore behaviors such as movement of the cat's head or ears may also be useful measures of the cat-human bond. Future research

should continue to examine both physiological effects and observable behaviors to determine the extent to which human familiarity influences cat behavior. Finally, the fact that cats display a large range of individual variation in their sociability, as seen in other cat research (Feaver et al., 1986; Turner et al., 1986), likely indicates that other factors, such as lifetime experience and individual predispositions or cat personality, may influence cat sociability. For example, kittens between 2-16 weeks old that have received frequent handling by an unfamiliar human display a reduction of distress and flight behavior in the presence of novel humans, indicating socialization to unfamiliar humans is necessary to shape sociability later on in life (Lowe and Bradshaw, 2002; for review see Vitale Shreve and Udell, 2015). Future research should investigate the influence of other life experiences, such as socialization or training, on an individual cat's sociability and preference for their owner to determine other factors influencing the human-cat relationship.

5. Conclusion

Together, this body of research indicates domestic cats cat detect human attentional state and modify their behavior in response, demonstrating they are sensitive to human social cues and tend to be more social when presented with an attentive human. Additionally, the population of the cat, either living in a home or shelter environment, can influence cat sociability, with shelter cats spending more time with humans despite the human's inattentive behavior or the cat's bond to that human.

Potter and Mills (2015) have suggested cat sociality exists on a continuum but may perhaps be skewed toward independency. Although we have found that indeed a wide range of individual variation exists in domestic cats, we have not necessarily seen this bias toward independence, especially in the shelter cat data where the mean proportion of time spent in proximity to the unfamiliar human was 0.47 in the inattentive and 0.75 in the attentive phase. Indeed, recent research examining individual cat preference for various stimuli found the majority of cats (50%) most-preferred social interaction with a human, with the next most-preferred item category being food (37%), followed by toys (11%), and then scent stimuli (2%) (Vitale Shreve et al., 2017). Therefore, we suggest that as facultatively social animals cats display much flexibility in their social behavior, with life experience - such as their environment and upbringing, playing a large role in shaping their sociability.

In respect to cat sociability and factors influencing the cat-human bond, many questions still remain unanswered (Vitale Shreve and Udell, 2015, 2017). Future research will continue to shed light on our scientific understanding of the domestic cat and ways to utilize this knowledge to increase cat welfare and the cat-human bond.

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Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This research complies with the Oregon State University Institutional Animal Care and Use Committee policies (ACUP #4444).

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References

- Ainsworth, M.D.S., Bowlby, J., 1991. An ethological approach to personality development. Am. Psychol. 46, 333–341.
- Ancillotto, L., Russo, D., 2014. Selective aggressiveness in European free-tailed bats (Tadarida teniotis): influence of familiarity, age and sex. Naturwissenschaften 101, 221–228. https://doi.org/10.1007/s00114-014-1146-6.
- Ainsworth, M.D.S., Bell, S.M., 1970. Attachment, exploration, and separation: illustrated by the behavior of one-year-olds in a strange situation. Child Dev. 41 (1), 49–67.
- Astrup, C.W., Gantt, W.H., Stephens, J.H., 1979. Differential effects of person in the dog and in the human. Pavlov J. Biol. Sci. 14, 104–107. https://doi.org/10.1007/
- Barrera, G., Jakovcevic, A., Elgier, A.M., et al., 2010. Responses of shelter and pet dogs to an unknown human. J. Vet. Behav. 5, 339–344. https://doi.org/10.1016/j.jveb.2010.
- Barry, K.J., Crowell-Davis, S.L., 1999. Gender differences in the social behavior of the neutered indoor-only domestic cat. Appl. Anim. Behav. Sci. 64, 193–211. https://doi. org/10.1016/S0168-1591(99)00030-1.
- Baun, M.M., Bercstrom, N., Lancston, N.F., Thoma, L., 1984. Physiological effects of human/companion animal bonding. Nurs. Res. 33, 126–129.
- Blumstein, D.T., Daniel, J.C., Evans, C.S., (2000) J Watcher. University of California Los Angeles.
- Boivin, X., Garel, J.P., Mante, A., Le Neindre, P., 1998. Beef calves react differently to different handlers according to the test situation and their previous interactions with their caretaker. Appl. Anim. Behav. Sci. 55, 245–257. https://doi.org/10.1016/S0168-1591(97)00050-6.
- Bowlby, J., 1973. Attachment and Loss: Separation: Anxiety and Anger. Basic Books. 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, 2nd edn. Cambridge University Press, Cambridge, UK, pp. 67–93.
- Capitanio, J.P., 2002. Sociability and responses to video playbacks in adult male rhesus monkeys (Macaca mulatta). Primates 43, 169–177.
- Collard, R.R., 1967. Fear of strangers and play behavior in kittens with varied social experience. Child Dev. 38, 877–891. https://doi.org/10.2307/1127265.
- Coppola, C.L., Grandin, T., Enns, R.M., 2006. Human interaction and cortisol: Can human contact reduce stress for shelter dogs? Physiol. Behav. 87, 537–541. https://doi.org/ 10.1016/j.physbeh.2005.12.001.
- 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. https://doi.org/10.1016/j.
- Cunningham, C.L., Ramos, M.F., 2014. Effect of training and familiarity on responsiveness to human cues in domestic dogs (Canis familiaris). Anim. Cogn. 17, 805–814. https://doi.org/10.1007/s10071-013-0714-z.
- 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. https://doi.org/10.2460/ajvr.2003.64.1151.
- Davis, H., Taylor, A.A., Norris, C., 1997. Preference for familiar humans by rats. Psychon. Bull. Rev. 4, 118–120. https://doi.org/10.3758/BF03210783.
- Defolie, C., Malassis, R., Serre, M., Meunier, H., 2015. Tufted capuchins (Cebus apella) adapt their communicative behaviour to human's attentional states. Anim. Cogn. 18, 747–755. https://doi.org/10.1007/s10071-015-0841-9.
- Dybdall, K., Strasser, R., Katz, T., 2007. Behavioral differences between owner surrender and stray domestic cats after entering an animal shelter. Appl. Anim. Behav. Sci. 104, 85–94. https://doi.org/10.1016/j.applanim.2006.05.002.
- 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. https://doi.org/10.1016/j.jveb.2007.06.004.
- Ellis, S.L.H., Thompson, H., Guijarro, C., Zulch, H.E., 2015. The influence of body region, handler familiarity and order of region handled on the domestic cat's response to being stroked. Appl. Anim. Behav. Sci. 173, 60–67. https://doi.org/10.1016/j. applanim.2014.11.002.
- Færevik, G., Andersen, I.L., Jensen, M.B., Bøe, K.E., 2007. Increased group size reduces conflicts and strengthens the preference for familiar group mates after regrouping of weaned dairy calves (Bos taurus). Appl. Anim. Behav. Sci. 108, 215–228. https://doi. org/10.1016/j.applanim.2007.01.010.
- Falk, J.L., 1971. The nature and determinants of adjunctive behavior. Physiol. Behav. 6, 577–588. https://doi.org/10.1016/0031-9384(71)90209-5.
- Feaver, J., Mendl, M., Bateson, P., 1986. A method for rating the individual distinctiveness of domestic cats. Anim. Behav. 34, 1016–1025.
- Gácsi, M., Topál, J., Miklósi, Á, et al., 2001. Attachment behavior of adult dogs (Canis familiaris) living at rescue centers: forming new bonds. J. Comp. Psychol. 115 (423).
- Galvan, M., Vonk, J., 2016. Man's other best friend: domestic cats (F. silvestris catus) and their discrimination of human emotion cues. Anim. Cogn. 19, 193–205. https://doi. org/10.1007/s10071-015-0927-4.
- Gosling, S.D., John, O.P., 1999. Personality dimensions in nonhuman animals a cross-

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- species review. Curr. Dir. Psychol. Sci. 8, 69-75.
- Győri, B., Gácsi, M., Miklósi, Á, 2010. Friend or foe: context dependent sensitivity to human behaviour in dogs. Appl. Anim. Behav. Sci. 128, 69–77. https://doi.org/10. 1016/j.applanim.2010.10.005.
- Handlin, L., Hydbring-Sandberg, E., Nilsson, A., et al., 2011. Short-term interaction between dogs and their owners: effects on oxytocin, cortisol, insulin and heart rate-an exploratory study. Anthrozoos 24, 301–315. https://doi.org/10.2752/175303711X13045914865385.
- Hartmann, D.P., 1977. Considerations in the choice of interobserver reliability estimates. J. Appl. Behav. Anal. 10, 103–116. https://doi.org/10.1901/jaba.1977.10-103.
- Heath, S., 2009. Aggression in cats. In: Horowitz, D.F., Mills, D. (Eds.), BSAVA Manual of Canine and Feline Behavioural Medicine. British Small Animal Veterinary Association, Gloucester, UK, pp. 223–235.
- Ito, Y., Watanabe, A., Takagi, S., et al., 2016. Cats beg for food from the human who looks at and calls to them: ability to understand humans' attentional states. Psychologia 59, 112–120. https://doi.org/10.2117/psysoc.2016.112.
- Leyhausen, P., 1988. The tame and the wild: another just-so-story? In: Turner, D.C., Bateson, P.P.G. (Eds.), The Domestic Cat: the Biology of Its Behaviour, 1st edn. Cambridge University Press, Cambridge, pp. 57–66.
- Lowe, S.E., Bradshaw, J.W., 2002. Responses of pet cats to being held by an unfamiliar person, from weaning to three years of age. Anthrozoos Multidiscip J Interact People Anim 15, 69–79.
- Maille, A., Engelhart, L., Bourjade, M., Blois-Heulin, C., 2012. To beg, or not to beg? That is the question: mangabeys modify their production of requesting gestures in response to human's attentional states. PLoS One 7, e41197. https://doi.org/10.1371/ journal.pone.0041197.
- Merola, I., Lazzaroni, M., Marshall-Pescini, S., Prato-Previde, E., 2015. Social referencing and cat-human communication. Anim. Cogn. 1–10. https://doi.org/10.1007/ s10071-014-0832-2.
- Mertens, C., Turner, D.C., 1988. Experimental analysis of human-cat interactions during first encounters. Anthrozoös 2, 83–97.
- 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. https://doi.org/ 10.1037/0735-7036.119.2.179.
- Nawroth, C., Ebersbach, M., von Borell, E., 2013. Are juvenile domestic pigs (Sus scrofa domestica) sensitive to the attentive states of humans?—The impact of impulsivity on choice behaviour. Behav. Processes 96, 53–58. https://doi.org/10.1016/j.beproc. 2013.03.002.
- Podberscek, A., Blackshaw, J., Beattie, A., 1991. The behavior of laboratory colony cats and their reactions to a familiar and unfamiliar person. Appl. Anim. Behav. Sci. 31, 119–130. https://doi.org/10.1016/0168-1591(91)90159-U.
- Poss, S.R., Kuhar, C., Stoinski, T.S., Hopkins, W.D., 2006. Differential use of attentional and visual communicative signaling by orangutans (Pongo pygmaeus) and gorillas (Gorilla gorilla) in response to the attentional status of a human. Am. J. Primatol. 68, 978–992. https://doi.org/10.1002/ajp.20304.
- Potter, A., Mills, D.S., 2015. Domestic cats (Felis silvestris catus) do not show signs of secure attachment to their owners. PLoS One 10, e0135109. https://doi.org/10. 1371/journal.pone.0135109.

- Powell, R., Honey, P.L., Symbaluk, D.G., 2012. Operant conditioning. Introduction to Learning and Behavior, 4th ed. Wadsworth Publishing, Belmont, CA, pp. 234.
 R Development Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rieger, G., Turner, D.C., 1999. How depressive moods affect the behavior of singly living persons toward their cats. Anthrozoos 12, 224–233. https://doi.org/10.2752/089279399787000066
- Saito, A., Shinozuka, K., 2013. Vocal recognition of owners by domestic cats (Felis catus). Anim. Cogn. 16, 685–690. https://doi.org/10.1007/s10071-013-0620-4.
- Schaffer, H.R., Emerson, P.E., 1964. The development of social attachments in infancy. Monogr. Soc. Res. Child Dev. 29, 1–77. https://doi.org/10.2307/1165727.
- Slingerland, L.I., Robben, J.H., Schaafsma, I., Kooistra, H.S., 2008. Response of cats to familiar and unfamiliar human contact using continuous direct arterial blood pressure measurement. Res. Vet. Sci. 85, 575–582. https://doi.org/10.1016/j.rvsc.2007. 12.008
- Spotte, S., 2014. Free-ranging Cats Behavior, Ecology, Management. Wiley, Hoboken.
- Thielke, L.E., Udell, M.A.R., 2015. The role of oxytocin in relationships between dogs and humans and potential applications for the treatment of separation anxiety in dogs. Biol. Rev. Camb. Philos. Soc. 92 (1), 378–388. https://doi.org/10.1111/brv.12235.
- Turner, D.C., 2014. Social organisation and behavioural ecology of free-ranging domestic cats. In: Turner, D.C., Bateson, P.P.G. (Eds.), The Domestic Cat: the Biology of Its Behaviour, 3rd edn. Cambridge University Press, Cambridge, UK, pp. 63–80.
- Turner, D.C., Feaver, J., Mendl, M., Bateson, P., 1986. Variation in domestic cat behaviour towards humans: a paternal effect. Anim. Behav. 34, 1890–1892.
- Turner, D.C., 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
- Udell, M.A.R., Dorey, N.R., Wynne, C.D.L., 2010. What did domestication do to dogs? A new account of dogs' sensitivity to human actions. Biol. Rev. 85, 327–345. https:// doi.org/10.1111/j.1469-185X.2009.00104.x.
- Vitale Shreve, K.R., Mehrkam, L.R., Udell, M.A.R., 2017. Social interaction, food, scent or toys? A formal assessment of domestic pet and shelter cat (Felis silvestris catus) preferences. Behav. Processes 141 (3), 322–328. https://doi.org/10.1016/j.beproc. 2017 03 016
- Vitale Shreve, K.R., Udell, M.A.R., 2015. What's inside your cat's head? A review of cat (Felis silvestris catus) cognition research past, present and future. Anim. Cogn. 18, 1195–1206. https://doi.org/10.1007/s10071-015-0897-6.
- Vitale Shreve, K.R., Udell, M.A.R., 2017. Stress, security, and scent: the influence of chemical signals on the social lives of domestic cats and implications for applied settings. Appl. Anim. Behav. Sci. 187, 69–76. https://doi.org/10.1016/j.applanim. 2016.11.011.
- von Bayern, A.M.P., Emery, N.J., 2009. Jackdaws respond to Human Attentional States and communicative cues in different contexts. Curr. Biol. 19, 602–606. https://doi.org/10.1016/j.cub.2009.02.062.
- Waiblinger, S., Menke, C., Fölsch, D., 2003. Influences on the avoidance and approach behaviour of dairy cows towards humans on 35 farms. Appl. Anim. Behav. Sci. 84, 23–39. https://doi.org/10.1016/S0168-1591(03)00148-5.
- Wolfe, R., 2001. The Social Organization of the Free Ranging Domestic Cat (Felis Catus). Unpublished Doctoral Dissertation. University of Georgia.