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Spatial interactions in a domestic cat population

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Abstract

The domestic cat (*Felis catus*) is one of the most popular pets globally, with hundreds or even thousands of individuals per km^2 in some areas. Domestic cats with outdoor access have both direct effects on wildlife through predation and indirect effects on wildlife through intimidation that alters prey behavior. Knowledge about space use by outdoor cats is important for understanding and mitigating their ecological impact. Little is known of how intraspecific interactions affect space use in cat populations. Yet, cat tracking studies typically include too few individuals or are spread across study areas that are too large to provide reliable inferences about intraspecific interactions.

In this study, I investigated the impact of intraspecific interactions on the combined space use of a cat population using GPS-tracking. This was made possible by the unprecedented high proportion of GPS-tagged cats: 75% of cats (n = 95) living in a 1.1 km^2 suburban neighborhood in Southern Norway. I used high-throughput GPS position data and analyzed it with a combination of Brownian Bridge Movement Models and an ecological null-model to assess the role of intraspecific spatial interaction on space use in the study population.

I found evidence that cats of both sexes tend to avoid conspecifics. This effect was particularly pronounced for females. Individuals less than 8 years old, regardless of sex, exhibited lower home range overlap with other individuals than older cats. I also detected indication that intraspecific avoidance led to a more widely spread population-level space use than would be expected by chance. In addition, I found that males had larger home ranges than females, and that cats below 8 years had larger home ranges than cats 8 years or older.

To my knowledge, this is the first study that explored the population-level manifestation of intraspecific interaction and its consequences for the spatial configuration of a free-ranging pet cat population. From my study, I conclude that age and sex explain the propensity of domestic cats to avoid each other, as well as the variation in home range size of domestic cats. This, in turn, will determine the overall space used by the population. Now, more studies are needed to investigate interactions and their ecological role, as intraspecific interaction is an important mechanism behind density-dependent effects.

Acknowledgments

Table of contents

Introduction

Domestic cats (*Felis catus*) have been implicated in the endangerment of 377 species of birds, mammals, and reptiles, and in the extinction of another 63 species (Doherty et al. 2016). It has been estimated that cats kill billions of birds and small mammals every year in the United States (Loss et al. 2013), and in Australia several hundred millions birds (Woinarski et al. 2017) as well as billions of mammals (Murphy et al. 2019). The Norwegian Ornithological Society has estimated that cats kill 6.95 million birds annually in Norway and that pet cats cause the majority of these kills as there is only a moderate population of unowned cats in Norway (Heggøy and Shimmings 2018). Cat predation may also hamper mammal reintroduction programs (Hardman et al. 2016).

Domestic cats, like other predators, may reduce prey densities through intimidation of which the effect on prey population demographics can be even greater than the effect of consumption (Preisser et al. 2005). The presence of cats can disrupt clustering in bat colonies and thereby interrupt allogrooming and parental care, as well as increase energy expenditure (Ancillotto et al. 2019). Cats can also reduce parental provisioning rates and nestling growth rates in birds, as well as increase the likelihood of nest predation by other predators (Bonnington et al. 2013). Bird abundances have shown as much as a 95% decrease even when consumption rate by cats is low (Beckerman et al. 2007). Cats, and especially unowned feral cats, can also be a source of zoonotic diseases that affect humans and wildlife alike (Gerhold and Jessup 2013, Hollings et al. 2013).

The massive ecological impact of domestic cats can to a large extent be attributed to their large numbers. The global domestic cat population is likely larger than all other felid populations combined (Kays et al. 2020). Pet cats alone number an estimated 600 million globally (Kays et al. 2020), of which an estimated 100 million live in Europe, and an estimated 750 000 live in Norway (FEDIAF 2020). The domestic cat is the most popular pet in Norway and around 31% of Norwegian households own at least one cat (FEDIAF 2020). Cat densities in suburban and urban areas can reach hundreds of individuals per km^2. In urban areas in the United Kingdom, cat density estimates range between 132 and 1580 cats/km^2 (Sims et al. 2008). A study in an urban area in New Zealand found an estimated density of 223 cats/km^2 (van Heezik et al. 2010). In the US, cat density was estimated to 137 cats/km^2 in suburban areas and 343 cats/km^2 in urban areas (Lepczyk et al. 2004). In comparison, density estimates of other carnivores in urban and suburban areas, such as the red fox (*Vulpes vulpes*), the Eurasian badger (*Meles meles*) and the stone marten (*Martes foina*), are much lower, with no more than an estimated 20 individuals/km^2 (Šálek et al. 2015).

Due to the small home ranges of pet cats, they kill about the same amount of prey per area as similar wild carnivores, although they kill fewer prey than expected based on body size and

metabolism (Kays et al. 2020). Hence, where cat density is high, the impact on wildlife can be significant (Kays et al. 2020).

In Felidae, phylogenetic evidence supports a solitary ancestor, and most extant species are solitary (Dalerum 2007). Of the species that exhibit group-living this is more often due to a flexible social organization, and only a few species exhibit group-living as their primary social organization (Dalerum 2007). In cheetahs (*Acinonyx jubatus*), adult females are solitary, while adult male siblings can form coalitions (Bradshaw 2016). There can be significant spatial overlap between the 99% home ranges of male cheetahs, but little to no overlap between 50% home ranges (Broekhuis et al. 2019). Direct interaction between males is avoided by use of scent marks, and occurrences of possible interactions is more common in the 50% home range, presumably due to territorial defense or the presence of receptive females (Broekhuis et al. 2019). In the Iberian lynx (*Lynx pardinus*) there are generally low levels of spatial overlap, but more so at low and high population densities. This is likely due to a positive relationship between population density and prey density - when population density is low due to low prey density, territoriality is beneficial to defend the scarce resources, and when population density is high due to high prey density, territoriality is beneficial to keep away increased intruder numbers (López-Bao et al. 2014). In Eurasian lynx (*Lynx lynx*), home range size in both sexes decrease as density increases. Home range size of male lynx also decreases in the mating season, presumably because males want to stay close to receptive females. Home range sizes of females decrease in the post-reproductive period, likely because they have dependent kittens that hamper movement (Aronsson et al. 2016). In cougars (*Puma concolor*), there is significantly more intersexual home range overlap than intrasexual home range overlap (Elbroch et al. 2016).

The domestic cat is unlike other small felids in that it can form social groups (Bradshaw 2016). Social domestic cat groups consist of related adult females that cooperate in kitten care and defense of their common core area (Bradshaw 2016, Braastad 2019). Domestic cats hunt alone and the members of social groups may at times only share core areas (Crowell-Davis et al. 1997, Braastad 2019). Social groups typically form when there is sufficient food access, as female home ranges are largely determined by food availability (Crowell-Davis et al. 1997, Braastad 2019). Domestic cats are typically not considered territorial as they do not actively defend their home ranges against intruders (Crowell-Davis et al. 1997). Home ranges can even be shared without confrontation by use of scent markings (Braastad 2019). However, females can exhibit territoriality in their core areas by actively driving away intruders, and they will only tolerate unfamiliar males when in heat (Braastad 2019). Males roam over large distances to seek out receptive females and are more tolerant of unfamiliar individuals of both sexes (Braastad 2019).

Avoidance and other spatial interactions between free-ranging animals are exceedingly difficult to study. For example, cat tracking studies typically do not include enough individuals of a population

2

to make reliable inferences about spatial interactions. Studies such as Kays et al. (2020) and Roetman et al. (2018) included large sample sizes (428 and 925 cats, respectively), but the cats tracked were spread across large study areas (six countries and State of South Australia, respectively). Morgan et al. (2009) and Izawa et al. (1982) tracked cats within small study areas ($< 2 \text{ km}^2$), but tracked no more than 5% of the estimated study populations. To my knowledge, the highest proportion of a cat population was studied by Edwards et al. (2001). They tracked an estimated 34.5% of a population of rural feral cats, though this study included only the male part of the population.

In this study, I tracked the majority of individuals of both sexes in a domestic cat population to measure intraspecific interactions between individuals and their impact on the spatial configuration of the entire population.
Specifically, I aimed to determine:

i)   Is there evidence of spatial avoidance in the population? If so, how strong is the effect and what are the implications for the spatial distribution of the population?

ii)   How do sex and age impact individual space use in relation to other cats?

As it has been reported in other studies (Hall et al. 2016, Bachmann 2020, Kays et al. 2020, Kisen 2021) and has a bearing for the spatial distribution in the population, I ask the following additional questions:

iii)   Do males in our study population have larger home ranges than females?

iv)   Does home range size decrease with age?

To answer the aforementioned questions, I GPS-tagged 75% of outdoor pet cats (n = 95) in a suburban neighborhood in Southern Norway. The cats were tracked over the course of four weeks with the help of cat owners.

Methods

Study area

The study was conducted in the town of Ås, Ås municipality, Norway. The study area (59°38-59°39 N, 10°46-10°48 E) is defined as the area in which cat owners were recruited and can be characterized as suburban. It measures approximately 1.1 km^2 and can be roughly divided into four zones (Fig. 1). It adjoins agricultural fields and mixed forest. Train tracks dissect the study area between the "East" and "South" zones (Fig. 1).

Fig. 1. *Map of the study area. The study area can be roughly divided into four zones, as delineated and labeled on the map. Google Earth, earth.google.com/web/*

GPS tracking occurred from May 1st to May 29th, 2021. During May 2021, the average temperature in the study area was 9.9°C, and total precipitation was 85.8 mm (temp. range: -2.1°C to 24.8°C, precipitation normal: 62.0 mm; Meteorologisk Institutt & NRK 2007-2022). The area was chosen as it held the potential to provide a large sample size while being isolated enough from other neighborhoods to decrease the likelihood of interference from visiting cats.

Participant recruitment and cooperation

Cat owners were recruited via social media, flyers in mailboxes, and direct contact. They signed up for participation through an online form. Participants were provided with GPS loggers and instructions on how to operate them. Technical assistance with GPS-tracking was provided on request throughout the study period. Midway through, and after the study period, each participant was provided with a map of the home ranges of all participating cats, with the home range of their cat(s) highlighted. Participants also filled out an online form collecting detailed information about each cat they wished to track.

Data collection

Participants were encouraged to track their cats when outdoors in the study period. The i-gotU GT120 GPS logger (Mobile Action Technology, Inc.) was used for tracking. The logger weighs 26 g and was attached to an adjustable elastic collar with a click buckle. The fix rate was set to 30 seconds. With this fix rate the GPS logger is estimated to have a battery time of at least 10 hours. Participants were instructed to charge the GPS logger when the cat was indoors. Data from the loggers were collected midway through the study period and at the end of it, using the software @Trip PC (Mobile Action Technology, Inc.).

Data pre-processing

GPS data was pre-processed to remove positions that were deemed unreliable. Positions were removed if they i) had an estimated horizontal position error (EHPE) $\geq$ 5000, as recommended by Morris and Conner (2017); ii) had an elevation outside the range 0-300 m, or iii) were obtained during the first two days of tracking or on days where the GPS logger was picked up for data download. Positions were also removed if they fell within clusters associated with the inside of participant homes. Finally, the fix interval was increased to $\geq$ 2 min for ease of processing. Additional details about the data processing can be found in Bischof et al. (2022).

Estimation of proportion of population tracked

To estimate the cat population size in the study area, and hence the proportion of the population tracked, camera trapping was utilized, along with knowledge about non-participating cats obtained from participants and cancelled sign-ups. Forty-seven participants had cameras set up in their backyards. The camera models used were Browning Dark Ops HD Pro Trail Camera BTC-6HDP (n = 37), Browning BTC-6HDPX Dark Ops HD Pro (n = 8), and Browning Spec Ops Full HD (n = 2).

The cameras had infrared flash and recorded 10 second videos when triggered. Cameras were set up 0.5-1 m above ground in places where the probability of detecting domestic cats was high while protecting the privacy of neighbors. Due to some late participant sign-ups, not all cats were GPS-tracked from the first day of the study period, so camera trapping started one week into the study period. The camera traps were removed after five weeks. Videos were visually examined to determine which cats were known from the GPS tracking study and which cats were unknown, evidenced by the presence or absence of GPS collars. The proportion of individuals in urban cat populations that can be identified by camera traps can be very high (Elizondo and Loss 2016). The use of camera traps combined with knowledge about tracked and non-tracked cats likely gives a very precise estimate of the population size and the proportion of individuals tracked. The spatial configuration and additional details on the camera trap survey are reported in Bischof et al. (2022).

Data analysis

All data processing and data analysis was done using R version 4.2.1 (R Core Team 2022). To estimate home ranges for each cat, 95% Brownian Bridge movement models (BBMM) were constructed using the R package *BBMM* (Nielson et al. 2013). R package *sf* (Pebesma 2018) was used for processing spatial data.

Determinants of home range size

To determine the effect of sex and age, as well as their interaction, on home range area, a linear regression was run on a model with log(home range area (ha)) as response variable and the interaction of sex (levels: female/male) and age category (levels: < 8 yrs / ≥ 8 yrs) as the predictor variables. The reason for using ordinal categorical age instead of continuous age was that the focus was on the effect of sex on space use. Age thresholds were chosen based on Hall et al. (2016).

Ecological null model for spatial configuration

To test for spatial interactions and determine their impact on population-level space use, an ecological null model was constructed where the effect of interaction on spatial configuration is minimized. For every iteration of 1000 simulations, each home range was assigned to a random participant household and randomly rotated around the centroid of the household. This resulted in 1000 simulated home range configurations. The observed home range configuration and first seven simulated home range configurations can be seen in Fig. 2.

For each of the 1000 null model simulations, the total area covered by all cats was calculated. This provided a null model distribution of the total area covered. The strength of the evidence in favor of rejecting the null hypothesis was calculated as the proportion of simulations from the null model with an outcome (simulated total area) that was less than, or greater, than the observed total area. The resulting number serves as an equivalent to a p-value, with lower values indicating lower support of acceptance of the null hypothesis. I chose a cutoff for significance of $p<0.05$ and considered $p<0.1$ indication of a trend, albeit non-significant.

Estimation of home range overlap

The overlapping area of 95% BBMM home ranges was calculated for each possible pair of cats, hereafter called "dyad". To quantify overlap, the General Overlap Index (GOI) was calculated for each dyad, as described in Ferrarini et al. (2021). A GOI of 0% equals complete separation of two home ranges, and a GOI of 100% equals complete engulfment of one home range in another (Ferrarini et al. 2021). A dyad was considered to overlap when $GOI \geq 10\%$. A network plot with connections between overlapping individuals was constructed using the R package *igraph* (Csardi and Nepusz 2006). The layout of the network plot corresponds to the relative positions of participant households, with a 25-50 m random offset and added jitter.

For each of the 1000 null model simulations, the average number of overlaps was calculated for females and males, and for cats < 8 yrs and ≥ 8 yrs of each sex. This provided a null model distribution of average overlap count for each group. The strength of the evidence in favor of rejecting the null hypothesis was calculated as the proportion of simulations from the null model with an outcome (average number of overlaps) that was less than, or greater, than the observed average number of overlaps.

For each of the 1000 null model simulations, the average GOI was calculated for male-male dyads, male-female dyads, and female-female dyads. This provided a null model distribution of average GOI for each group. The strength of the evidence in favor of rejecting the null hypothesis was calculated as the proportion of simulations from the null model with an outcome (average GOI) that was less than, or greater, than the observed average GOI. Assessments were made on sex-specific pairings.
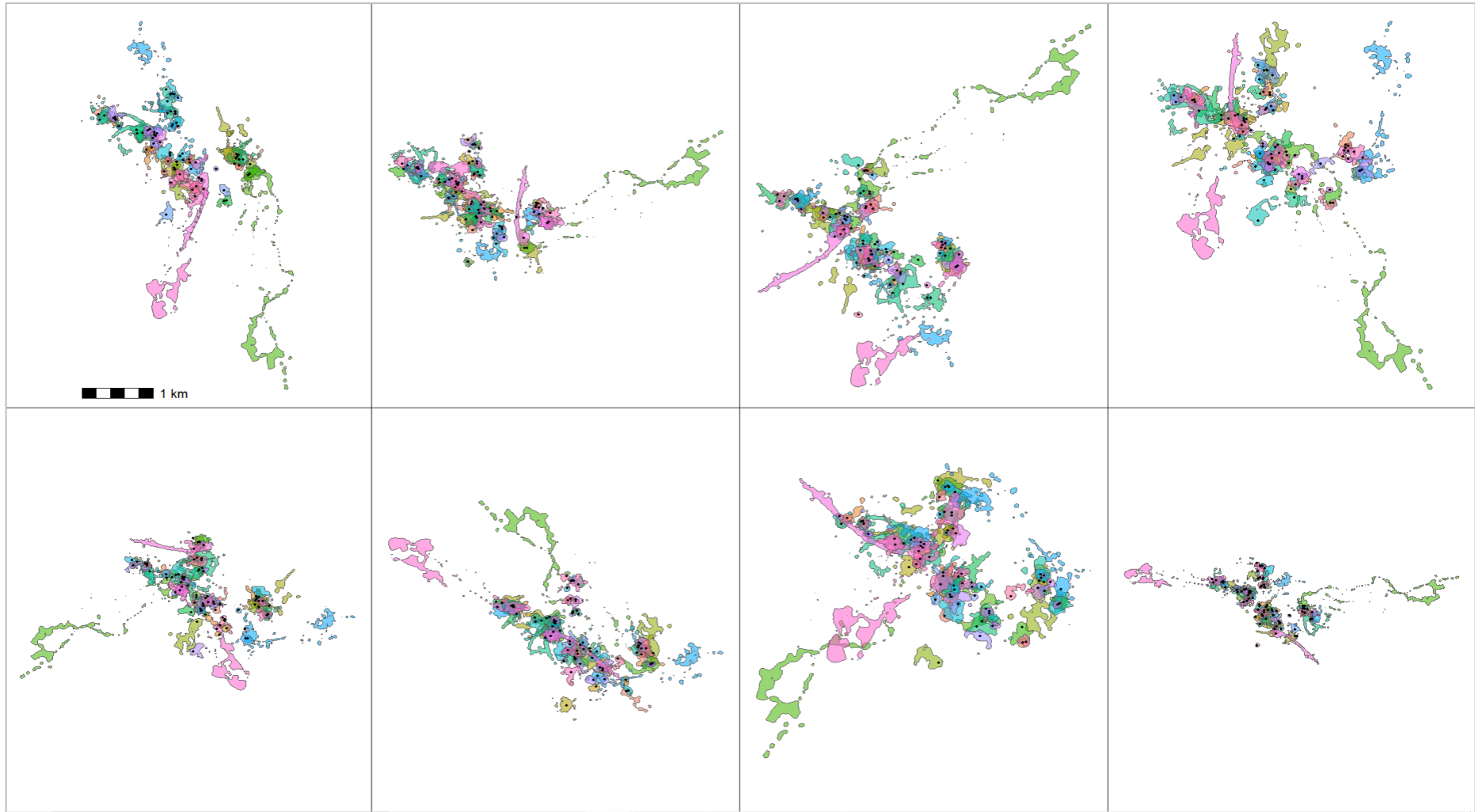
Fig. 2. *Observed (top left panel) and examples of simulated home range configurations. Brownian Bridge Movement Models were constructed to derive 95% home ranges estimates. Each configuration contains home ranges of all 95 cats included in the study. Centroids of participant residences are represented by black points and remain unchanged across configurations. The simulated home range configurations are based on an ecological null model where the purpose is to remove the effect of conspecific interaction on space use. Each home range has been assigned to a random participant residence and rotated randomly around the centroid of the residence.*

Results

Participant recruitment, data collection and processing, and estimated proportion of population tracked

In total, 79 participants with 95 cats were recruited to the study (Table 1). Based on camera trapping and knowledge of non-participating cats, the population size was estimated to be 126 cats (see also Bischof et al. (2022), and so the 95 cats tracked made up 75% of the estimated population. Participants provided information about the sex, neutering status, and method of release to the outdoors of 88 of the cats, and the age of 83 of the cats. The number of females and males was equal. The number of cats < 8 yrs was 52, and the number of cats ≥ 8 yrs was 31. Regarding neutering status, 86 cats were sterilized or castrated and 2 were intact. Most cats were released to the outdoors by their owners opening the door to let them out (Table 1). The median number of days tracked was 25 (range: 2-28 days). The median number of fixes was 4004 (range: 175-8975 fixes). The median number of fixes/day was 167 (range: 30-345 fixes/day). Camera traps were operational for an average of 22.6 days (SD = 12.4) due to memory limitations.

Table 1. *Overview of tallies regarding participation and cats.*

	n
Estimated population size	126
Households	79
Cats total[i]	95
Females[ii]	44
Males[iii]	44
< 8 yrs[iv]	52
≥ 8 yrs[v]	31
Neutered	86
Intact	2
Released through door	62
Free access through cat flap	24
Limited access through cat flap	2

[i] 75% of estimated population size.
[ii] 25 < 8 yrs, 16 ≥ 8 yrs.
[iii] 27 < 8 yrs, 15 ≥ 8 yrs.
[iv] 25 females, 27 males.
[v] 16 females, 15 males.

Home range area

BBMM (95%) home range size ranged between 0.11 ha and 26.32 ha (median = 1.49 ha; Fig. 3). Linear regression revealed that males had significantly larger home ranges than females, on average 2.66 ha larger ($\beta = 0.98$ log(ha), $t = 3.44$, $p = 0.0009$). Cats ≥ 8 yrs had significantly smaller home ranges than cats < 8 yrs, on average 2.80 ha smaller ($\beta = -1.03$ log(ha), $t = -3.11$, $p = 0.0026$). The interaction between sex and age category had no significant effect on home range size ($\beta = 0.09$ log(ha), $t = 0.185$, $p = 0.85$). The cats covered a total area of 176.9 ha, which was larger than expected from the null model distribution, though not significantly ($p = 0.087$; Fig. 4).

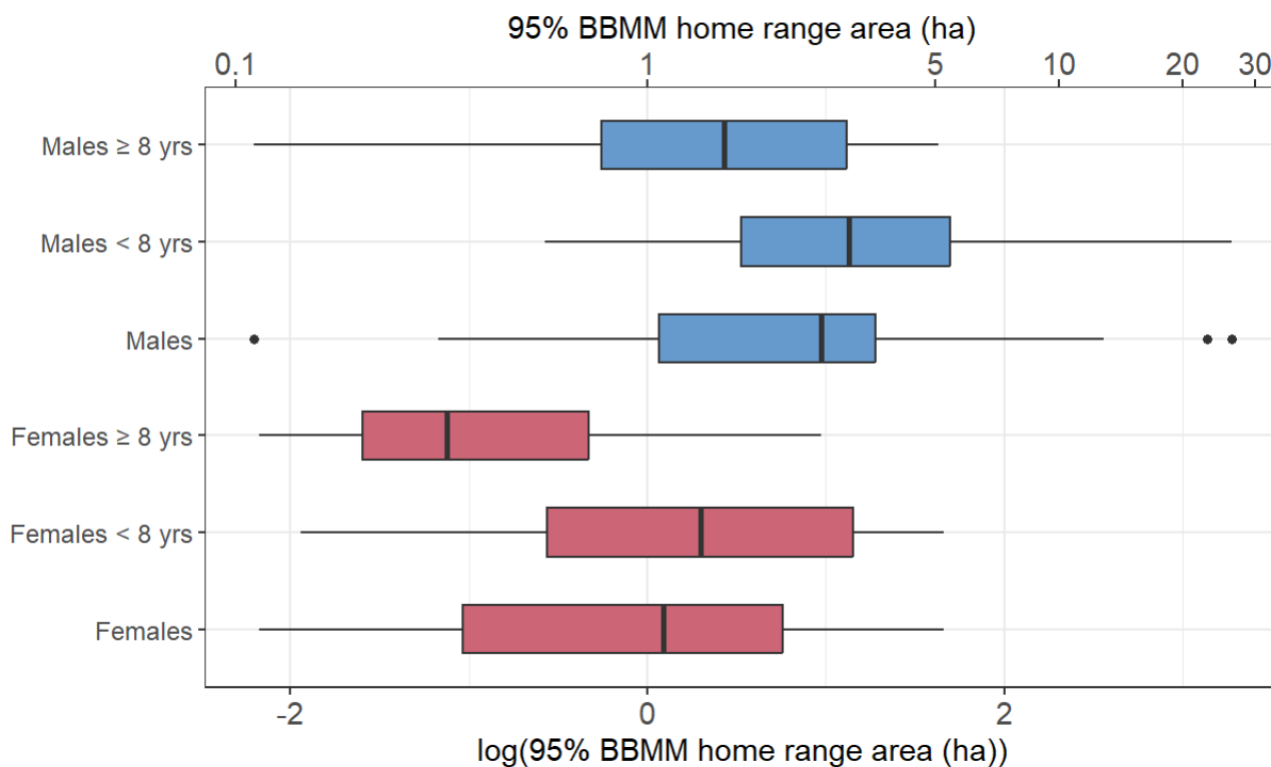**Fig. 3.** *Distribution of 95% home range area (ha and log(ha)) derived using Brownian Bridge Movement Models for females and males, and for cats < 8 yrs and ≥ 8 yrs of each sex.*
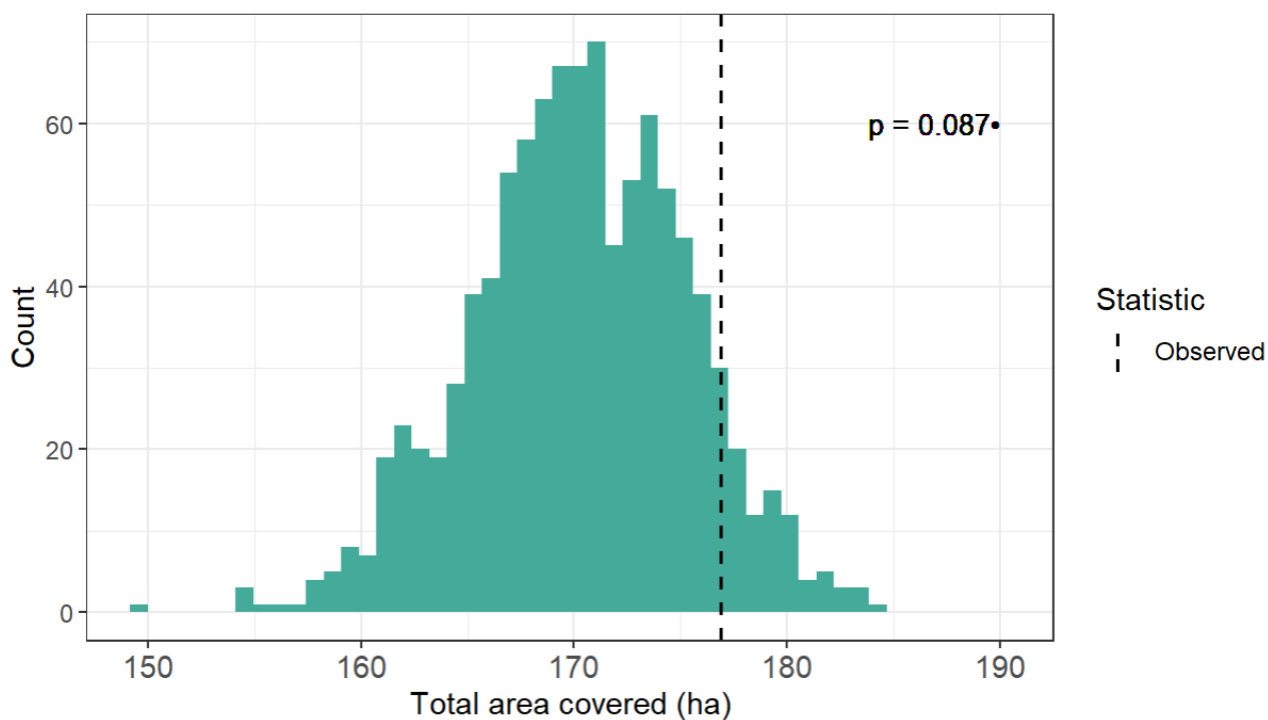

Fig. 4. *Null model distribution of total area covered (ha) by all cats. Observed total area covered as a dashed black line.*

Home range overlap

The network plot in Fig. 5 visualizes the spatial interactions in the population with connections between individuals that are considered to overlap (GOI ≥ 10% between individuals). The majority of cats with overlapping home ranges lived within the same study zone (see Fig. 1), while there was minimal overlap between cats of different zones (Fig. 5). The number of overlapping dyads were 34 in the East zone (n = 20 cats), 62 in the North zone (n = 32 cats), 61 in the South zone (n = 32 cats), and 17 in the West zone (n = 11 cats). Cats in the East zone and the South zone did not overlap with cats from any other zone, and only one cat in the North zone formed dyads with cats in the West zone. The network plot in Fig. 5 shows that there is a clear divide between the cats to the right ("East"), the middle ("South), and to the left ("North" and "West"), with connections between the North and West zone via only one male in the North zone.
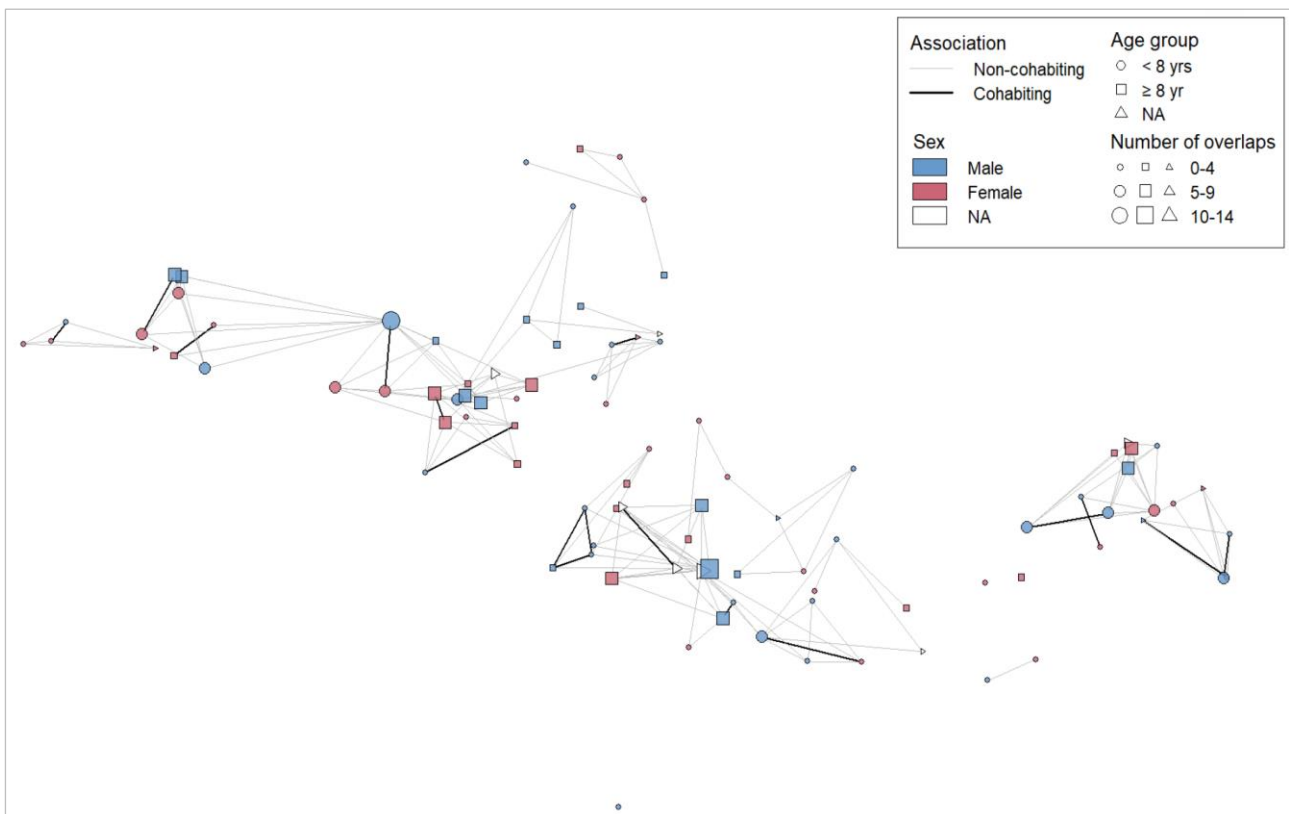

Fig. 5. *Network plot of 95 cats where each node is a cat and each connection corresponds to a GOI ≥ 10% (overlap) between the cats. Layout of nodes based on real locations of participant households, with 25-50 m random offset and added jitter to nodes.*

Table 2. a) *The ten cats that overlapped with the highest number of conspecifics, and the ten cats that overlapped with the fewest conspecifics. b) The ten cats with the largest home ranges, and the ten cats with the smallest home ranges. Only cats with known sex and age are included. Number of overlaps, sex, age in years, zone in which household is located, number of conspecifics that live within 100 m, and 95% BBMM home range (ha) for each cat are shown.*

a

n overlaps	Sex[1]	Age (years)	Zone[2]	n conspecifics within 100 m	BBMM (95%) home range area (ha)
Top 10					
14	M	3	N	2	12.88
10	M	10	S	6	3.56
9	M	7	N	5	12.10
8	F	2	E	9	5.14
8	M	10	N	2	2.20
7	M	3	S	2	4.36
6	M	8	N	4	3.33
6	M	10	S	2	2.82
6	M	10	S	5	2.71
6	F	8	N	5	2.22
Bottom 10					
1	F	7	E	3	0.60
1	F	10	S	2	0.49
1	F	5	N	2	0.44
1	M	9	N	2	0.31
1	F	14	S	1	0.29
1	F	>15	S	2	0.18
1	F	1	S	2	0.14
0	M	5	S	0	3.40
0	F	11	E	0	1.95
0	F	5	E	0	0.37

[1] F: Female, M: Male.
[2] W: West, N: North, S: South, E: East.

b

BBMM (95%) home range area (ha)	Sex[1]	Age (years)	Zone[2]	n conspecifics within 100 m	n overlaps
Top 10					
26.32	M	7	E	4	4
23.06	M	6	S	0	3
12.88	M	3	N	2	14
12.10	M	7	N	5	9
9.71	M	5	S	2	4
9.06	M	7	E	6	5
5.82	M	4	E	6	5
5.25	F	5	E	4	4
5.14	F	2	E	9	8
5.10	M	9	S	1	2
Bottom 10					
0.31	F	13	N	4	5
0.29	F	14	S	1	1
0.21	F	11	N	6	4
0.18	F	>15	S	2	1
0.18	F	6	N	4	2
0.17	F	9	E	5	2
0.14	F	1	S	2	1
0.12	F	9	S	3	2
0.11	M	13	E	6	5
0.11	F	>15	S	7	6

[1] F: Female, M: Male.
[2] W: West, N: North, S: South, E: East.

It was most common to overlap with 0-4 conspecifics (n = 65 cats), followed by 5-9 conspecifics (n = 27 cats), and 10-14 conspecifics (n = 3 cats; Fig. 5). The cats that overlapped with the highest number of conspecifics and had the largest home ranges were predominantly male, and the cats that overlapped with the lowest number of conspecifics and had the smallest home ranges were predominantly female (Table 2a-b). Only three cats did not overlap with any conspecifics (Fig. 5; Table 2a), and there were no cats living within 100 m of the homes of these cats. The individual that overlapped with the highest number of conspecifics was a 3-year-old male with a 12.88 ha home range. It overlapped with 14 conspecifics, and there were two other individuals living within 100 m of his home (Table 2a). A 10-year-old male with a 3.56 ha home range overlapped with 10 conspecifics. This male lived within 100 m of six other individuals (Table 2a). The two cats with the largest home ranges were a 7-year-old male and a 6-year-old male. They overlapped with 4 and 3 conspecifics, respectively (Table 2b). The two cats with the smallest home ranges were a 13-year-old

male and a female older than 15 years. They overlapped with 5 and 6 conspecifics, respectively (Table 2b).

Females overlapped with an average of 3.02 conspecifics (Fig. 6a), while males overlapped with an average of 4.27 conspecifics (Fig. 6d). Both females and males overlapped with significantly fewer individuals on average than expected from the null model distribution (Figs. 6a and 6d, respectively). Females overlapped with fewer individuals on average than males regardless of age (Figs. 6b-c, 6e-f), and cats < 8 yrs overlapped with fewer individuals on average than cats ≥ 8 yrs regardless of sex (Figs. 6c and 6f vs. 6b and 6e). Cats < 8 yrs of either sex overlapped with significantly fewer individuals than expected from the null model distribution (Figs. 6c and 6f), while cats ≥ 8 yrs did not (Figs. 6b and 6e).
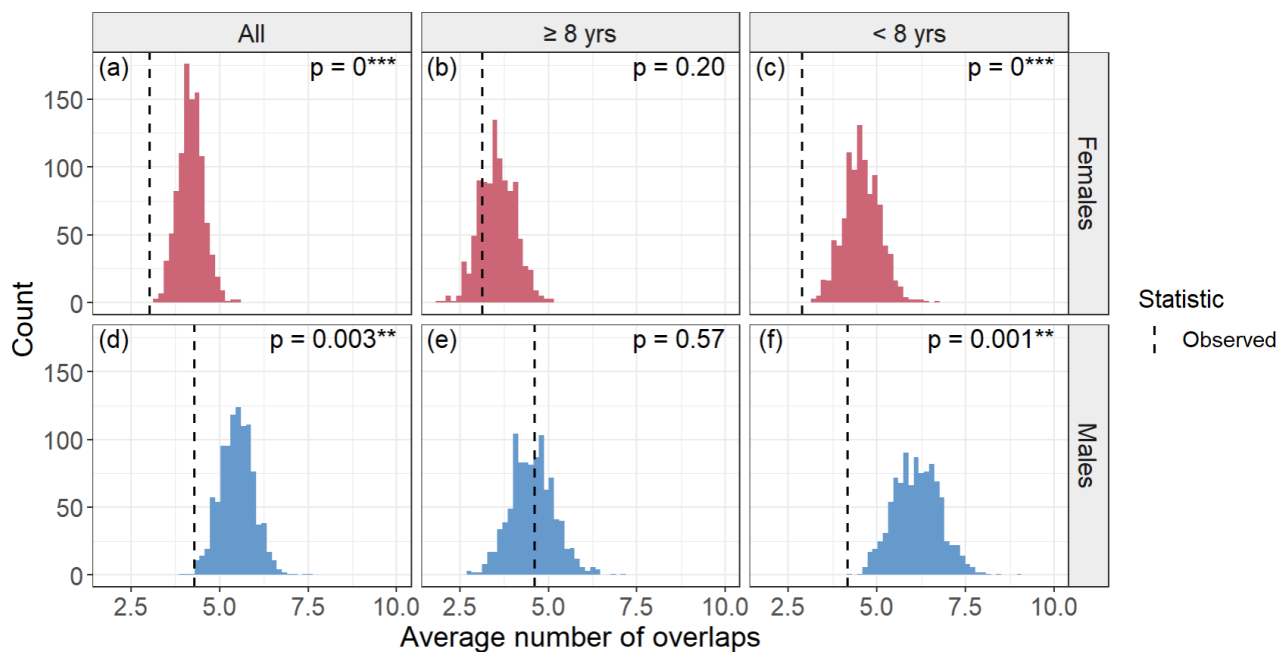

Fig. 6. *Null model distribution of average number of overlaps for a) all females, b) females ≥ 8 yrs, c) females < 8 yrs, d) all males, e) males ≥ 8 yrs, and f) males < 8 yrs. Observed average number of overlaps for each group as dashed lines.*

There were 4465 possible dyads in the population (Table 3) and 181 overlapping dyads (Table 4). All cohabiting cats (cats that lived together) overlapped (n = 17 dyads), with an average home range overlap area of 1.36 ha (range: 0.31-3.97 ha, interquartile

Table 3. *Summary statistics of General Overlap Index (GOI; %) for all possible dyads in the population and all possible cohabiting and non-cohabiting dyads.*

	n dyads	Mean	Range	IQR
All dyads				
All	4465	2.2	0-100	0-0
Cohabiting	17	83.8	45.3-100	73.1-97.8
Non-cohabiting	4448	1.9	0-100	0-0

13

range (IQR): 0.58-165 ha) and average GOI of 83.8% (range: 45.3-100%, IQR: 73.1-97.8%; Table 3). Excluding dyads with cohabiting cats, the average GOI in the population was 1.9% (range: 0-100%; IQR: 0-0, Table 3). Of the 164 dyads with overlapping non-cohabiting cats there were 22 female-female dyads, 65 male-female dyads, 40 male-male dyads, and 37 dyads where the sex of at least one individual was unknown (Table 4). Average home range overlap area and distance between participant households in overlapping non-cohabiting dyads was smallest in female-female dyads, followed by male-female dyads and male-male dyads (Table 4).

Table 4. *Summary statistics of overlap area (ha) and distance between homes (m) for all overlapping dyads, overlapping female-female dyads, overlapping male-female dyads, overlapping male-male dyads, and overlapping NA dyads (dyads where the sex of at least one individual is unknown).*

	n dyads	Overlap area (ha)			Distance between homes (m)		
		Mean	Range	IQR	Mean	Range	IQR
All dyads							
All	181	0.64	0.02-3.97	0.2-0.77	98.3	0-520	36-116
Cohabiting	17	1.36	0.31-3.97	0.58-1.65	0.0	0-0	0-0
Non-cohabiting	164	0.57	0.02-2.22	0.18-0.72	108.5	3-520	42-124
Female-Female dyads							
All	24	0.49	0.05-2.15	0.16-0.54	68.8	0-283	38-83
Cohabiting	2	0.80	0.31-1.29	0.55-1.04	0.0	0-0	0-0
Non-cohabiting	22	0.46	0.05-2.15	0.13-0.47	75.1	5-283	44-83
Male-Female dyads							
All	73	0.60	0.02-3.97	0.17-0.66	82.2	0-373	35-97
Cohabiting	8	1.46	0.58-3.97	0.93-1.38	0.0	0-0	0-0
Non-cohabiting	65	0.49	0.02-2.22	0.16-0.59	92.3	5-373	38-99
Male-Male dyads							
All	46	0.81	0.03-3.84	0.39-0.85	130.7	0-520	36-167
Cohabiting	6	1.58	0.54-3.84	0.58-2.09	0.0	0-0	0-0
Non-cohabiting	40	0.70	0.03-2.22	0.37-0.79	150.3	23-520	73-188
NA dyads							
All	38	0.62	0.06-2.09	0.18-0.74	108.9	0-449	40-121
Cohabiting	1	0.44	0.44-0.44	0.44-0.44	0.0	0-0	0-0
Non-cohabiting	37	0.63	0.06-2.09	0.18-0.75	111.8	3-449	41-123

Average GOI was smallest in female-female dyads (1.39%; n = 24 dyads), followed by male-female dyads (2.10%; n = 73 dyads) and male-male dyads (2.65%; n = 46 dyads; Figs. 7a-c). Average GOI in male-female dyads and female-female dyads was significantly lower than expected from the null model distribution (Figs. 7b and 7c, respectively), while average GOI in male-male dyads was not (Fig. 7a).
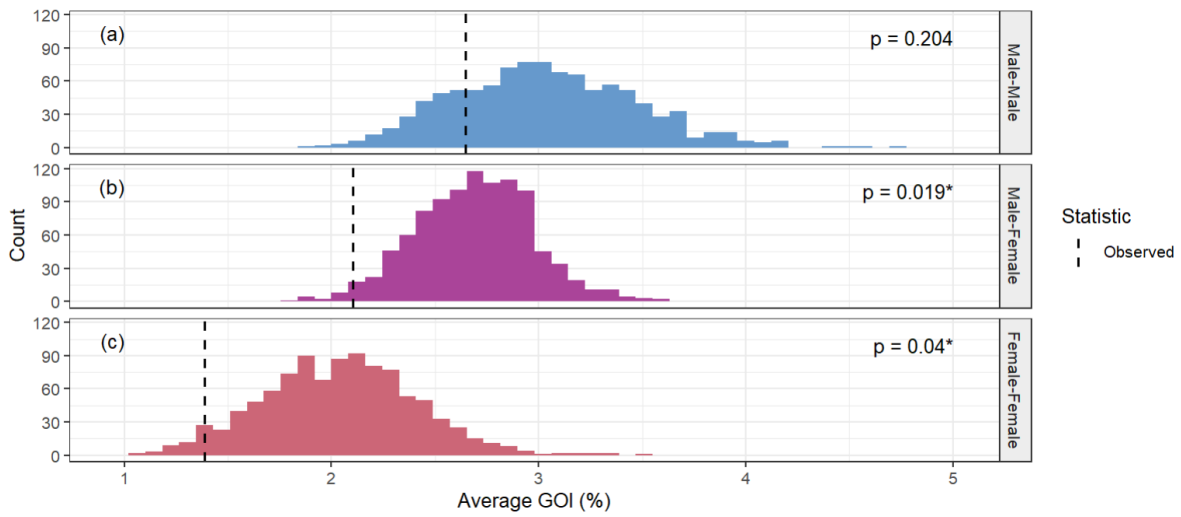
Fig. 7. *Null model distribution of average GOI (%) for a) male-male dyads, b) male-female dyads, and c) female-female dyads. Observed average GOI (%) for each dyad as dashed line.*

Discussion

This is one of the most intensive cat tracking studies thus far, with an unprecedented proportion of the population included. This in turn allowed me to draw population-level inferences about intraspecific interactions which have eluded other tracking studies. My results provide clear evidence of intraspecific avoidance. I also found indication that avoidance may have positively affected the spatial extent of the population

Sex and age differences in home range size and overlap measures

Both females and males overlapped with significantly fewer individuals than expected by chance. However, the magnitude of overlap between two cats depended on their sex. Average GOI was significantly lower than expected by chance both in female-female dyads and female-male dyads, while this was not the case in male-male dyads. These results suggest that females were overall less tolerant of conspecifics than males were, and that they were especially intolerant of other females. Studies on cats have shown that the extent of overlap between females can be small or even non-existent compared to the extent of overlap between males and between males and females (Liberg 1980, Barratt 1997, Guttilla and Stapp 2010, McGregor et al. 2015). In mammals, frequent interactions with neighbors may lead to reinforcement of exclusive home ranges, even if this results in smaller home ranges. Conversely, the larger an area an individual occupies, the harder it is to maintain exclusive use of the area (Jetz et al. 2004). Males had significantly larger home ranges than females, which is consistent with previous research on both pet cats (Hall et al. 2016, Bachmann 2020), and feral cats (Warner 1985, Yamane et al. 1994, Goltz et al. 2008, Guttilla and Stapp 2010, Gehrt et al. 2013, Recio and Seddon 2013, McGregor et al. 2015, Bengsen et al. 2016, Normand et al. 2019). Due to their larger home ranges, males should be more likely to encounter conspecifics and less likely to be able to maintain exclusive use of their home ranges, at least within the constraints of an artificially configured population that is driven by pet ownership.

Cats < 8 yrs overlapped with fewer individuals than cats ≥ 8 yrs, despite having significantly larger home ranges. Larger home ranges in younger cats has been found in other research (Hall et al. 2016, Kays et al. 2020, Kisen 2021). Cats < 8 yrs also overlapped with fewer individuals than expected by chance, while this was not the case for cats ≥ 8 yrs. Perhaps younger cats are more capable of excluding intruders from their home ranges than older cats, who must settle for smaller home ranges but are nonetheless overlapping with more individuals.

The role of cohabitation

All cohabiting cats overlapped to a large degree. Barratt (1997) found that home ranges of cohabiting cats overlapped extensively, with related cohabiting cats having completely overlapping home ranges and unrelated cohabiting cats having completely overlapping core areas. It is unknown whether the cohabiting cats in my study were related or not. Nevertheless, my results show a clear distinction in spatial overlap between cats that live in the same household and cats that live in separate households.

The role of neutering

The results of this study must be seen in the context that a large proportion of the cats were known to be neutered (91%). In Norway, approximately 85% of cats are neutered, and neutered cats are most common in suburban and urban areas (Braastad 2019). Hence, this population likely represents a typical suburban cat population in Norway. One review found no significant difference in home range size between neutered and intact cats within either sex (Hall et al. 2016). However, another study found that males exhibited smaller home ranges and less home range overlap with other males post-castration (Ferreira et al. 2020), and so neutering may have a larger effect on the individual level. As male home ranges are largely determined by access to females (Braastad 2019), castration may result in reduced home range size and reduced contact with conspecifics if it causes decreased interest in seeking out receptive females. A study on a feral cat colony found that the general activity level and proximity between individuals decreased post-neutering, though the proximity between some males increased (Cafazzo et al. 2019). Altogether, it can be suggested that the cats in my study are at the lower end of the scale of reported conspecific interaction when considering the effect of neutering.

Density-dependence

The null-model approach revealed that combined space use of the cat population in this study was larger than would be expected by chance, at least as a trend. At first glance, this could be taken to mean that avoidance facilitates larger overall space use, as avoidance of surrounding home ranges forces cats to use unoccupied areas instead of overlapping more. However, this reasoning assumes that cat home ranges sizes remain unchanged in response to changes in cat density and associated interactions. This is unlikely - in fact, it has already been shown that cat home ranges are smaller in denser cat populations (Edwards et al. 2001, Tennent and Downs 2008, Bengsen et al. 2016). Home range size is affected by, among other factors, conspecific density. Reduced densities can reduce competition and result in increased home ranges, while increased densities can increase intruder

pressure and result in decreased home ranges (Mcloughlin and Ferguson 2000). Thus, it is possible that overall space of the cat population in this study would have been similar in size or even larger in the absence of active avoidance. Further study is needed to untangle the role of density dependence and avoidance on home range size and population-level space use. In fact, more information on this aspect of cat population space use could be critical for better understanding and mitigating ecological impacts of pet cats.

Individual variation

A striking result of this study is the high individual variation in both home range size and measures of spatial interaction. The network plot was particularly revealing. It shows an intricate web of spatial interaction with most cats having little spatial contact with other cats, and a few cats interacting with many. The cats who overlapped with the highest number of individuals were predominantly male with relatively large home ranges, and the cats who overlapped with the lowest number of individuals were predominantly female with relatively small home ranges. Interestingly, the two cats with the largest home ranges (males) overlapped with fewer conspecifics than the two cats with the smallest home ranges (a male and a female), despite their home ranges being 200-fold larger. The former were 6-7 years old and the latter were > 12 years old, which supports the earlier finding that older cats overlapped with more individuals than younger cats despite having smaller home ranges. Another explanation for the apparent discrepancy between home range size and number of spatial interactions for the two individuals with the largest home range sizes is that they roamed relatively long distances away from the study population and so did not encounter other tracked individuals very often. This could be further anecdotal evidence for a density dependent effect on home range size. Contrary to these two males, the cat with the third largest home range interacted with quite a few conspecifics – in fact, this 3-year-old male overlapped with the highest number of individuals of any cat in the population. This cat was also the only cat to overlap with individuals outside the zone it lived in. It is possible that the distinct interaction patterns of these three males are attributable to differences in personality (Litchfield et al. 2017). The variation in number of conspecifics that a cat can interact with is also obviously affected by the location of their owner's home. The three aforementioned males all lived on the suburban edge, but the male that showed large spatial interaction had access to other residential areas across a field, while the other two had largely unobstructed access into natural habitats.

Reach of spatial interactions

Ultimately, mapping and understanding the social network of cats could be a useful tool not only for investigating interactions, but also to explore the epidemiological potential within pet cat populations. In this regard, and despite the small and relatively compact study area, I observed little connection between cats living in the different study zones. A combination of infrastructure (train tracks, larger roads) and discontinuity in urban habitat can partially explain this apparent segregation. Bischof et al. (2022) showed that the cats in this population spent on average 79% (range: 32-100%) of their time outdoors within 50 m of their household, which can also explain the low connectivity between study zones.

Future research

Further research is needed into how spatiotemporal interactions shape population-level space use in domestic cats. There is evidence of significant positive relationship between home range overlap and intraspecific contact rate in racoons (*Procyon lotor*; Robert et al. 2012), but it is unclear if this also pertains to other species, like domestic cats. It would be especially interesting to see to what degree cats that share home ranges avoid or seek each other out spatiotemporally. The manner in which the avoidance observed in my study comes about is unknown without observing direct contact between cats. The form that direct contact between cats take should be addressed; whether interactions are aversive or amicable, and how this affects space use. Another topic for further research is the level of intraspecific interaction within core areas of home ranges and how this varies with sex and age. A limitation of my study is that not all outdoor activity was captured by GPS tracking (~44 % of outdoor activity tracked; see Bischof et al. (2022)). A possible explanation for this is that the GPS loggers needed to be charged frequently. Utilizing GPS loggers with more battery power that can stay on cats for longer could help capture the full extent of space use and intraspecific interaction in populations. Research into how intraspecific interactions affect space use along the housing density gradient from rural to urban is also needed.

Conclusion

This study gives unique insight into spatial interaction in a domestic pet cat population and how it affects space use. Ideally, domestic cats with outdoor access would be kept at low population size and constrained to small areas to limit their ecological impacts. This, however, is not the current situation. Alternatively, the demographic composition of the population should facilitate as narrow spatial distribution of the population as a whole. Findings from my study may help in this regard, as

I found clear evidence that cats tend to avoid conspecifics, and that this tendency depends on sex and age. The demographic composition of a pet cat population could be influenced actively by owners' choice of sex and age of pet cats with outdoor access. As pet cats are strongly associated with the homes of their owners, knowledge about the extent of interaction with neighboring pet cats can also help inform cat owners on the best management regimes for their cats. This study shows that urban cat populations are likely fragmented by infrastructure, and this can be useful in management of urban cat populations and mitigation of their impact on wildlife. A closer look is needed into how intraspecific interactions influence space use at lower and higher cat densities. Further, this study revealed large variation between cats when it comes to their tendency to spatially interact with conspecifics. My study demonstrates the necessity of observing a complete or near complete population to reliably quantify interactions and their effect on space use in animal populations.

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