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Research Article

GPS-based seasonal home ranges of neutered pet cats *Felis catus* along a habitat gradient

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Abstract

Understanding the habitat-related hunting behavior of house cats *Felis catus* is needed to evaluate their potential predatory effect on areas they actively visit within their home range. As part of a citizen science program, 30 neutered cats from 25 households were equipped by their owners during, on average, 2 consecutive days per month between January and November 2016 with a GPS programmed to acquire fixes at 1 to 5 min intervals. Nine cats were located in rural environments, 9 in suburban landscapes, and 12 in urban habitats. For 16 of these cats, preys brought home were recorded daily. Using the recursive distribution movement-based kernel density estimator, rural cats had the largest mean home range area (3.5 ± 0.3 ha), followed by suburban (2.1 ± 0.2 ha) and city cats (1.4 ± 0.1 ha). Moreover, suburban cats enlarged their frequently visited areas in April–June, which corresponded to a peak in small bird preys brought home. Our results suggest that a more diversified landscape may drive domestic cats to increase their home range by benefiting from higher numbers of exploitable areas.

Introduction

Domestic cats *Felis catus* are opportunistic predators that can reach high densities in urbanized environments (Thomas et al., 2012). These cats prey upon a large range of small terrestrial vertebrate species, with the potential to exert an important pressure on these prey populations (Baker et al., 2008). Understanding the habitat-related movement behaviour of these pet carnivores is therefore needed to evaluate the predatory pressure within areas they select for hunting activities (Thomas et al., 2014). Indeed, domestic cat predatory behaviour has recently been shown to vary spatially and temporally across an urban landscape gradient (Krauze-Gryz et al., 2017).

In the last decade, several studies have used lightweight GPS loggers with a high rate of position fixes to infer the size of the home range of domestic cats (Thomas et al., 2014). None of these studies however applied recent developments in data analysis that integrate behavioural processes detected through movement paths during tracking position acquisitions (Castañeda et al., 2018). Individuals often restrict their movement to a subset of areas within their home range, within which they repeatedly visit at various frequencies as long any attractive resource is present (Benhamou and Riotte-Lambert, 2012). Movement-based kernel density estimation (MKDE: Benhamou, 2011) allows active utilization distributions to be computed, by incorporating information on the movements undertaken by an individual within its home range (Benhamou and Cornélis, 2011).

Here, we provide an analysis from data collected over one year under a citizen science program, to study spatial and seasonal variation in space use of 30 neutered domestic cats. Using modern MKDE analysis, we focused on areas frequently visited in influencing their home range size, under the assumption that this behaviour may concentrate a large part of their hunting activities. We expected that, after controlling for the effect of age and sex on the variation of home range (Castañeda et al., 2018; Kays et al., 2020), different habitats features such as dense urban matrix with lower numbers of places available with prey for hunting would yield in smaller home range areas than in suburban or rural landscapes (Baker et al., 2008). We also expected that cats would show a habitat-related temporal pattern in actively visiting their home range under the hypothesis that these pet predators would follow some demographic characteristics of their available prey populations (Baker et al., 2005; Krauze-Gryz et al., 2017). We explored this last hypothesis with an analysis of prey return home by a subset of our studied cats.

Materials and methods

Followers of the citizen science project ("Chat et Biodiversité": https://www.chat-biodiversite.fr/) were asked if they wanted to participate to the GPS monitoring of their cat. A total of 25 cat owners, 24 distributed across the Ile-de-France region and one in Normandie (Fig. 1), volunteered to the monitoring of their pets. Thirty cats were equipped for on average two days each month with a GPS Position Logger (CatTrack I, Perthold Engineering™ containing a Sirf III chipset) programmed to acquire fixes at 1 to 5 minutes intervals between January and November of 2016 (Supplementary Table S1). Of the 30 neutered cats, 11♀ and 12♂ were 2–14 years old. An additional 6 neutered cats, not aged (4♀ and 2♂), and one individual neither aged nor sexed, were also monitored. We kept locations for estimated horizontal position error (EHPE) recorded by the GPS Position Logger of less than 50 m (Morris and Conner, 2017), and manually eliminated all visually aberrant locations well outside of the area formed by the 99% Minimum Convex Polygon.

The monthly home range area of each cat was calculated using the movement-based kernel density estimator method (Benhamou, 2011) that accounts for patterns in behavioural processes detected through movements during tracking positions acquisition. We aimed to identify areas that were frequently visited by cats using the recursive distribution model: this model evaluates the spatial distribution of the num-

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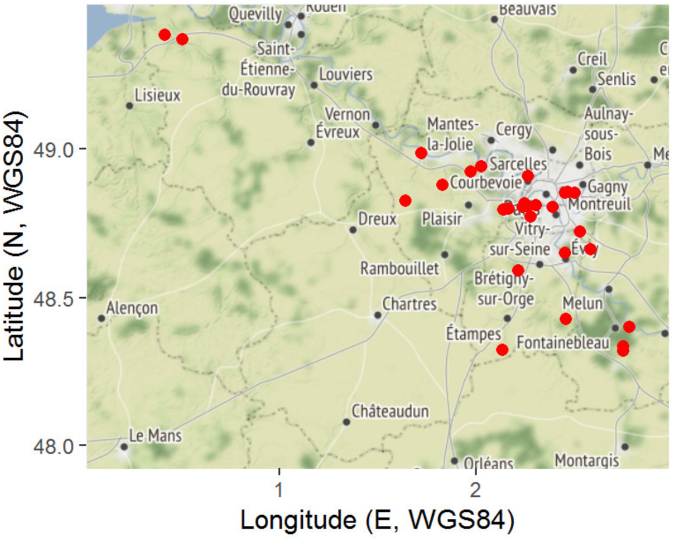

Figure 1 – Spatial distribution of the 30 domestic cats *Felis catus* monitored in 2016.

ber of visits in places within the home range (Benhamou and Riotte-Lambert, 2012). Based on studies that have investigated GPS-based fine-scale movement behaviour of domestic or feral cats (George, 2010; Martin et al., 2013; Recio et al., 2010), the minimum distance between successive relocations was set L_{min} = 5 m in order to define intensive or resting activity. The maximum duration allowed for a step built by successive relocations was set T_{max} to 1800 s (Supplementary Figure S2). The minimum smoothing parameter was set to h_{min} = 5 m, and the radius of the patches was set to 3*h_{min} (see Benhamou, 2011 for definition). The maximum time that the animal was allowed to spend outside the patch before considering it actually left it was set to maxt = 60 s.

A total of 12 cats, each belonging to a single owner (Supplementary Table S1) were assigned to an urban habitat because the area formed by the 100% minimum convex polygon encompassing outermost locations included patches corresponding to "discontinuous or continuous urban fabrics", and partly "urban green spaces" and "sport and leisure facilities" (CORINE Land Cover 2018, Supplementary Table S1). For 9 cats, each belonging to a single owner (Supplementary Table S1), locations matched an area characterized by "discontinuous urban fabrics", along with fixes recorded on a mix of small patches of "agricultural lands", and "deciduous or mixed forests". These cats were assigned to a suburban habitat type. The remaining 9 cats almost exclusively matched areas corresponding to large "agricultural grasslands", and were assigned to a rural habitat. Three of these cats belonged to the same owner (Supplementary Table S1).

Throughout the year of 2016, we found 12 of the previous 25 owners that recorded the date and identified as far as possible prey brought home by their pets on the website of the citizen science project "Chats et Biodiversité". A total of 234 prey-brought-home events were recorded (Supplementary Table S3a and S3b). Preys were identified to species level, or only at the genus or order levels, also accounting for unknown items, which were included in two categories: small birds, micromammals (i.e., < 100 g), and other preys involving medium to large sized birds and mammals, amphibian and reptiles, macro-invertebrates, and unidentified items.

Nonlinear variation in range areas, and frequency in preys brought home, were investigated with time (Julian day) and according to habitat (three levels: rural, suburban, urban; Supplementary Table S4), using Generalized Additive Mixed models (GAMM: Zuur et al., 2014). Home range area was also analyzed according to age and sex (two-ways interactions with four levels; female, male, aged less than 5 years old, aged 5 years and older), and smoothed to the number of fixes (with a cubic regression spline) a cat was tracked each month (Anile et al., 2017). GAMM models for range areas were adjusted to a Negative binomial error (with a log link and theta parameter inferred from observed mean and variance of the response variable), and run using a cyclic cubic regression spline smoother (noted 'cc'). Binomial GAMMs with a logit link were used to model the variation in the probability of preys brought home with time and habitat, also smoothed with a 'cc' (Krauze-Gryz et al., 2017). For each prey category, small birds or micromammals, a prey return event was encoded 1, and otherwise 0. In all models, a cat identity random intercept was included to cope with consistent individual-specific patterns in movement or hunting behavior. Variance homogeneity was graphically checked (Supplementary Figure S5) and an index of dispersion was calculated for Binomial GAMMs (Zuur et al., 2014). Mean is always followed by ±1SE throughout the article. All analyses were performed in R 3.5.2 (R Core Team, 2018).

Results

Cat identity had a strong effect in all models (Tab. 1). No differences were found for mean range areas according to sex and age. The 10 cats aged 2–4 years old had similar mean monthly range areas to the 13 cats aged 5–14 years old (respectively: 1.8±0.2 ha, n=76; 2.6±0.2 ha, n=108). The 11 females had a mean range area of 2.1±0.2 ha (n=92) and the 12 males, 2.4±0.2 ha (n=92). Including the 7 cats for which no information on sex or age was recorded, the 12 monitored urban cats had the lowest range areas (1.4±0.1 ha), followed by suburban (2.1±0.2 ha) and rural cats (3.5±0.3 ha; Tab. 2). While urban and rural cats did not show temporal variation in their range area, suburban cats

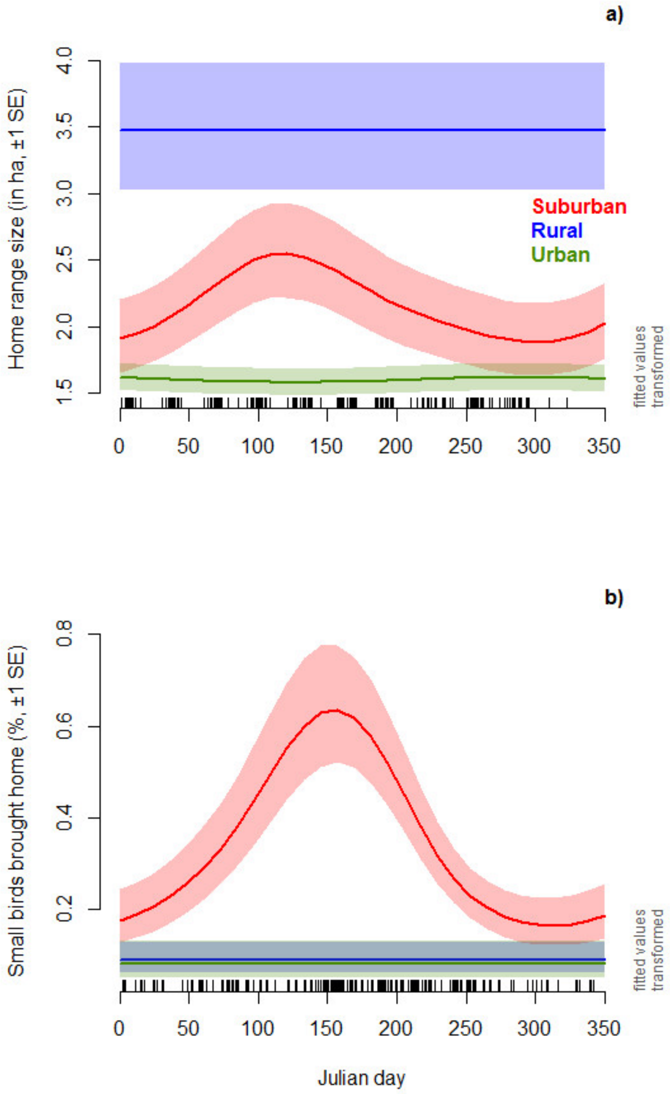

Figure 2 – Habitat-related temporal variation of a) monthly home range areas and b) proportion of small and medium sized bird preys brought to home, from domestic cats between January and November in 2016.

Table 1 – Details of the generalized additive mixed models analysing the habitat related temporal variation of monthly estimates of the RD-MKDE home range areas and preys-brought-home of domestic cats throughout the year of 2016.

Model	Predictors	Estimates	Statistics	P-value
Home range areas				
N=23 cats fully sexed and aged	Intercept	0.84±0.39	t=2.13	0.0346
n=184 areas	$\text{Habitat}_{\text{Suburban vs Rural}}$	−0.26±0.47	t=−0.56	0.5788
R^2_{adj}=0.761	$\text{Habitat}_{\text{Urban vs Rural}}$	−0.87±0.38	t=−2.28	0.0242
Negative binomial θ=4.37	$\text{Sex}_{\text{Females vs Males}}$	−0.68±0.60	t=1.12	0.2644
	$\text{Age}_{< 5 \text{ yrs old vs} \geqslant 5 \text{ yrs old}}$	−0.03±0.07	t=0.41	0.6821
	$\text{Sex:Age}_{\text{Males} < 5 \text{ vs Females} \geqslant 5}$	−0.09±0.10	t=−0.89	0.3743
	$\text{Number of Fixes}_{(\text{scale[fixes]})}$	edf=3.87	F=4.62	0.0157
	$\text{Rural}_{(\text{scale[Julian day]})}$	edf<0.01	F<0.01	0.4765
	$\text{Suburban}_{(\text{scale[Julian day]})}$	edf=2.64	F=14.13	0.0011
	$\text{Urban}_{(\text{scale[Julian day]})}$	edf<0.01	F<0.01	0.5972
	Cat ID	edf=16.27	F=23.80	0.0000
N=30 cats	Intercept	1.05±0.18	t=5.68	0.0000
n=244 areas	$\text{Habitat}_{\text{Suburban vs Rural}}$	−0.45±0.26	t=−1.74	0.0836
R^2_{adj}=0.702	$\text{Habitat}_{\text{Urban vs Rural}}$	−0.77±0.25	t=−3.15	0.0019
Negative binomial θ=5.68	$\text{Number of Fixes}_{(\text{scale[Fixes]})}$	edf=3.18	F=2.05	0.1024
	$\text{Rural}_{(\text{scale[Julian day]})}$	edf<0.01	F<0.01	0.7230
	$\text{Suburban}_{(\text{scale[Julian day]})}$	edf=1.95	F=1.09	0.0205
	$\text{Urban}_{(\text{scale[Julian day]})}$	edf=0.75	F=0.17	0.2103
	Cat ID	edf=25.07	F=15.07	0.0000
Small birds brought home				
N=16 cats	Intercept	−2.67±0.55	t=−4.86	0.0000
n_{event}=234	$\text{Habitat}_{\text{Suburban vs Rural}}$	1.44±0.69	t=2.08	0.0379
R^2_{adj}=0.227	$\text{Habitat}_{\text{Urban vs Rural}}$	−0.10±1.00	t=−0.10	0.9242
Binomial φ=1.05	$\text{Rural}_{(\text{scale[Julian day]})}$	edf<0.01	χ^2<0.01	0.9355
	$\text{Suburban}_{(\text{scale[Julian day]})}$	edf=1.64	χ^2=5.90	0.0350
	$\text{Urban}_{(\text{scale[Julian day]})}$	edf<0.01	χ^2<0.01	0.9444
	Cat ID	edf=4.59	χ^2=10.32	0.0133
Micromammals brought home				
N=16 cats	Intercept	1.64±0.57	t=2.86	0.0043
n_{event}=234	$\text{Habitat}_{\text{Suburban vs Rural}}$	−1.24±0.76	t=−1.63	0.1022
R^2_{adj}=0.276	$\text{Habitat}_{\text{Urban vs Rural}}$	−1.32±0.91	t=−1.45	0.1462
Binomial φ=1.03	$\text{Rural}_{(\text{scale[Julian day]})}$	edf<0.01	χ^2<0.01	0.8715
	$\text{Suburban}_{(\text{scale[Julian day]})}$	edf=1.06	χ^2=2.07	0.2182
	$\text{Urban}_{(\text{scale[Julian day]})}$	edf=1.58	χ^2=5.25	0.0452
	Cat ID	edf=8.20	χ^2=24.15	0.0003

enlarged their area up to 2.5 ha for the period April–June, whereas it remained around 2.0 ha for the rest of the study (Tabs. 1 and 2; Fig. 2a).

For the 5 rural cats, small birds (n=7) and micromammals (n=86) represented 92% of prey-return events (n=104; Tab. 2). For the 7 suburban cats, small birds (n=34) and micromammals (n=46) represented 81% of prey-return events (n=99; Tab. 2). For the 4 urban cats, small birds (n=2) and micromammals (n=18) represented 63% of prey-return events (n=32; Tab. 2). Small bird preys were brought home more often by suburban cats during May–June (Fig. 2b). Such temporality was neither observed for small bird preys brought home by rural or city cats, nor for micromammals brought home by any cat.

Discussion

We highlight that domestic cats enlarge the area they use in their home range depending on the increased availability of agricultural land, wooded or forested patches they encounter in the vicinity of their house of residence. Our results also show that habitat use by suburban domestic cats varies seasonally, with a peak increase of the areas they frequently visit in spring. This monthly pattern in space use activity matched the increased frequency at which small bird preys were brought home. Such temporal patterns in both spatial activity and hunting behaviour were not detected for cats living in rural or in deep urban habitats.

A spring peak of juvenile small bird species or prey individuals in poor body condition brought home by domestic cats has already been detected (Baker et al., 2005; Krauze-Gryz et al., 2017; Tschanz et al., 2011; van Heezik et al., 2010). However, seasonality in space use by domestic cats in varying habitats has been poorly investigated (Hervías et al., 2014; Thomas et al., 2014), and no marked seasonal change in home range area has ever been found (Baker et al., 2008; Morgan et al., 2009; Thomas et al., 2012, 2014). Collectively, our results suggest that the enlargement of the home range area observed during the April–June months for suburban cats did partly involve hunting activity of small bird species. It should be noticed however that prey return do not reflect the complete hunting behaviour by pet cats, as demonstrated by video-based records during cat hunting activities (Loyd et al., 2013; Bruce et al., 2019; Seymour et al., 2020).

Such temporal relationships between space use and prey returns were not evidenced for cats that almost exclusively frequented rural habitat comprised of agricultural lands. We expected both a spring peak for small bird preys brought home, and an autumnal peak for rodent preys, as recorded in similar rural landscapes in central Poland (Krauze-Gryz et al., 2017). It should be noted that only 5 cats — of which 4 belonging to the same owner — were monitored for prey brought home in rural

Table 2 – Details of the habitat related seasonal mean home range area (RD-MKDE ±1 SE, in ha) and number of events of preys brought to home (PBH; SB: Small birds, MM: Micromammals; O&U: Other and unknown) recorded by owners for their pet cats over the year 2016.

Habitat	Number of		Analysis		Winter		Spring		Summer		Autumn	
	cats	owners			n	Jan–Mar	n	Apr–Jun	n	Jul–Sep	n	Oct–Nov
Rural	9	5	RD-MKDE		11	3.0±0.6	18	3.5±0.4	14	3.7±0.4	7	3.6±1.0
	5	2	PBH	SB	-	1	-	3	-	2	-	1
				MM	-	14	-	25	-	34	-	13
				O&U	-	1	-	2	-	3	-	2
Suburban	9	8	RD-MKDE		19	1.9±0.3	21	2.5±0.4	16	2.1±0.3	5	1.2±0.2
	7	7	PBH	SB	-	5	-	17	-	12	-	0
				MM	-	10	-	19	-	17	-	2
				O&U	-	1	-	10	-	8	-	0
Urban	12	12	RD-MKDE		27	1.4±0.2	24	1.4±0.2	17	1.4±0.2	5	1.5±0.3
	4	3	PBH	SB	-	0	-	1	-	0	-	1
				MM	-	8	-	6	-	3	-	1
				O&U	-	4	-	1	-	7	-	0

habitats and only 4 cats belonging to 3 owners in the urban habitat. Such small samples must not have allowed for the detection of temporal pattern in hunting behavior through prey returns. Moreover, we found a strong cat identity effect, meaning that some individuals consistently returned more preys than others, supporting the presence of "super predators" (Kauhala et al., 2015; Tschanz et al., 2011). Indeed, 2 rural cats housed by a single owner returned a total of 75 micromammal preys, representing 75% of the total return events (n=101; Supplementary Table S3a). Nevertheless, a marked difference was seen in number of prey items brought home: 63% of events including both small bird and micromammal preys were recorded for the four urban cats, compared to 92% recorded for the five rural cats, and 81% for the seven suburban cats. Overall, these results are in accordance with a habitat gradient-related prey availability for domestic cats, as urban habitats may both provide fewer hunting sites and lower prey diversity (Clergeau et al., 2001). A switch in preys brought home between micromammals and small birds between rural and suburban habitats also indicates that the latter habitat must be most beneficial to birds because of the presence of a large number of gardens enriched by a variety of feeding plants and bird-feeding activities (Clergeau et al., 2001; Kauhala et al., 2015; Morgan et al., 2009; Pavisse et al., 2018; Woods et al., 2003).

Our results also agree with most studies on neutered domestic cats that did not find a difference in home range size according to sex, or at least a weak effect of age on domestic pet cats (e.g.: Castañeda et al., 2018; Thomas et al., 2014, but see Hervías et al., 2014). It should be noted however that the comparison of home range size with biological or environmental factors is made difficult because of the many different methods used to calculate home range size in published studies (e.g., Castañeda et al., 2018; Kays et al., 2020). Moreover, our method, based on 1.5 to 2 days monitoring, may not have fully revealed the complete home range area of the cats, impeding the detection of a stronger effect of age on home range area where young individuals may move less than older ones (but see Kays et al., 2020).

The present study highlighted that small bird preys returned home could be associated to seasonal changes in cat space use in suburban habitats. Understanding such a fine-scale spatial and temporal process could be improved by analyzing larger datasets for both prey return records and GPS tracking data from a larger panel of citizen participants (Thomas et al., 2012; Tschanz et al., 2011). The threat facing urban wildlife posed by domestic cats living in the vicinity of green areas that can serve as refugia to many small vertebrates is evident (Baker et al., 2008; Kauhala et al., 2015; Krauze-Gryz et al., 2017; Thomas et al., 2012, 2014; Tschanz et al., 2011; Woods et al., 2003). Thus, identifying hot spots where cats repeatedly concentrate their hunting behaviour is of importance (Benhamou and Riotte-Lambert, 2012). It could allow for a focus of monitoring effort on prey populations inhabiting these patches, in order to more finely evaluate the impact of cat predation. Connecting citizens, academic researchers, and conservation managers or stakeholders to collectively gather high quality data on what, where and when cats catch their prey, could greatly assist in the development of a consensual management scheme (Bassett et al., 2020; Crowley et al., 2020; Mori et al., 2019; Roetman et al., 2018), in order to reduce their impact on urban wildlife, especially small bird species.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Supplemental Table S1 Detailed synthesis of the high frequency GPS-acquisition locations of the 30 castrated house cats *Felis catus* between January and November 2016. Time records in seconds, distances in meters, coordinates in decimal degrees (WGS84), areas in ha.

Supplemental Figure S2 Influence of varying T_{max} parameter on 95%RD-MKDE home range area estimates.

Supplemental Table S3 a) Details of the seasonal number of events of preys brought to home recorded by owners of 16 cats over the year 2016; b) Details of the daily events of small birds and mammals preys brought to home recorded from 16 cats housed by 12 owners over the year 2016.

Supplemental Table S4 Raw data from the RD-MKDE analysis.

Supplemental Figure S5 Graphical variance checking of the Negative binomial error GAMM model a) with 184 monthly home ranges from n=23 aged and sexed cats, and b) with n=244 monthly home ranges from n=30 neutered cats.