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Activity patterns and interspecific interactions of free-roaming, domestic cats in managed Trap-Neuter-Return colonies

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ABSTRACT

There is very little information on the activity and experiences of stray cats living in managed Trap-Neuter-Return colonies. We explored this issue on a barrier island in the southeastern USA. We analyzed activity patterns relative to both individual cat and colony variables. We used 645 h of point-of-view (Kittycam) video from 26 cats to determine that cats spent an average of 89.5% of time in inactive states (resting, sleeping), 9% of time roaming, 0.6% eating or drinking at colony feeding stations and 0.9% of time hunting wildlife. The averages did not differ by sex nor did activity levels differ by colony location (close to developed or undeveloped island habitat). A total of 142 interspecies interactions were recorded between 29 TNR colony cats and local wildlife. Non-predatory encounters were primarily comprised of interactions with four species: raccoons, black vultures, white-tailed deer, and Virginia opossums. All interactions occurred at cat feeding stations, the majority within 2 h of the daily feeding time. Understanding stray cat activity patterns may provide insight into the welfare of domestic cats in the environment, including their exposure to injury and disease from interacting with other animals.

1. Introduction

Domestic cats (*Felis catus*) are a common sight in urban and suburban neighborhoods throughout the world and their numbers continue to grow (American Pet Products Association, 2016). Domestic cats may be feral (stray, unfriendly, often untamed and unsocialized), stray but somewhat or completely tame, or pets (outdoor “barn cats” and, more commonly, indoor-outdoor house cats). Stray cats roam free in the environment without supervision and current numbers estimate up to 70 million in the U.S. (Loss et al., 2013). Unowned cats present a variety of population management concerns to wildlife managers, public health officials, and veterinary epidemiologists (Slater, 2001; Gerhold and Jessup, 2013; Loss et al., 2013).

Trap-Neuter-Return (TNR) programs have received significant attention as a means of both managing cat populations and avoiding lethal alternatives (Levy et al., 2014). In theory, this management program reduces stray cat populations by limiting recruitment through reproductive control. Cats are reintroduced into resident colonies following their capture and sterilization, with the expectation that population growth will be halted without resorting to euthanasia (Levy et al., 2003). Cats subjected to TNR reside in colonies that are fed and monitored by volunteers on a regular basis, often attracting newcomers to an area where they can be trapped and sterilized (Slater, 2004).

Understanding stray cat activity patterns may provide insight into the welfare of cats in the environment, including their exposure to injury and disease from roaming in the environment or interacting with other animals and people. Stray cats serve as reservoirs or facilitate the transmission of potentially important zoonotic pathogens like raccoon variant rabies virus, *Toxoplasma gondii*, *Bartonella henselae*, plague, tularemia, and various nematode parasites (Campagnolo et al., 2014). Disease, pathogen, and parasite prevalence in free-roaming cats is well-documented (Yamaguchi et al., 1996; Nutter et al., 2004; Hill et al., 2000; Akucewich et al., 2002) but varies by region and colony size. Cat roaming and foraging behavior have important implications for pathogen exposure and transmission, and concerns extend to people and wildlife (Lepczyk et al., 2015). Unfortunately, cat colonies with subsidized food may also attract wildlife that artificially aggregate at higher densities than normal (Jessup, 2004) and interact with cats.

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Wildlife that visit feeding stations may be more likely to come into contact with people because they will forage outside of their natural activity patterns (e.g. raccoons feeding during the day) to take advantage of subsidies.

To date, most studies of stray cat activity have been limited to determinations of range on remote islands (Apps, 1986; Barratt, 1997; Konecny, 1987). These studies found male home range to be larger than female and nocturnal activity to be greater than diurnal. Activity levels of cats in Brooklyn, New York correlated with season and variation in weather (increasing with increasing temperature, decreasing with rain) (Haspel and Calhoon, 1993). Habitat use, range and activity levels of stray cats in exurban Champaign-Urbana Illinois revealed that habitat preference changed seasonally as did percent of time spent in higher levels of activity (Horn et al., 2011). There is very little information on activity and experiences of stray cats living in managed colonies, where cats are neutered, vaccinated, and fed by caretakers. Research from TNR cats on Catalina Island, California suggests that even sterilized cats roamed across large areas, often entering sensitive natural areas far away from feeding stations (Guttilla and Stapp, 2010). Large numbers of stray cats in the USA today visit feeding stations or receive some care from caretakers, yet their primary activities while away from the colony or while roaming are unknown.

To create successful and socially acceptable management plans for stray cats and to understand their interactions with wildlife, it is critical to understand cats' daily behavior patterns. Time budget analyses are normally achieved using data obtained from small parts of the day when humans are able to observe the subjects in their natural habitat. Understanding how often and what time of day cats engage in specific activities will help inform management decisions and also has implications for cat welfare, wildlife health, and pathogen transmission among cats, wildlife and people.

This study utilized point-of-view cameras to: 1) describe the time budget and activity patterns of stray cats living in managed colonies on a barrier island, 2) determine if there are differences in activity patterns due to cat age, sex, or colony location, and 3) document the frequency, timing, and type of interspecies interactions occurring with cats in colonies managed by TNR. Because younger, male cats are more likely to exhibit risky behavior (Loyd et al., 2013,b), we predicted age (younger) and sex (male) would have an influence on the proportion of time spent roaming. We also predicted that cats residing in colonies close to undeveloped, natural areas would spend more time roaming. Lastly, we hypothesized that cat interactions with other wildlife would happen most often at colony feeding stations and be associated with feeding times.

2. Methods

2.1. Study site

Our research took place on Jekyll Island (31°4′12″N, 81°25′13″W), a 5847 acre barrier island on Georgia's Southeastern coast. Jekyll Island is comprised of numerous habitats, including intermixed maritime hardwood forests (19%), maritime pine and pine-hardwood forests (16%), shrub scrub habitats (6%), marshes dominated by *Spartina* spp. (28%), maintained grass (18%), and paved, impervious urbanized settings (3%) (Fig. 1). Jekyll Island is a Georgia state park known for its beautiful and well-protected natural lands. The weather on Jekyll is moderate with long, hot and humid summers and short, mild winters. The most recent US Census numbers (2014) estimate 621 residents on the island, but this varies seasonally, with peaks during tourist season (May–July).

2.2. Technology

The use of animal borne CritterCams® have been implemented in many studies to provide an "animal-eye view" of behaviors such as

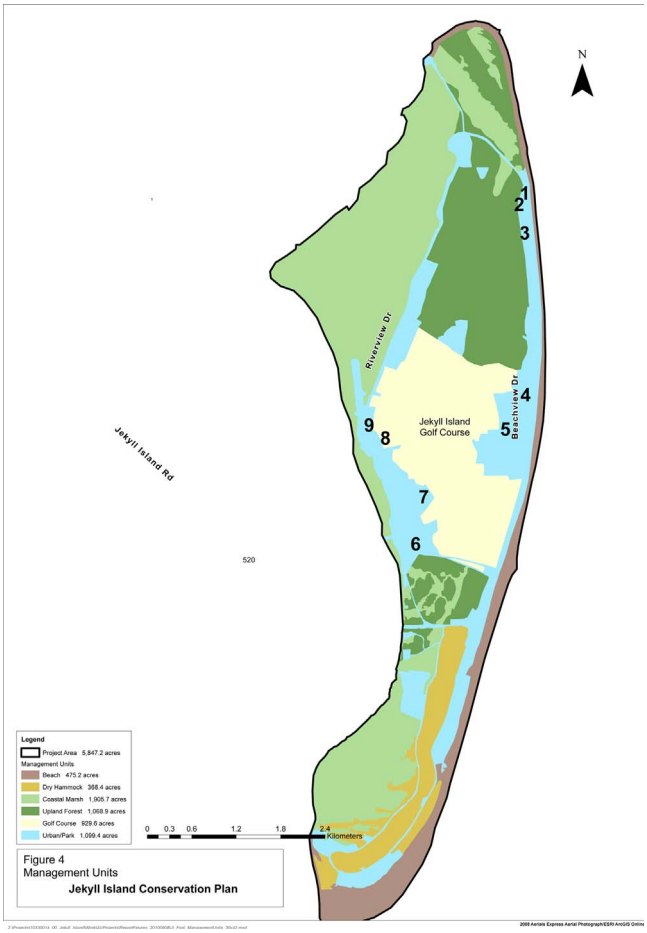

Fig. 1. Map of Jekyll Island, Georgia, USA showing locations of 9 colonies where stray cat activity was monitored in 2014–2015. Sites 1, 2, and 3, are along forest edges and within close proximity to the beach and large expanses of undeveloped, natural area. Sites 4 and 5 are located in neighborhoods. Site 6 is located in the Historic District of Jekyll Island where there are shops, a hotel, restaurants, and significant human activity. Site 7 is located at the golf course maintenance buildings, adjacent to forested habitat. Site 8 is located behind a small church on the edge of dense, old growth oak forest. Site 9 is located in a neighborhood but also adjacent to undeveloped forested land.

hunting and intra- and interspecies interactions (most recently: American Alligators, Nifong et al., 2013; and Bull Sharks, Meynecke et al., 2015). Developed by National Geographic's CritterCam Program, our engineered "KittyCams" monitored stray cats living in colonies managed by TNR. Each camera weighs approximately 90 g, is set in a water-resistant housing, and attached to a breakaway collar (Fig. 2). KittyCams are equipped with VHF transmitters so they could be located if separated from the cats. An ternal motion sensor eliminated most of the recording while the cats were sleeping; however, it was sensitive enough to pick up important activities such as stalking. The cameras included infrared lights, to allow recording of nocturnal activity. After deployment, the camera batteries lasted an average of 24 h at which time the cameras were removed, video downloaded, and units charged for the next deployment.

2.3. Subjects

There were approximately 120 un-owned stray cats on Jekyll Island at the time of this research. Of those, 50 were managed in a TNR program in 9 colonies primarily concentrated in the northern part of the island (Fig. 1). The TNR program was started by a Jekyll Island resident in 2005 in an attempt to decrease the island's population of free-roaming cats. At its onset, the program involved trapping and removing cats that were ill or injured, and placing cats for adoption whenever

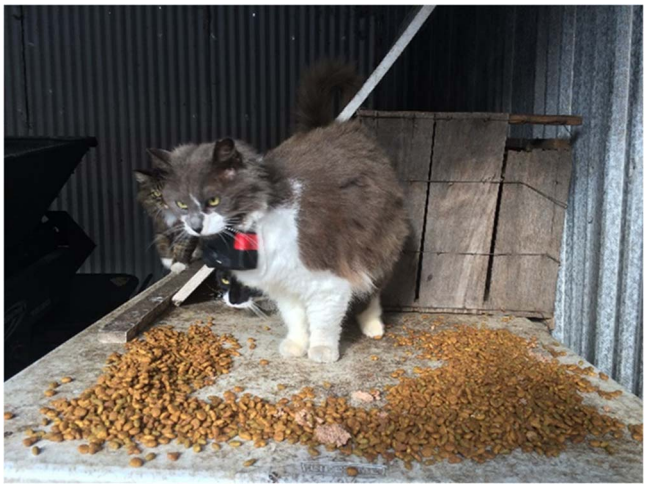

Fig. 2. A colony cat fitted with a National Geographic Kittycam on Jekyll Island, Georgia, USA 2014.

possible. The remainder of the cats were sterilized, vaccinated, and returned to their site of capture. They are currently maintained within designated colonies through daily feeding and monitoring by the TNR manager or his employee. New cats that cannot be adopted or socialized are added to colonies following vaccination and sterilization. They do not receive additional vaccines. The cats were fed daily around the same time, and provided with medical care if needed. We outfitted cats with KittyCams from May to December 2014 and again from February to August 2015. Previous research noted above, as well as our Kittycam work with pet cats, demonstrated that most activity takes place during warmer seasons, February through November (Loyd et al., 2013a). We placed cameras on cats by quickly scruffing habituated cats and slipping the collar over the head. All procedures received approval from the University of Georgia's Institutional Animal Care and Use Committee (AUP #A2010 05-091-Y3-A0).

We outfitted 31 individuals with cameras (17 male, 12 female). Cat colonies were located at various forested and suburban spots on Jekyll Island (Fig. 1). Sites located in suburban neighborhoods were categorized as "developed" whereas those in close proximity to natural forest or beach were labeled "undeveloped."

2.4. Video analysis

We collected and analyzed 681 h of video and used a total of 645 h in analysis (after removing data where camera malfunctions could skew the activity budget calculations). We collected an average of 22 video hours (range 3.8–60 h) from each cat, depending on how frequently the cat could be handled. The data represents a relatively complete account of cat behavior for a 24-h period, with cameras deployed on sampled individuals in the morning before feeding times and removed the following day at feeding time. While reviewing video, we calculated how much time the cats spent in active or inactive states. We used definitions described by Stanton et al., 2015 as a guideline (Table 1). Active states included eating/drinking provided food, hunting, and roaming. Roaming was defined as any movement such as walking, running, and interacting with other cats or wildlife. Hunting included stalking, chasing, batting, harassing, pouncing, eating prey, or playing with prey. Inactive states included sleeping, grooming, and resting.

We also specifically examined interaction events with wildlife. Interactions with other animals included encounters where the cat was aware that the other animal was present (for example, lifted its head and looked at the other animal). Interaction events included: watching, pursuing, approaching, avoiding/fleeing, attacking, fighting, eating or drinking in close proximity, and anything else eliciting a response from the cat that was unrelated to hunting. Interactions lasted from a few seconds to over 30 min. We recorded the time of day and the species involved in each interaction. Since non-predatory interactions were our focus for this study, we only counted interactions between cats and larger or like-sized animals. In order to understand if the cat interactions with wildlife correlated with feeding-site activity, we compared the frequency of interactions around the colony sites during a designated feeding period to interspecies interactions recorded outside of this period. The designated feeding period was constructed by adding a two-hour buffer before and after each colony's 0845 h feeding time. We considered interactions that occurred within this four-hour timeframe to be facilitated by, or related to, the provision of food at a central feeding station location for colony inhabitants.

Table 1
Ethogram of behaviors observed in free roaming cats on Jekyll Island, GA.

Modifier	Description
Active States	
Hunting	Actively pursuing/stalking/harassing live prey
Eating/Drinking	Ingesting food/water provided by humans
Roaming	Walking/running/interacting with cats or wildlife in non-predatory way
Inactive States	
Sleeping	Lying still with minimal movement and not easily disturbed[a]
Grooming	Cat cleans itself by licking/biting/chewing its fur
Resting	Cat is not moving but is alert and easily disturbed

[a] time the camera is off is assumed equivalent to sleeping because the motion sensor is not triggered.

2.5. Statistical analysis

We used the average percent of time cats spent in alternative states of behavior to compare activity by age, sex and location. We tested for association among numerical variables using Pearson correlations (time spent in alternative behaviors, cat age), then used these variables with cat sex and colony location (developed or undeveloped), as potential predictors in a general linear regression model (95% confidence level) with percent of time roaming as the response. In our second regression model, we used the average percent of time cats spent hunting as a response. We investigated differences in behavior by location (colonies close to undeveloped natural area or located within a developed, more urban/suburban area of the island). Fifteen cats had deployments over two seasons. We used a Wilcoxon signed ranks test (95% confidence interval level) to determine whether there was a difference in percent of time spent roaming between two seasons for these fifteen cats. We used circular statistics to examine timing of frequent cat-wildlife interactions. Circular statistics are used to analyze variables that are cyclic in nature, like directional data (Mardia, 1975). Time of day data is also cyclic and we used these analyses to compare the frequency of interactions around the TNR feeding stations during a designated feeding period to interspecies interactions recorded outside of this period. The designated feeding period was constructed by adding a two-hour buffer before and after each colony's 0845 h feeding time. Interactions that occurred within this four-hour timeframe were considered facilitated by, or related to, the provision of food at a central feeding station location for colony inhabitants. We used the Rayleigh test to investigate whether timing of cat-wildlife interactions was uniform in distribution or whether frequencies exhibited a pattern.

3. Results

3.1. Stray cat activity patterns

We were able to use video collected from 152 camera deployments on 26 individual cats for behavior analysis. Deployments with less than 2 h of recording due to malfunction were eliminated, and three of our

Table 2
The average stray cat activity budget by colony location for 9 managed cat colonies on Jekyll Island GA.

Colony Location	Cats visiting feeding station	Cats sampled (n)	Sex ratio M:F	Avg video hrs per cat	Avg% time inactive	Avg% time roaming	Avg% time eating	Avg% time hunting
Site 1 (undeveloped)	5	2	1:1	8.4	0.894	0.102	0.003	0.002
Site 2 (undeveloped)	2	2	0:2	35.75	0.883	0.107	0.004	0.006
Site 3 (undeveloped)	10	3	1:2	17.63	0.91	0.07	0.007	0.012
Site 4 (developed)	2	1	0:1	32.98	0.869	0.123	0.006	0.002
Site 5 (developed)	7	5	1:4	29.01	0.893	0.091	0.007	0.009
Site 6 (developed)	2	2	1:1	37.26	0.881	0.103	0.009	0.007
Site 7 (developed)	9	6	3:3	25.81	0.888	0.099	0.007	0.007
Site 8 (undeveloped)	1	1	1:0	14.7	0.874	0.117	0.001	0.008
Site 9 (undeveloped)	6	4	3:1	15.69	0.943	0.054	0.002	0.001

total 29 cats were excluded after determining that they behaved more like pets to their caretakers than stray cats. The average total deployment length was 1257 min or 20.8 h (Min = 126 Max = 2732, SD = 467 min), including the time the camera was recording due to motion triggering the sensor and when off due to inactivity. On a typical deployment, the cats spent an average of 18.9 h in inactive states and 2.06 h in active states. Cats spent an average of 89.5% of time resting or sleeping (min = 68% max = 96%, SD = 5%), 9% of time roaming (min 4% max 30%, SD = 5%), 0.6% eating or drinking at colony feeding stations (min = 0.1% max = 2%, SD = 0.5%), and 0.9% of time hunting wildlife (min = 0 max = 3%, SD = 0.7%). The averages did not differ by sex nor did activity levels differ by colony (either close to developed or undeveloped property, Table 2). Cats spent an average of 9% of their time roaming, regardless of whether they were at a colony in a developed area or bordering undeveloped natural area. The average percent of time hunting did not differ by site location, either. Overall, the cats that were the least active were from the colony that lived around the cat colony manager's home (Site 9) (Table 2). These cats were fed more often and rarely had to compete with other wildlife (i.e. raccoons and vultures) for food like cats at the more rural sites such as Site 2 and 3. The cat at Site 4 roamed more than cats at other sites. This site contained two cats, only one of which could be captured, so this result may be an anomaly. The cat colony with individuals that spent the most time hunting was Site 3. which is directly between a small residential area and a dense area of natural forest lands. Cat demographics (age, sex, colony location) were not significant predictors of time spent in active states, including roaming or hunting. Individual cats were more active during some seasons then others (P = 0.05). Cats with deployments in both fall and spring were more active in the fall (average 10% of time roaming vs. 9% respectively) and cats were less active in the summer (7% of time roaming on average) than in fall or spring (10%).

3.2. Stray cat interactions with wildlife

A total of 142 interspecies interactions were recorded between colony cats and local wildlife. These non-predatory encounters were primarily comprised of interactions with four species: 49% with raccoons (*Procyon lotor*), 37% black vultures (*Coragyps atratus*), 13% white-tailed deer (*Odocoileus virginianus*), and 1% Virginia opossums (*Didelphis virginianus*) (Fig. 3). Raccoons visited all colony feeding stations but black vulture interactions were only recorded at three colony study sites: Site 3, 5 and 7. Our analysis of non-predatory interspecies interaction timing using circular statistics indicates that cat encounters with all species occurred at a mean time of 0939 h (Table 3 and Fig. 4; 95% Confidence Interval = 0851 h–1027 h). Interactions between cats and raccoons occurred at a mean time of 0859 h (95% Confidence Interval = 0813 h–0945 h), and cat interactions with black vultures occurred at a mean time of 1003 h (95% Confidence Interval = 0916 h–1050 h). Average timing of observed interactions with white-tailed deer (μ = 2015 h, 95% Confidence

Fig. 3. An example of close proximity of cats and willdife of Jekyll Island, Georgia, USA 2015.

Interval = 1851 h–2140 h) occurred over two standard deviations away from the overall mean (Table 3; circular σ = 0424 h/140.5°). A Rayleigh test of all interspecies interactions found the probability of a uniform distribution of interaction timing to be very low (Table 3; p < 1E-12). A significant majority of the these interactions occurred within two hours of the colonies' 0845 h feeding time; the overall 95% confidence interval for the timing frequency of interspecies interactions was well within a two-hour feeding time buffer. The overall median interaction time, in addition to the means, medians, and 95% confidence intervals for both raccoon and black vulture interactions, also fell within this 2-h buffer. We counted a total of 173 predatory interactions with invertebrates and amphibians captured more frequently than reptiles, mammals, or birds (Hernandez et al., 2018).

4. Discussion

This is the first analysis of stray cat activity and interactions with wildlife using animal borne cameras. Surprisingly, our hypotheses were not supported as neither colony location, cat age, nor sex influenced cats' roaming behavior. The fact that cameras were deployed on cats at feeding stations may influence activity budget data for those cats with fewer hours of video recording (because cats may sleep or be more active after feeding and deployment). Additionally, some of the most timid colony cats were unable to be captured for study, thus our data may not represent the activities of especially wary individuals. A larger sample size with a greater diversity in ages and more even representation in cats per colony may influence results. Most cats were more active in spring and fall than in summer, and this is consistent with research on free-roaming farm cats in Illinois (Warner, 1985). Only one other study documented activity levels of unowned cats. Horn et al. (2011) found unowned cats in Illinois spent an average of 62% of their time resting/sleeping and 37% of their time roaming, grooming, hunting, and feeding (n = 15). The primary reason for the discrepancy between their results and our results may be that the Illinois cats were not part of a managed colony, thus most were not sterilized and would

Table 3
Statistical summary of the timing and frequency of interactions between stray colony cats and wildlife on Jekyll Island, GA, 2014–2015.

Species	OVERALL	Raccoon	Black Vulture	Virginia opossum	White-tailed Deer
Number of Observations	142	68	54	2	18
Mean Vector (μ)	09:39 (144.849)	08:59 (134.971)	10:03 (150.91)	23:28 (352.125)	20:15 (303.964)
Length of Mean Vector (r)	0.515	0.7	0.739	0.756	0.724
Median	09:22 (140.5)	09:00 (135)	09:34 (143.5)	23:28 (352.125)	19:57 (299.25)
Concentration	1.196	2.006	2.278	0.241	2.162
Circular Variance	0.485	0.3	0.261	0.244	0.276
Circular Standard Deviation	04:24 (66.039)	03:13 (48.39)	02:58 (44.526)	02:51 (42.84)	03:04 (46.075)
95% Confidence Interval (−) for μ	08:51 (132.834)	08:13 (123.478)	09:16 (139.131)	11:04 (166.236)	18:51 (282.801)
95% Confidence Interval (+) for μ	10:27 (156.865)	09:45 (146.464)	10:50 (162.689)	11:52 (178.014)	21:40 (325.127)
ONE SAMPLE TESTS					
Rayleigh Test (Z)	37.614	33.322	29.52	1.143	9.428
Rayleigh Test (p)	< 1E-12	< 1E-12	< 1E-12	0.371	0.0000185

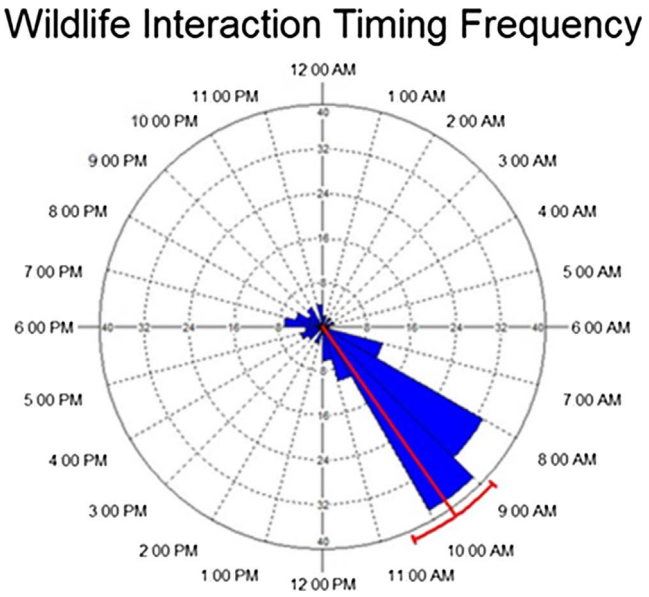

Fig. 4. Rose plot representation of circular statistics depicting frequency of nonpredatory interspecies interactions between TNR colony cats and all wildlife within a 24-h period. The red vector represents mean interaction time (0939 h) and 95% confidence interval (0851 h–1027 h). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

be expected to have larger home ranges and exhibit more roaming behavior (Schmidt et al., 2007). Additionally, Illinois cats did not receive subsidized food at feeding stations and activity may be explained by an increased need to search for food. Our results suggest that offering food for stray cats may reduce their levels of activity and roaming, though confirmation of this would require empirical research on cat activity in the presence and absence of subsidized food. If feeding reduces roaming, this may reduce risks to individual cat welfare (for example, crossing roads, and consuming unsafe substances (Loyd et al., 2013b)). This may also confine the impact of hunting cats to a localized area near the colony feeding station. However, there are many negative aspects to offering subsidized food for stray cats, including support of continued population growth. Subsidized food eliminates the need for cats and wildlife like raccoons to be territorial, allowing them to exist in higher densities. The food attracts newcomers to the colony and any unsterilized individuals can breed more often with higher juvenile survival in the presence of abundant resources (Gunther et al., 2011). From a human dimensions perspective, colonies may provide the public a place to abandon animals under the pretense that they are “being cared for” (Castillo and Clarke, 2003).

Our research indicates that feeding stations and food subsidies are responsible for many non-predatory interactions colony cats experience with wildlife. Cats on Jekyll Island only spent an average of 1–10 min a day eating and drinking at the feeding stations, but even a small amount of time may expose cats to parasites and infectious pathogens. Although the managed cats received one initial set of vaccinations (rabies and common feline pathogens) when they were sterilized, immunity is not life-long, putting these cats at risk for future infections. Cat activity at feeding stations also has implications for zoonotic disease. In fact, the risk of rabies transmission among cats at feeding stations and the potential human exposure of cat colony volunteers has risen over the past 10 years (Gerhold and Jessup, 2013). Curiously, the first case of rabies in a raccoon on Jekyll island was documented in 2015 (Ortiz et al., 2018), despite a relatively long history of wildlife vigilance. The island is currently experiencing regular outbreaks of both rabies and canine distemper epizootics among its raccoon population. Both of these pathogens are density-dependent and our results, along with these events, suggest that research on the role of feeding colonies on raccoon populations is needed.

Colonies managed through TNR attract and aggregate wildlife (Jessup, 2004), and our research provides documentation of multiple occurrences of non-predatory interspecies interactions between free-roaming cats and wildlife, across all studied colony sites, associated with human-provided food at colonies. At times, cats were observed hissing and batting at raccoons. Similar activities were recorded at feeding stations in Bakersfield, CA between cats and kit foxes (Harrison et al., 2011). While the majority of observed interactions were non-aggressive, with little direct physical contact, the close proximity of the species (e.g. less than 30 cm, Fig. 4) observed interacting with cats around the feeding site is concerning for cats and other species of wildlife. Intraspecific interactions within aggregated raccoon populations frequently occurred, increasing the probability of potential pathogen transmission among conspecifics (Totton et al., 2002) and between raccoons and cats. Raccoons are one of the top five species of wildlife frequently infected with the rabies virus and the most significant terrestrial reservoir of rabies in Georgia (Gerhold and Jessup, 2013; CDC, 2016). Aside from rabies, cats are reservoirs for pathogens that can infect raccoons, such as *Bartonella spp* and feline parvovirus, the latter of which is considered an emergent pathogen for wild raccoons (Allison et al., 2013). Even when close proximity does not occur, many of the pathogens for which cats and raccoons are reservoirs are highly environmentally persistent.

Interactions between black vultures and colony cats were frequent around morning meal times. This is likely a result of vulture natural history, the omnivorous nature of their diet, and their ability to quickly adapt to new feeding situations (Buckley, 1999; Sazima, 2013). Black vultures, along with other scavenging raptors and aquatic birds that feed at areas of aggregated anthropomorphic resources, have been shown to be asymptomatic carriers of *Salmonella* spp (Tizard, 2004), shedding bacteria in the feces close to where they feed, with the potential to infect cats. With regards to zoonoses, cats can be an important bridge between wildlife and cat caretakers.

We quantified interspecific interactions through animal-borne

cameras for the purpose of this study but further analysis is necessary to determine the magnitude of the interactions occurring. Because of the limitations of camera lenses, quantitative measurement of distance between interacting individuals is imperfect when animals are more than 1 m from another. Further evaluation of the interaction in terms of spatial proximity would be beneficial for an analysis of the probability for pathogen transmission. Other limitations of this study include the relatively homogenous age structure of the colony cats that may not represent the behavior of all stray cats (particularly juveniles) and study location on an isolated barrier island where the biodiversity of terrestrial mammals with which cats could interact is limited.

Despite limitations, our findings have important management implications for colony cats. Our results suggest that managing strays in well-monitored colonies where cats are fed daily may mean that cats roam less. Although these cats still engage in risky and hunting behaviors (undesirable for both cats and wildlife, respectively), this may be with less frequency than truly feral cats or even cats in poorly-managed colonies where volunteers cannot sustain a daily schedule. Although TNR allows cats to remain in the environment unsupervised (a practice we do not support), it may be possible to design feeding stations that exclude the majority of other animals yet allow cats to obtain food. For example, through positive reinforcement training and the use of enclosures with trap doors or other methods. Additionally, the location of feeding stations may be positioned to keep cats from roaming in close proximity to sensitive habitats or species (e.g. shore bird nesting sites).

Conflict of interest

None.

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