

Predictors of proximity to others in colony housed shelter cats (*Felis silvestris catus*)

Malini Suchak, Michael Piombino, and Kalina Bracco

Abstract

Colony housing of cats allows shelters to maximize the number of cats housed in limited space. Most research on colony-housed cats examines stress in relation to group size or enclosure size. While this is important for evaluating welfare, it is equally important to understand how cats are interacting socially in these colonies. We observed 259 adult cats housed in groups of two to eight individuals. Scan samples were used to assess how frequently individual cats were in close proximity to other cats. These data were used to measure individual differences in sociability and patterns of proximity to certain partners. We used information about the past history of the cat, which was collected upon admission to the shelter to identify predictors of time spent in proximity. There was a high degree of inter-individual variability in sociability. Strays tended to spend less time in proximity to other cats, and this effect was most pronounced in females. However, none of the information collected upon admission predicted patterns of proximity to certain partners, or which cats spent time in association with each other. Future studies should explore the implications of differences in sociability by associating observations of social behavior and stress behaviors.

HIGHLIGHTS

- Cats showed high variability in time spent near conspecifics in the shelter
- Cats who were surrendered as strays were most likely to be classified as non-social
- None of the data collected upon intake significantly predicted which cats tended to be in proximity to each other

1. INTRODUCTION

From an evolutionary standpoint it is unknown exactly when or how the domestic cat (*Felis silvestris catus*) evolved from a solitary ancestor to a species that, under the right circumstances, can and will form social bonds with each other (Bradshaw et al. 2012). The best-studied examples of social behavior in cats come from free-ranging or feral cats who will form groups when there are ample resources as a result of provisioning (Crowell-Davis et al. 2004; Bradshaw 2009; Carfazzo and Natoli 2009). These cats show a wide variety of affiliative behaviors including allogrooming, allorubbing, and sleeping in close proximity to each other. In general, agonistic behaviors are not frequently observed within feral cat colonies, although avoidance behavior such as turning the head away to avoid a direct stare may suggest that the cats are resolving

Pet Behaviour Science | 2016, Vol.2, 24 - 33
DOI: [10.21071/pbs.v0i2.5186](https://doi.org/10.21071/pbs.v0i2.5186)

Malini Suchak, Michael Piombino, and Kalina Bracco

Animal Behavior, Ecology, and
Conservation
Canisius College, Buffalo, NY

Paper Research
Email:
suchakm@canisius.edu

United States

Keywords:
Cats, colony housing,
Felis catus, multi-cat
household, proximity,
shelters

conflicts through subtle signals rather than overt fighting (Dards 1983). Given their large home ranges, avoidance may be more important than overt aggression for cats.

The potential use of large spaces by free-ranging cats to avoid conflict has led many to question how they adapt to social living in the home, where the space per cat is typically of an order of magnitude less than outdoors. Cats may form individual territories or home ranges within the house and frequently spend time out of sight of each other (Bernstein and Strack 1996; Barry and Crowell-Davis 1999). They even seem to “time share” favored spots, each occupying the spot at a different time of day (Bernstein and Strack 1996). Familiarity and relatedness are important factors in whether or not household cats spend time together, with related individuals spending the most time together (Bradshaw and Hall 1999; Curtis et al. 2003; Crowell-Davis et al. 2004). Overall, the rates of aggression observed in the household are low and are most often negatively correlated with familiarity (Bernstein and Strack 1996; Barry and Crowell-Davis 1999; Bradshaw and Hall 1999).

The role of familiarity on aggression and affiliation has significant implications for shelters that wish to house cats in groups. Group housing may have several benefits. Depending on the amount of space and provisioning of environmental enrichment, cats that live in a larger enclosure may have more hiding places and perches, which are important for reducing stress (Casey and Bradshaw 2007; Kry and Casey 2007; Ellis 2009). Furthermore, cats housed in communal housing are adopted just as quickly as cats housed in enriched, single cages, and more quickly than those housed in basic, single cages (Gourkow and Fraser 2006). However, given that the space per cat is significantly less than they would have in the household, there may also be costs to living in a group without the opportunity to avoid one another by leaving (Ottaway and Hawkins 2003).

Most of the work done on group housing and cats has focused on the stress levels of cats (Finka et al. 2014). While stress is undoubtedly important in assessing the welfare of shelter cats, little attention has been given to whether or not the cats are engaging in positive social

interactions or avoiding each other. Since socialization appears to occur during a critical period of 3-7 weeks of age (Landsberg 1996), it is unlikely a shelter will have knowledge of the socialization of an adult cat, particularly for those individuals who are surrendered with unknown histories or from single-cat households. Coming from a multi-cat household may ease the adjustment of a cat even in single caging, as they are used to having other cats around (Broadley, McCobb and Slater 2014).

The goal of the current study was to identify predictors of time spent in proximity to conspecifics from the information collected upon admission to the shelter. Many previous studies have established that proximity is a reliable measure of affiliation between cats (Macdonald and App 1978; van den Bos 1994; Barry and Crowell-Davis 1999; Curtis et al. 2003; Crowell-Davis et al. 2004) and many other species (Dunbar and Shultz 2010; Silk et al. 2013,). Based on the literature, we hypothesized that cats who were surrendered together from the same household were more likely spend time in proximity than cats who were previously strangers. Furthermore, we hypothesized that if the individual history of the cat, such as their previous living situation (owned versus free-ranging), or the number of other cats they lived with reflected social experience, then cats that had indicators of previous social experience may spend more time in proximity to others. Alternatively, if the cats were primarily seeking to avoid each other in the shelter colony (*sensu* Ottaway and Hawkins 2003), we predicted that a higher density of cats in the room (number of cats per m² of space) would lead to increased proximity between cats.

2. METHODS

Participants and setting.

Participants were 259 adult cats (128 males and 131 females) of various breeds, including mixed breeds, housed at the SPCA Serving Erie County. Group sizes ranged from two to eight cats, with a median of three cats per group. The staff at the SPCA decided group composition upon admission. There were no strict criteria for inclusion in a group, although cats that had contagious medical issues or were surrendered for a

history of aggression towards other pets were excluded from the groups. Upon introduction, a staff member or volunteer observed the group for approximately an hour in case of severe aggression. In total, we observed 87 groups of cats in this study. Among the groups we observed there were single-sex (N = 32) and mixed sex groups (N = 55), as well as groups of individuals that were brought in together (N = 41) and groups where individuals were introduced at the shelter (N = 46).

The groups were built on an all-in, all out policy, that is, individuals were placed together and no new individuals were added until all of the individuals were adopted out. Thus, there were cats leaving the groups, but not entering the groups during the time of the study. The average length of stay (LoS) in the shelter was 39 days (range: 1-205) for our participants. This measure, called Shelter LoS throughout, represents the total amount of time from intake to the date of observation, including time when the cat was not available for adoption or present in the colony housing. On average, cats only spent 15 days in the colony setting (range 1-85, but note that only 6 cats spent more than 39 days in colony housing). This measure is called Colony LoS throughout. Since groups were created using an all-in, all-out policy, this represents the length of time each group was together, on average.

The cats were housed in one of four colony rooms, ranging in size from 3.06m² to 5.41m². Each room contained 1-2 litterboxes, several beds and towels, and typically contained a Karunda bed[®], 1-2 plastic milk crates, and a long shelf approximately 1.19m high. The two larger rooms also contained a mid-level shelf (approximately 0.6 m high). Food and water were provisioned by the shelter staff and at no time were participants food or water deprived as part of this study. This study was approved by the SPCA serving Erie County prior to the commencement of data collection. This study did not require approval of the Canisius College IACUC because it was observational in nature.

Background data on the cats.

Using the SPCA's PetPoint database, we gathered background information on each of our participants

that was collected upon admission to the shelter. This included the cause for relinquishment (owner surrendered (N=192), stray (N=37), or seized (N=30)), number of cats in the intake (number admitted together, M=6.6, range 1-50), and names of cats that came in together. For the purposes of this study, any individuals that were brought in together were considered "familiar" and any individuals that were not brought in together were considered "strangers." Based on the intake data we were unable to determine relatedness or length of time spent together for familiar individuals. We also recorded demographic information including sex, age, and spay/neuter status.

Procedures.

Observations were collected from January 2014-December 2015 (92.6 hours of observation). Each group was observed for 10 minutes, twice per day, 2 to 4 times per week. Because we could not control when cats were adopted, not all cats were observed for the same amount of time, but all cats were observed for at least two sessions. The average number of scans each cat was observed was 71.3 (range: 22-251). All observations occurred between 10:00h and 16:30h, during the normal operating hours at the shelter, and were balanced across time of day. Observations were suspended during husbandry procedures, or if shelter staff or visitors entered the room. Thus, observations were limited to periods when just the cats were present in the room without any human interference.

During each 10-minute observation period, the observer stood outside the clear glass door of the colony room. Scan samples were taken at 1-minute intervals to record the proximity of each cat to all others. Two short, separate observation periods per day ensured that we were not overestimating the preferences of 2 cats who happened to be sleeping near each other at any given time. Each cat was scored as being in contact with another cat, within one body length but not touching, or greater than one body length away from each other cat. Only cats who were resting, sleeping, or grooming with another cat were scored as in proximity. Thus, cats who were transiently passing by other cats were not counted as in proximity. As per previous research (Macdonald and App 1978; van den Bos 1994; Barry and Crowell-Davis 1999;

Curtis et al. 2003; Crowell-Davis et al. 2004) time spent in proximity can be used a proxy for tolerance towards another. Although previous research has used <1m as a measure of proximity, we chose one body length as a more conservative measure given that the size of the room would automatically put most cats within one meter, rendering this measure useless in determining tolerance. Body length is a frequently used measure of proximity in other species (i.e., primates: Perry 1996; cetaceans: Conner et al. 2006) and is defined as the length from nose to tailbase of an adult individual. We also recorded all occurrences of any aggressive interactions including swat, hiss, growl, and chase. Inter-rater reliability was excellent on all measures (97.78% agreement between raters), and was collected by two live scorers present in front of the colony enclosure for a random subset of sessions. Cats were not videotaped due to blind spots in the room (e.g., hiding places).

Analysis

Each cats' individual propensity to spend time near conspecifics (regardless of partner) was calculated using as the percentage of scans in which an individual was in proximity (defined as a body length or closer) to another cat. Because the data from each scan are not independent from each other (a cat sleeping in proximity during one scan is likely to be in proximity the next), data were collapsed across the day. Due to the large number of zeros (cats who were never within a body length of another cat) in the data, we collapsed this measure into a binary sociability index, designating each cat as either sociable or non-sociable (1/0). Cats who were never within a body length or closer of another cat were scored as non-sociable (0), and cats who were, at some point, within a body length or closer of another cat were scored as sociable. We used the background data collected from the PetPoint database to see if any characteristics of the cats predicted whether or not an individual might be classified as sociable.

To control for repeated sampling of individuals, we ran a Generalized Linear Mixed Model (GLMM), using the Information Criterion (IC) method for selecting the best model (Bolker et al 2009). The IC method uses model selection to compare fits of models, estimating their

predictive power on the dependent variable. Since the current study was interested in which factors were predictive of proximity to other cats in the shelter, the IC method was used to identify these factors. The purpose of running multiple models testing different combinations of the fixed effects is to determine which fixed effect or combination of effects is the best predictor of sociability. We determined the model with the most explanatory power by comparing the Akaike Information Criteria (AIC) values for all of the possible models. We then tested the best fit model against a full model with all of the fixed effects and a null model with only the random effects. All analyses were run using R statistical software (R Development Core Team, 2014) using the *glmer* function of the *lme4* package (Bates, Maechler, and Bolker 2012). After obtaining AIC from all of the models, we used the *anova* function to determine which model had the most explanatory power. The significant interaction was explored using the *ggplot* function.

The binary sociability index (1/0) was the dependent variable. Individual, date of observation, and observer were entered as random effects. Fixed effects tested included the density of cats in the room (cats/m²), number of cats in the intake, source of intake (categorical: owner surrendered, stray, or seized), spay/neuter status (1/0), age, sex, length of stay at the shelter and length of stay in the colony housing. Since data were aggregated by day, we calculated the length of stay measures specific to each observation day; that is, for Shelter LOS, we calculated the difference (in days) between the date the animal came into the shelter and the date of observation, for Colony LoS it was the difference between when the cat came into the colony and the date of observation. We tested density, number in intake, and source of intake individually and also the 2-way interaction of these effects with demographic information such as spay/neuter status, age, sex and the two LoS measures. Since Shelter LoS and Colony LoS were highly correlated ($r = 0.507$, $P < 0.001$), we did not include those two measures in the same model together, but rather ran separate models for each of them. See Table 1 for a summary of models.

Due to frequent changes in group composition, most typical measures of patterns of proximity (e.g., affinity matrices, social network analysis, etc.), are not

Model	Model DF	AIC	Deviance
Null (random effects only)	4	932.55	924.55
Full (all fixed effects)	13	934.02	908.02
Source * sex (best fit)	9	921.18	903.81
Other models tested			
Source	6	926.20	914.20
Source * Age	9	923.48	905.48
Source * Colony LoS	9	928.01	910.01
Source * Shelter LoS	9	930.88	912.88
Source * Spay/Neuter status	9	931.56	913.56
Density (cats/m²)	5	934.49	924.49
Density * Age	7	937.59	923.59
Density * Colony LoS	7	937.17	923.17
Density * Shelter LoS	7	937.74	923.74
Density * Spay/Neuter status	7	933.08	919.08
Density * sex	7	935.36	921.36
Number in intake	5	934.40	924.40
Number * Age	7	935.36	921.36
Number * Colony LoS	7	938.26	924.26
Number * Shelter LoS	7	932.96	918.96
Number * Spay/Neuter status	7	938.10	924.10
Number * sex	7	933.74	919.74

Table 1. Summary of models tested for predictors of proximity. A model including source of surrender, sex, and the interaction between source and sex was the best fit model.

appropriate for this setting. We calculated patterns of proximity using the percentage of scans in which two individuals were in proximity (a body length or closer) to each other. There were also a large number of zeros for this measure (e.g., pairs of cats who were never in proximity to each other), so we again created a binary variable, designating each pair as either in proximity or

not (1/0). We again used a GLMM to determine which predictors had the most explanatory value in proximity, our dependent variable. Random effects were dyad, date and observer, to control for repeated sampling of the same individuals across multiple days. Fixed effects tested included whether the cats were familiar or strangers, sex composition of the dyad (e.g., M-M, M-F,

and F-F), and days together in the colony setting. Among dyads who were at some point in proximity (dyads scored as 1 above, $N = 142$) we ran a follow-up analysis to see if there was a difference in dyads who were in contact (e.g., touching) vs. those who were within a body length, but not in contact. The dependent variable was contact, the random effects, fixed effects, and models were the same as above. We were unable to analyze aggression as it occurred too rarely (only on 3 occasions).

3. RESULTS

Sociability.

There was extremely high inter-individual variability in sociability (as measured by percent of scans in proximity to another individual; Figure 1). One hundred ten cats (42.47%) were never seen in proximity to another individual, the remaining ranged from 4.34% to 100% percent of scans in proximity to another cat (median = 4.50%). Only 40 cats (15.4%) were recorded in proximity to other cats more than 50% of the time.

The results of the GLMM revealed that a model including the reason for surrender and the sex of the cats had the most explanatory power in whether or not a cat was categorized as sociable ($AIC = 921.81$, $\chi^2 = 20.74$, $\chi^2 DF = 5$, $P < 0.001$; Table 1). The intercept was not significantly contributing to the fit of the model.

There was a main effect of source ($Z = -3.53$, $P < 0.001$) and a significant interaction with sex ($Z = 2.59$, $P = 0.01$). A closer look at the data revealed that both males and females that were surrendered to the shelter as strays were less likely to be classified as social (Figure 2). However, this difference was much more pronounced for females than males, with female strays only having a 0.10 probability of being classified as social.

The results of the second GLMM on patterns of proximity revealed that the model including familiarity had the most explanatory power ($AIC = 929.24$, $\chi^2 = 2.5$, $\chi^2 DF = 1$, $P = 0.11$; Table 2), however it was not significantly better at explaining the variance than either the null or full model. A closer look at the best fit model revealed that the intercept was significant ($Z = -3.54$, $P < 0.001$), but familiarity was not ($Z = 1.61$, $P = 0.11$). Thus, none of the fixed effects tested in this study significantly predicted time spent in proximity to a specific partner. When the analysis was limited to only cats that were in proximity, and compared those in contact versus those within a body length, but not in contact, the null model had the most explanatory power ($AIC = 287.67$, Table 3). Again, none of the fixed effects predicted time spent in contact over general proximity, there was only a trend towards significance for the random effects ($Z = -1.92$, $P = 0.052$).

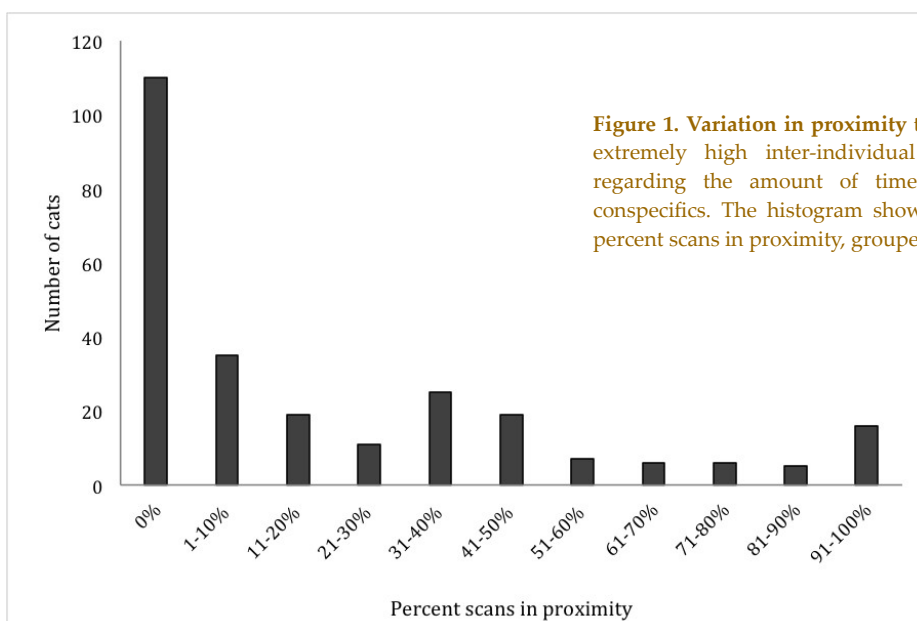


Figure 1. Variation in proximity to conspecifics. There was extremely high inter-individual variability among cats regarding the amount of time spent in proximity to conspecifics. The histogram shows the number of cats by percent scans in proximity, grouped into blocks of 10%.

Model	Model DF	AIC	Deviance
Null (random effects only)	4	929.75	921.75
Full (all fixed effects)	8	934.21	918.58
Familiarity (best fit)	5	929.24	919.24
Other models tested			
Sex composition	6	932.90	920.90
Time together	5	931.56	921.56
Familiarity * Sex composition	9	933.91	915.91
Familiarity * time together	7	933.13	919.13
Sex composition * time together	9	936.58	918.58

Table 2. Summary of models tested for patterns of proximity. A model including whether the cats were familiar (came from the same intake), was the best fit model, but did not explain the variance better than the null and full models.

Model	Model DF	AIC	Deviance
Null (random effects only)	4	287.67	279.67
Full (all fixed effects)	8	295.24	279.24
Other models tested			
Familiarity	5	289.35	279.35
Sex composition	6	291.56	279.59
Time together	5	295.24	279.66
Known * Sex composition	9	291.72	273.72
Known * Time together	7	291.73	277.73
Sex composition * Time together	9	295.37	277.37

Table 3. A summary of the models tested for predictors of which days might be in contact versus simply within a body length, but not touching. The null model had the most explanatory power.

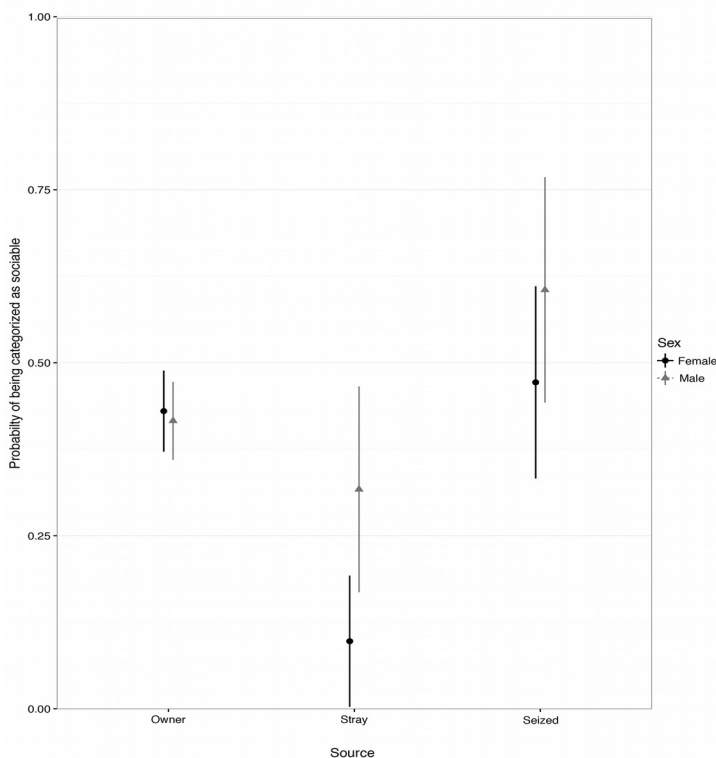


Figure 2. Cats surrendered as strays are less likely to be classified as social. This effect was more pronounced in females (circles) than males (triangles). Error bars represent interquartile range (first through third quartile).

4. DISCUSSION

In this study we used proximity as a behavioral measure to assess how cats in colony housing interact with each other. Overall, the cats varied highly on propensity to be sociable with one another. Approximately 42% of the cats were never in proximity to another cat during the period of observation. There might be several reasons why cats may try to maintain some distance in the colony room. First, cats may wish to avoid social contact with other cats. The use of body length as a measure in other work is often chosen because it is close enough between two individuals that there is potential for contact (i.e., Perry 1996). Keeping a further distance may allow individuals more of an opportunity to avoid contact. Although nearly half of the cats observed in this study were more than a body length away, if they were seeking to avoid contact, we cannot determine from the current data if there was sufficient space for them to do so. An alternative explanation is that non-social cats were avoiding other cats due to stress. Stress can lead to suppression of behavior, and while this is typically applied to

maintenance behavior, it could impact social behavior as well (Rehnberg, Robert, Watson and Peters 2015; Stella, Croney and Buffington 2013). A behavioral or physiological measure of stress could shed light on how frequently highly stressed cats are in proximity to others.

On the other hand, a large number of cats spent time in proximity to each other, some of them frequently so. As determined by the GLMM, the best predictor of sociability was a model including sex and source of intake (owner surrendered, stray, or seized). Overall, cats that were surrendered as strays were less likely to be categorized as sociable. It is important to note that this cannot merely be explained by number in intake or number in the room, as both of these factors were accounted for in the analysis and source alone was the best predictor.

The observed interaction between source and sex is puzzling, as female strays were less likely to be categorized as sociable than male strays. Many studies have found that female feral cats tend to have much stronger social bonds than males (Macdonald and Apps 1978; Crowell-Davis et al. 2004; Bradshaw 2009; Carfazzo and Natoli 2009; Houpt 2011) and have smaller home ranges, suggesting greater tolerance than males (Dards 1983). However, these cats were classified by the shelter as “stray” rather than feral, since they were socialized enough with humans to be placed on the adoption floor. Far more is known about the social interactions of owned cats (i.e. Bernstein and Strack 1996; Barry and Crowell-Davis 1999) and feral cats (i.e. Carfazzo and Natoli 2009), than free-ranging socialized cats.

Previous work has shown owner surrendered cats tend to be more stressed than strays (Dybdall, Strasser and Katz 2007) and that male cats tend to be more stressed than females (Rehnberg et al 2015). Thus, our findings demonstrate cats less likely to be stressed (females, strays) are also less likely to be in proximity to other cats. Although above we note that stress may lead to the suppression of social behavior, theoretically it might also lead to increased proximity. For example, if an individual is very inactive, they may not move away from another individual, even if they prefer to be alone. This would, on the surface, look like proximity, but

have nothing to do with tolerance or a preference to be near others. Second, the cats observed in this study are on the adoption floor. Members of the public frequently enter the rooms to interact with the cats. There may be a “safety in numbers” effect, whereby proximity to other cats lessens the chance of someone directly approaching a particular cat for interaction. More detailed knowledge of how cats end up in proximity (e.g., who approaches whom?), measures of stress, and observations of the distance between cats when people are in the room may help determine how the setting is impacting their social spacing.

We also looked at patterns of proximity to see if there were particular individuals who tended to be near each other. Such a measure has implications for the cats’ well being if not adopted together or moved independently while at the shelter, and also might help shelters decide which cats to place in rooms together. However, none of the data collected upon intake predicted patterns of proximity, and our hypothesis was not supported. This is in contrast to previous reports where familiarity predicted proximity; however, it is important to note that those were studies of homed cats whose histories were known in much more detail (e.g., Bradshaw and Hall 1999; Curtis et al. 2003). We did not know how long two cats had been together or kin relationships, two factors, which in these previous studies of homed cats have been implicated in affiliation patterns. Behavioral signs that two individuals are closely bonded, such as allogrooming, or signs of distress when separated may be informative to shelter staff in addition to time spent in contact or proximity. However, it is important to consider that stress may also suppress these behaviors as well.

In addition to collecting stress data, longer data collection periods may also shed light on patterns of proximity better than the short, multiple data collection periods used in this study. We chose to use two short sessions per day so as to capture, but not over-represent proximity between two cats who might be sleeping near each other. This created a significant limitation as doing two short sessions may have missed some opportunities for particular pairs to be near each other. We also rarely observed activity, limiting our opportunity to observe aggression and affiliative behavior (such as approaches with a tail up, nose to

nose sniffing), which occur randomly and infrequently throughout the day. Furthermore, because our observations were live, we were limited to only the times in which the shelter was open to the public. Given the potential role of stress in social behavior, collecting data when the shelter is not open could be highly useful in understanding the patterns observed in our study.

5. CONCLUSION

Understanding the group dynamics of cats living in shelter colonies can help shelter employees make informed decisions about how to place cats upon admission. Our data contribute to this growing body of knowledge, specifically by suggesting that strays are less likely to be in proximity to other cats in colony housing. However, given the puzzling sex difference observed and limited observation time, our results should be interpreted with some caution. Future research should investigate the interaction between stress and social behavior in colony housed cats.

6. ACKNOWLEDGEMENTS

We would like to thank the SPCA Serving Erie Country for allowing us to collect data on their colony housing and Julia Watzek for statistical advice. This research was funded in part by a grant from the AI and Noura Gress Foundation.

7. REFERENCES

- Barry, K.J., and Crowell-Davis, S.L. 1999. Gender differences in the social behavior of the neutered indoor-only domestic cat. *Applied Animal Behaviour Science* 64: 193-211.
- Bates, D., Maechler, M., and Bolker, B. (2012). *Lme4: Linear mixed effects models using s4 classes (2011)*. R package version 0.999375-42. <http://www.R-project.org>
- Bernstein, P.L., and Strack, M. 1996. A game of cat and house: Spatial patterns and behavior of 14 domestic cats (*Felis catus*) in the home. *Anthrozoos* 9: 25-29.
- Bolker, B.M. et al. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24: 127-135.
- Bradshaw, J. (2009). Behaviour of cats. In *The ethology of domestic animals, 2nd ed.*, 204-216, ed. P. Jensen. Oxfordshire, UK: CABI.
- Bradshaw, J.W.S., and Hall, S. (1999). Affiliative behaviour of related and unrelated pairs of cats in catteries: A preliminary report. *Applied Animal Behaviour Science* 62: 251-255.
- Bradshaw, J.W.S., Casey, R.A., and Brown, S.L. 2012. *The Behaviour of the Domestic Cat, 2nd edition*. Oxfordshire, UK: CABI press.
- Broadley, H.M., McCobb, E.C. and Slater, M.R. 2014. Effect of single-cat versus multi-cat home history on perceived behavioral stress in domestic cats (*Felis silvestris catus*) in an animal shelter. *Journal of Feline Medicine and Surgery* 16: 137-143.
- Cafazzo, S., and Natoli, E. 2009. The social function of tail up in the domestic cat (*Felis silvestris catus*). *Behavioural Processes* 80: 60-66.
- Casey, R.A., and Bradshaw, J.W.S. 2007. The assessment of welfare. In *The welfare of cats*, 23-46, ed. I. Rochlitz. Doordrecht, The Netherlands: Springer.
- Connor, R.C., Smolker, R., and Bejder, L. 2006. Synchrony, social behaviour, and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Animal Behaviour* 72: 1371-1378.
- Crowell-Davis, S.L., Barry, K., and Wolfe, R. 1997. Social behavior and aggressive problems of cats. *Veterinary Clinics of North America: Small Animal Practice* 27: 549-568.
- Crowell-Davis, S.L., Curtis, T.M., and Knowles, R.J. 2004. Social organization in the cat: A modern understanding. *Journal of Feline Medicine and Surgery* 6: 19-28.
- Curtis, T., Knowles, R., and Crowell-Davis, S. 2003. Influence of familiarity and relatedness on proximity and allogrooming in domestic cats (*Felis catus*). *American Journal of Veterinary Research* 64: 1151-1154.

- Dards, J.L. 1983. The behaviour of dockyard cats: Interactions of adult males. *Applied Animal Ethology* 10: 133-153.
- Dunbar, R.I. and Shultz, S. 2010. Bondedness and sociality. *Behaviour* 147: 775-803.
- Ellis, S. 2009. Environmental enrichment: Practical strategies for improving animal welfare. *Journal of Feline Medicine and Surgery* 11: 901-912.
- Finka, L.R., Ellis, S.L.H., Stavisky, J. 2014. A critically appraised topic (CAT) to compare the effects of single and multi-cat housing on physiological and behavioural measures of stress in domestic cats in confined environments. *BMC Veterinary Research* 10: 73. Doi: 10.1186/1746-6148-10-73
- Gourkow, N., and Fraser, D. 2006. The effect of housing and handling practices on the welfare, behaviour, and selection of domestic cats (*Felis silvestris catus*) by adopters in an animal shelter. *Animal Welfare* 15: 371-377.
- Houpt, K.A. 2011. *Domestic animal behavior for veterinarians and animal scientists*. Wiley-Blackwell.
- Kessler, M.R., and Turner, D.C. 1997. Stress and adaptation of cats (*Felis silvestris catus*) housed singly, in pairs, and in groups in boarding catteries. *Animal Welfare* 6: 243-254.
- Kessler, M.R., and Turner, D.C. 1999. Socialization and stress in cats (*Felis silvestris catus*) housed singly and in groups in animal shelters. *Animal Welfare* 8: 15-26.
- Kry, K., and Casey, R. 2007. The effect of hiding enrichment on stress levels and behaviour of domestic cats (*Felis silvestris catus*) in a shelter setting and the implications for adoption potential. *Animal Welfare* 16: 375-383.
- Landsberg, G. 1996. Feline behavior and welfare. *Journal of the American Veterinary Medical Association* 208: 502-505.
- Macdonald, D.W., and Apps, P.J. 1978. The social behaviour of a group of semi-dependent farm cats, *Felis catus*: A progress report. *Carnivore Genetics Newsletter* 3: 256-268.
- Ottaway, D.S., and Hawkins, D.M. 2003. Cat housing in rescue shelters: A welfare comparison between communal and discrete-unit housing. *Animal Welfare* 12: 173-189.
- Perry, S. 1996. Female-female social relationship in wild white-faced capuchin monkeys (*Cebus capucinus*). *American Journal of Primatology* 40: 167-182.
- R Development Core Team (2014). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org>
- Rehnberg, L.K., Robert, K.A., Watson, S.J. and Peters, R.A. 2015. The effects of social interaction and environmental enrichment on the space use, behaviour and stress of owned housecats facing a novel environment. *Applied Animal Behaviour Science* 169: 51-61.
- Silk, J., Cheney, D., Seyfarth, R. 2013. A practical guide to the study of social relationships. *Evolutionary Anthropology: Issues, News, and Reviews* 22: 213-225.
- Stella, J., Croney, C and Buffington, T. 2013. Effects of stressors on the behavior and physiology of domestic cats. *Applied Animal Behaviour Science* 143: 157-163.
- Stoinski, T.S., Kuhar, C.W., Lukas, K.E., and Maple, T.L. 2004. Social dynamics of captive western lowland gorillas living in all-male groups. *Behaviour* 141 169-195.
- Turner, D.C. and Bateson, P. 2014. *The Domestic Cat: The Biology of its Behaviour*. Cambridge, UK: Cambridge University Press.
- van den Bos, R., and Bruning, T.D.C. 1994. Social behaviour of domestic cats (*Felis lybica f. catus* L.): A study of dominance in a group of female laboratory cats. *Ethology* 98 14-37.