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Pet cats (*Felis catus*) from urban boundaries use different habitats, have larger home ranges and kill more prey than cats from the suburbs

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HIGHLIGHTS

- Cats living next to natural areas have larger home ranges, using nearby natural habitats.
- Cats living next to natural areas returned over twice as many prey than suburban cats.
- Mammal returns greatly increased with natural habitat availability, but bird returns did not.
- The intersection of urbanization and prey availability may alter the impact of pet cats on wildlife.

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ABSTRACT

The domestic cat (*Felis catus*) is a predator of global significance. In Great Britain there are ca. 9.5 million owned pet cats, with their population determined by human population density. As urban areas expand and encroach on areas of conservation value, it is not known how cats use these areas and how habitat availability influences predation rates. To address this, over a year we recorded the movement and prey of 79 owned cats in inner suburban areas (non-boundary cats) and in areas adjacent to natural habitats on the edge of the suburban area (boundary cats). Boundary cats had larger home ranges (mean 3.42 S.E. $\pm$ 0.61 ha) and returned more prey (mean 7.91 S.E. $\pm$ 2.70 prey cat^{-1}year^{-1}) than cats in non-boundary areas (2.01 S.E. $\pm$ 0.70 ha; 3.35 S.E. $\pm$ 1.06 prey cat^{-1}year^{-1}respectively). Assuming a prey return rate of 23%, extrapolated predation rates equate to 34.40 (S.E. $\pm$ 11.74) and 14.57 (S.E. $\pm$ 4.62) prey cat^{-1}year^{-1} in our boundary and suburban study sites respectively. While non-boundary cats had little access to natural habitats, natural habitats made up > 25% of the home range of boundary cats. Boundary cats travelled a mean distance of 64.9 m (S.E. $\pm$ 6.8) into these natural habitats, with some cats ranging > 300 m inside these areas. Bird predation rates did not differ between boundary and non-boundary cats, but boundary cats killed three times more mammals. This is of relevance to urban planning, as the hunting behaviour of pet cats extends the ecological effects of urbanisation into surrounding habitats.

1. Introduction

The global population size of the domestic cat (*Felis catus*) is not accurately known, although previous estimates of ~ 600 million (O'Brien & Johnson, 2007) suggests that they are one of the most widely distributed terrestrial mammals (Long, 2003). The popularity of cats as pets is increasing (Lepczyk et al., 2010) and cats may soon overtake dogs as the preferred animal companion of humans. In Great Britain, 23% of households own an average of 1.6 cats and, with an estimated population of 9.5 million cats (Murray, Gruffydd-Jones, Roberts, & Browne, 2015), they greatly outnumber the total wild British terrestrial mammalian carnivore population of ~ 1.8 million (Sainsbury et al., 2019).

Although domesticated, cats have retained their predatory nature and are considered to be one of the most problematic of invasive species (GISD, 2018). Introduced cats have contributed to, or been directly responsible for, 26% of modern vertebrate extinctions (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016) and are believed to be the primary threat to 8% of critically endangered mammals, birds and reptiles (Medina et al., 2011). Cats annually kill an estimated 1.3–4 billion birds and 6.3–22.3 billion mammals in the United States (Loss, Will, & Marra, 2013), and 100–350 million birds in Canada (Blancher, 2013). In

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Britain, estimates from a single study suggests 92 million prey over five (spring and summer) months (Woods, McDonald, & Harris, 2003).

Predation estimates are largely based upon cats returning prey to their homes, but prey returns alone may not show a complete picture. Video data suggests that only 23% of the total prey caught is returned (USA, Loyd, Hernandez, Carroll, Abernathy, & Marshall, 2013) and scat analysis shows a difference in species that are consumed rather than returned (Poland, Krauze-Gryz, Gryz, & Goszczyński, 2012). Nevertheless, UK studies agree that rodents are the main prey taxon of cats (mainly wood mice *Apodemus sylvaticus*), followed by small urban birds (house sparrow *Passer domesticus*, blackbird *Turdus merula,* great tit *Parus major*, robin *Erithacus rubecula,* and dunnock *Prunella modularis*; Churcher & Lawton, 1987; Woods et al., 2003; Baker, Bentley, Ansell, & Harris, 2005; Thomas, Fellowes, & Baker, 2012).

Cat predation studies are primarily from urban and suburban habitats, which may bias estimates of predation and behaviour. Given that species of conservation concern are more likely to be found outside of urban areas, consideration should be given to cat predation in non-urban areas, particularly as urban development (and hence increased numbers of cats; Thomas et al., 2012) encroaches on areas of conservation value. There is some evidence that prey returns by cats is greater when living next to natural areas in the UK (Churcher & Lawton, 1987), but studies from New Zealand have found no difference in bird returns (Gillies & Clout, 2003; van Heezik, Smyth, Adams, & Gordon, 2010) and indeed a Polish study found that more birds were returned by urban cats (Krauze-Gryz, Żmihorski, & Gryz, 2017). However, it is not known where these cats were hunting, and the ranging behaviour of domestic cats will determine where (and therefore what) they hunt.

Cat ranging behaviour can be affected by a variety of factors, with some studies finding age (less than eight years old), being male (Hall et al., 2016), not wearing a collar (Coughlin & van Heezik, 2014), or not being owned (Horn, Mateus-Pinilla, Warner, & Heske, 2011) to be significantly associated with larger home ranges. Other studies suggest that where they live (urban vs peri-urban; Hanmer, Thomas, & Fellowes, 2017) and cat density (Barratt, 1997; van Heezik et al., 2010) also influences range size, with larger ranges occurring where cat density is lower. Although the range size of cats living next to natural habitat, where cat density should be relatively low, has not been investigated in the UK, two New Zealand studies did not find ranges to be significantly larger next to the natural habitat (Morgan et al., 2009; van Heezik et al., 2010), but ranges were found to increase with increasing size of natural habitat (van Heezik et al., 2010).

Therefore, while we have some understanding of the home range size of pet cats, how does this affect where they hunt? Do cats prefer to hunt in surrounding areas, or to remain in domestic gardens? The answer to this will be of considerable interest for conservation. Four global studies tracking cats suggest that they rarely use natural areas (USA Albany pine bush forest, Kays & DeWan, 2004; Australian heathland, Meek, 2003; New Zealand, Metsers, Seddon, & van Heezik, 2010; New Zealand native bush, van Heezik et al., 2010). However, little can be generalised from these studies. While the reasons for lack of use of natural areas in New Zealand areas was unknown, the relatively dense vegetation (Australia) or presence of larger predators (USA) could have been deterrents from using natural habitats in these areas. In contrast, a recent study found that 11% of 925 GPS tracked cats from Australia, New Zealand, USA and the UK did use natural habitat for > 50% of their time (Kays et al., 2020), but it is unclear how far the cats roamed into the area or how far they lived from the area.

Roaming behaviour and habitat use may determine prey returns due to differences in the abundance of potential prey and opportunities for hunting between areas. Therefore, determining whether pet domestic cats living next to natural habitats use and hunt in these areas is important, in order to understand the potential impact on nationally threatened species. For example, in our study area, the declining European nightjar *Caprimulgus europaeus*, and near threatened Dartford warbler *Sylvia undata* (Eaton et al., 2015; IUCN, 2018) inhabit heathland, a habitat which is being increasingly affected by urban development.

As urban areas grow and increasingly encroach on areas of biodiversity value, the answers to the questions posed above will help us understand the consequences for conservation of increased cat density associated with the growth of domestic housing. Given that rates of cat predation are likely to be affected by cat roaming behaviour (i.e. where they hunt) and prey diversity and abundance (i.e. what they have available to hunt), we tested the hypotheses that a) domestic cat home range is positively affected by availability of natural habitats; b) that the predation rate of domestic cats will be greater in areas with greater access to natural habitats; and c) that the identity of prey returned will vary with availability of natural habitat. To test these hypotheses we compared these traits between pet cats living on urban boundaries, with ready access to natural areas of biodiversity value (heathland and woodland in southern England), with the behaviours of owned cats dwelling in nearby suburban areas.

2. Material and methods

2.1. Study site

We chose nine sites (Fig. 1) within the counties of Berkshire and Hampshire, UK. Sites were all situated within a radius of 30 km from the town of Reading and met the criteria of having a residential area located adjacent to woodland or heathland, with five sites situated next to, or within the vicinity of the Thames Basin Heaths Special Protection Area, which have populations of nationally scarce European nightjar, woodlark *Lullula arborea* and Dartford warbler (Joint Nature Conservation Committee, 2005; Sussex Wildlife Trust, 2012; Appendix 1).

2.2. Data collection

2.2.1. Home range

The study was approved by the University of Reading School of Biological Sciences ethical review committee (reference SBS16-17 18). A total of 123 cat owners were initially recruited between April and June 2017 using a combination of door knocking and leaflet distribution at the nine sites. Houses were targeted at each site in two locations; up to 100 m from natural areas (termed boundary residents, with 73 trialled) and a kilometre from the green boundary surrounded by other residential buildings (termed non-boundary residents, with 50 trialled). Where enrolment was not successful for non-boundary residents, recruitment occurred in areas surrounded by houses and roads at a minimum of 200 m from a natural area. Of the 97 cats accepted for the study, 18 dropped out due to the owner changing their mind about participating (3 cats), the owner detecting distress in their cat (4), repeated loss of the tracker (4), the owner moving (2), the cat dying of age-related illness (2), the cat moving (1), the owner became unwell (1), or the cat was kept inside after being attacked (1), leaving a total of 79 cats that completed the study (general characteristics; Appendix 2).

We enlisted a single cat per household and recorded information about the study cat (mass, age, neuter status, collar or bell wearing, if it had moved house with the owner or was a rescue cat, had access to food and what type, and what prey the cat usually returned (small mammal, large mammal, bird, reptile, amphibian, insects) and how often (once, rarely, once a month, once a fortnight and once a week). Only cats that were over a year old, in good health, had outside access and weighed over 2 kg were accepted to ensure the tracker would not weigh >2% of their body mass (Coughlin & van Heezik, 2014).

Before the cat was entered into the full study, a trial was conducted for a week to confirm that the cat was not averse to wearing a collar and GPS device. GPS units were attached to quick release collars for cat safety reasons. Cats were monitored by their owners during the initial trial and throughout the main study period to ensure no signs of distress. Cats that showed distress at any time during the monitoring period or

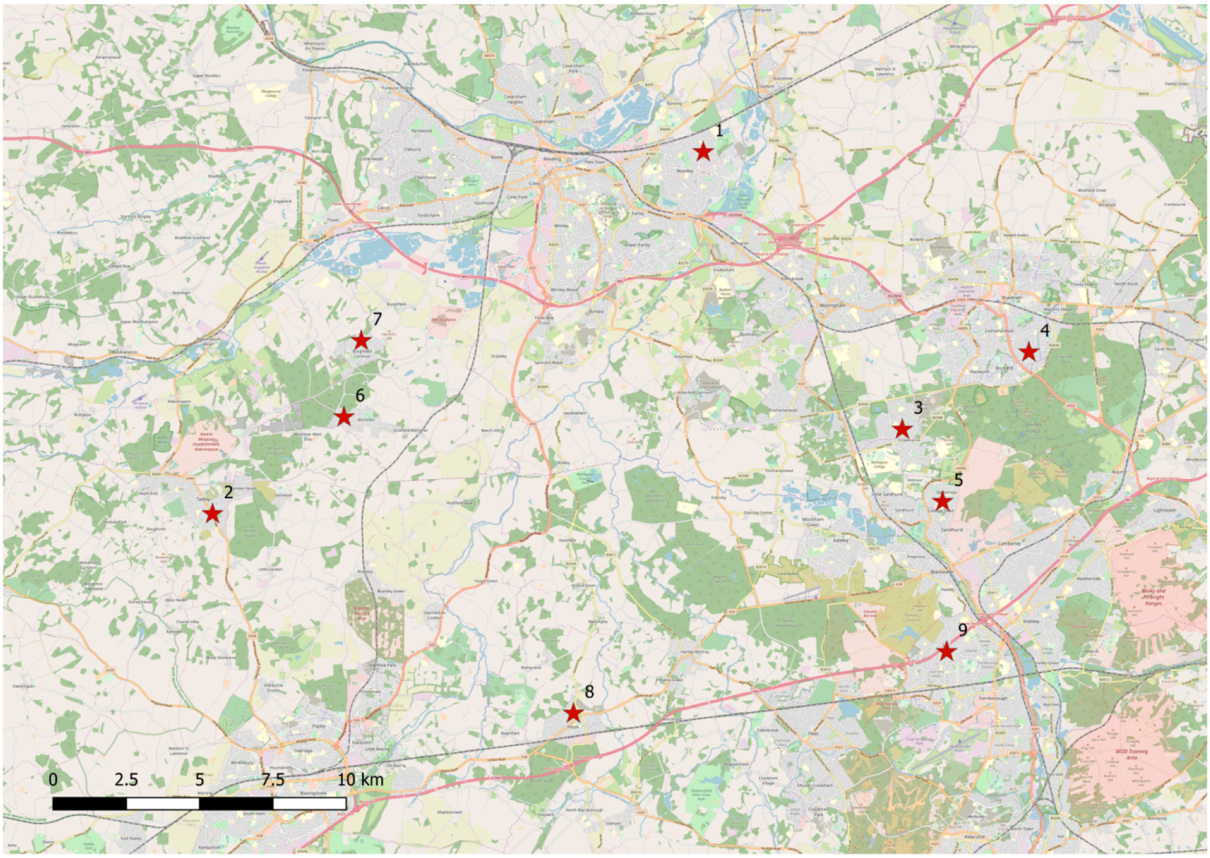

Fig. 1. Site locations marked with stars and numbered 1–9 (2–5 and 9 are situated next to or within the vicinity of the Thames basin heaths special protection area; Appendix 1). Produced with QGIS version 3.2.0 and open source maps.

main study were immediately removed from the study.

Tracking was conducted between 1st June 2017 and 31st May 2018. Cats that progressed to the main study (97) were tracked between seven and ten days for each month, except September – November. We used i-got U GT120 USB GPS receiver tracking devices (MobileAction, Taiwan) which were 44.5 × 28.5 × 13 mm and weighed 20 g. The trackers can return positional accuracies of 10.03 m in the open and 29.96 m in foliage (Coughlin & van Heezik, 2014). Although waterproof, the device was wrapped in cling film in order to protect it further from snow or water before being placed in a blue gel case for attachment to the collar. Fixes were initially recorded every 2.5mins to allow for a high number of fixes per day (between June and December), however the download time was extended to every 15mins (Coughlin & van Heezik, 2014), from January to May in order to extend the number of days the cats were tracked. Data were downloaded from retrieved trackers after completion each month using @trip PC.

2.2.2. *Prey returns*

Owners recorded both dead and live prey that were brought home between 1st June 2017 and 31st May 2018. In addition, they also noted prey type (bird, rodent, small mammal, large mammal, reptile, insect), the species if known, the date it was returned and how confident they were it was the study cat which returned it. We requested that owners saved any dead prey items that were returned so we could collect and accurately identify them. Zip lock bags and labels were supplied and specimens were frozen until collection was possible. Samples were collected to coincide with tracker delivery or within 24 h of reporting a return if freezing was not possible.

2.3. *Statistical analysis*

2.3.1. *Home range*

Tracking data (collected datum: WGS 84) were cleaned prior to analysis. Fixes from each cat were compared visually across all months for extreme single points in QGIS (Quantum GIS, version 3.2.0) following Hanmer, Thomas, and Fellowes (2017). Extreme differences in distance travelled (Coughlin & van Heezik, 2014) and altitude (Moen, Pastor, & Cohen, 1997) compared to fixes either side were used to confirm errors.

The home-range kernel density estimate (95% KDE) were calculated from all the fixes (projection: WGS 84 / UTM zone N30) for each cat and then fixes for three months were combined for each season (summer: Jun-Aug; winter: Dec-Feb; spring: Mar-May; to ensure > 10 days to increase the likelihood of a fully revealed home range) using the “adehabitatHR” package in R (R Core Team, 2018, version 3.5.1). ESRI shape files of the KDEs were saved using the “maptools” package. The furthest point was found by measuring from the centre of the cat owner’s house to the furthest point of the home-range. The distance into the natural area was measured perpendicular from the edge of the green area to the furthest point of the home-range. Seasonal home ranges were not normal therefore a paired Kruskal Wallis test was used to compare boundary and non-boundary cats (termed locations) by calculating the mean home range per site for both locations. Furthest point data was normal therefore a paired *t*-test was used to compare means per site for locations.

A generalized mixed model was run in R (R Core Team, 2018, version 3.5.1, package ‘lme4’), with home-range size as the response variable and site as a random factor. Factors which have been found by other studies to influence home range were included as explanatory variables; cat age (rounded to nearest year) and sex (Hall et al., 2016), and collar wearing (Coughlin & van Heezik, 2014), plus location (boundary/non-boundary) and amount of natural habitat within 300 m of the cats' home. In addition, if the cat moved house with the owner (yes/no), or if it was a rescue cat (yes/no) were also included in case historic movement affected home range size. Core range was not considered here as we were interested in what influences the extent of a cat's range. Home-range data were not normally distributed but were transformed with the reciprocal and all continuous variables were standardised. Data were investigated for best fit prior to model selection and checked after selection. Model selection (including a null model) was conducted using AICc values, rejecting models ΔAICc of > 2 (Burnham & Anderson 2002) and averaging those < 2 ΔAICc. Selected models were checked for collinearity and dispersal, and residuals for normality and heteroskedasticity.

2.3.2. Habitat used

The home-range shape file polygons were overlaid with the EDINA Digimap Ordnance Survey Service (2018) in QGIS (QGIS Development Team, 2018; version 3.2.0). Using the EDINA classifications the percentage of buildings and roads (termed built-up surfaces), mixed surfaces (patio, grass, hedging; termed gardens) and natural habitat within the home range polygons were calculated. This was repeated for a 300 m radius around the house for each cat. Means of each habitat within the home range and 300 m radius around the house were taken for each site to use in the Jacobs' index. This compared the use of the three habitat types with the availability to detect any preference or avoidance for all cats and then for each location separately. This was calculated using $D = (r - p)/(r + p - 2rp)$, where p is the proportion of habitat available within a 300 m radius of the house, r is the proportion of habitat use within the home-range. The index (D) indicates the habitat preference with + 1 indicating a complete preference, −1 a complete avoidance and 0 illustrates no preference (Jacobs, 1974). Significance threshold was set at $p = 0.05$.

2.3.3. Prey returned

Only prey that could be identified as an animal that were returned to the house or garden by the study cat were considered for analysis (i.e. organs and blood were omitted). G-tests were used on counts of total recorded prey (alive and dead), mammals or birds only and individual species (Yates's correction was applied where numbers were < 5). Predicted values were weighted based on proportions of cats at either location to compare returns equally. Total numbers of returned mammals and birds per cat were correlated with owner's perception of how often the taxa were returned using a Spearman's rank test.

Generalized linear mixed models (R package lme4) were used to investigate what factors influenced total prey returns, and for mammal and bird returns only. Site was included as a random factor. The total number of cats living at the house, if the cat was kept in at night (Barratt, 1998), cat age (rounded to the nearest year), and if a bell was worn (yes/no; Gordon, Matthaei, & Van Heezik, 2010), were all included as explanatory variables as they have been found to influence prey returns. Additionally, size of the home-range, amount of natural habitat within 300 m and location (boundary/non-boundary), were also included as explanatory factors. In addition, although not found to affect prey returns in previous studies, sex (Barratt, 1998) and access to wet food were included to ensure they were not significant in this study. All continuous variables were standardised, models and residuals were checked and the average model was calculated as stated for the previous models.

2.3.4. Home range and habitat selection by cats returning prey

Only cats returning prey were used in the following analyses. To examine if the wearing of a GPS unit affected predation rates, the daily mean number of prey returned by individual cats when GPS units were worn and not worn were compared using a paired Kruskal-Wallis test. Daily home-ranges were calculated for each cat based on the following adjusted 24 h period owing to the unknown prey capture time. Fixes were taken from 20:00 h on the previous day to the date of discovery of the prey to 20:00 h on the same day due to the nocturnal behaviour of cats (Meek, 2003) and potential for predation any time (George, 1974). The times would also coincide with when owners returned home from work and potentially discovered the returned prey. Due to a mean of 3.19 days tracked [S.E. ± 0.49; mean 494 fixes (±129)] when prey were returned compared to a mean of 57.07 days [S.E. ± 1.99, mean 6884 fixes (±772)] when not, daily home-range were calculated for each cat. The mean daily home-range was taken for each cat when prey was returned and not and compared using a paired Kruskal-Wallis test. Home-ranges were then calculated for each cat based on all fixes when prey was returned and not, in order to determine habitat use using Jacob's index as previously described.

2.3.5. Predation rates

For predation rates, the mean total prey returned per cat annually was calculated by dividing the total full animal prey returned per site by the number of cats at that study site, then taking the mean prey return rate across the nine study sites. The mean total prey per location was found using the same method for only boundary or non-boundary cats. These figures represent an estimated 23% of the total prey caught (following Loyd et al., 2013). Therefore, the remaining 77% was extrapolated for the total, boundary and non-boundary means to give the total annual cat predation rate for each.

3. Results

3.1. Home range

A mean of 1.8% (SE ± 0.57) of points per cat were removed during the data cleaning and the mean number of tracking days over the combined nine months was 55.30 (SE ± 1.41), with mean spring tracking as 23.39 days (SE ± 0.93), summer 11.76 days (SE ± 0.47) and winter 18.15 (SE ± 0.66). There was no significant difference between locations for distance travelled (Table 1) or seasonal home-ranges. Home ranges were significantly larger for boundary cats and males (Table 2). Models that included number of cats, owners moved house or the cat was a rescue cat were not selected due to ΔAICc being greater than two.

3.2. Habitat used

Built-up surfaces were significantly avoided by cats in general (D = −0.67, 95% CI values −0.66 and 0.99), but selection for gardens and natural areas were not significant (D = 0.49; D = 0.71 respectively). This pattern was maintained by both boundary and non-boundary cats, with cats in both locations significantly avoiding built-up surfaces (D = −0.75, 95% CI −0.74 and 1, D = −0.53, 95% CI −0.52 and 0.86 respectively). The mean proportion of natural habitat (area) in the home ranges of boundary cats was 25.92% (S.E. ± 2.66%) and boundary cats moved a mean distance into the natural area of 64.9 m (S.E. ± 6.8, Table 1). Given possible tracker location recording errors, it is sensible to check against the unlikely scenario that the errors were biased in one direction (i.e. over-recording use of natural habitats). The great majority (38; 90%) of boundary cats had home-ranges which extended >12 m, and 37 of boundary cats (86%) >29 m, into the natural habitats, allowing us to reject the hypothesis that GPS error accounts for differences in habitat use.

3.3. Prey returned

There was a total of 604 prey items recorded of which 499 could be confirmed as being attributed to the study cat. The remaining 105 items were returned to multiple cat households where the owner could not confirm which cat was responsible for returning the item; therefore,

Table 1
Number of cats tracked for boundary cats (B) and non-boundary cats (NB) and mean 95% kernel density estimates (ha) per site, the furthest point from the residence (metres) and mean distance into the natural area (metres).

Site	Total N	N (B)	Mean 95% KDE (B) ha	Furthest point (B) m	Mean distance into natural habitat (B) m	N (NB)	Mean 95% KDE (NB) ha	Furthest point (NB) m
1	10	6	6.45	650.3	103.8	4	1.56	690.3
2	8	4	1.99	950.3	83.0	4	1.74	754.8
3	8	2	2.70	828.0	68.4	6	3.03	547.3
4	8	5	2.25	430.6	87.0	3	1.19	501.0
5	4	3	5.06	760.3	52.9	1	2.38	1069.0
6	17	10	2.44	606.0	44.0	7	3.16	606.6
7	9	5	5.81	623.4	63.6	4	1.37	578.8
8	9	5	1.82	499.0	40.5	4	1.87	625.5
9	6	2	2.23	501.0	51.3	4	1.81	655.8
Mean (se)	9	4	3.42 (0.61)	649.9 (56.5)	64.9 (6.8)	4	2.01 (0.70)	669.9 (55.9)
Max			27.06	1,502	368		6.23	1,294
Min			1.14	250	0		0.75	177
Total cats	79	42			42	37		

Table 2
Generalized linear mixed models within 2Δ AICc of the top model and averaged model containing significant variables for 95% KDE range sizes of all cats (N = 79); NB = non-boundary).

Dependent variable Family (Link)	Top Models	*df*	AICc	Δ AICc	Wgt	Contributing variables to averaged model	Contributing weight to averaged model	Averaged model Independent Variables	Est.	SE	*p*
95% KDE (N = 79)	A	5	−12.43	0	0.27	1,3	0.53	**Intercept**	**2.01**	**0.26**	**<0.001**
								1. Location (NB)	**−0.45**	**0.22**	**0.04**
	B	7	−11.09	1.34	0.14	1,3,4,5	0.27	2. Age	−0.00	0.01	0.80
Gaussian (Inverse)	C	7	−10.54	1.90	0.11	1,2,3,4	0.20	**3. Sex (Male)**	**0.46**	**0.17**	**0.01**
								4. Collar worn (Yes)	0.05	0.19	0.80
								5. Location (NB): collar worn (Yes)	0.09	0.24	0.70

Table 3
Total recorded (all prey recorded by owners) and checked prey (prey checked by researcher) returned by boundary cats (B, N = 42) and non-boundary cats (NB, N = 37) divided by prey category.

Prey category	N confirmed species	N recorded live	N recorded dead	N checked	N recorded total	N in B	N in NB
Amphibian	–	**5**	**1**	**0**	**6**	**3**	**3**
Bird	**14**	**14**	**96**	**76**	**110**	**64**	**46**
Erithacus rubecula				*11*		*10*	*1*
Periparus ater				*8*		*6*	*2*
Prunella modularis				*7*		*6*	*1*
Carduelis carduelis				*7*		*5*	*2*
Turdus merula				*5*		*0*	*5*
Parus major				*6*		*5*	*1*
Columba palumbus				*5*		*4*	*1*
Cyanistes caeruleus				*4*		*1*	*3*
Other species				*17*		*6*	*2*
Unknown				*6*		*21*	*28*
Egg	**1**	–	**2**	**2**	**2**	**2**	**0**
Invertebrates	**4**	**3**	**3**	**3**	**6**	**2**	**4**
Mammal	**10**	**74**	**238**	**160**	**311**	**220**	**91**
Chiroptera	***1***	***0***	***1***	***1***	***1***	***0***	***1***
Eulipotyphlan	***2***	***1***	***9***	***8***	***10***	***8***	***2***
Lagomorph	***1***	***4***	***10***	***2***	***14***	***14***	***0***
Rodent	***6***	***69***	***217***	***149***	***286***	***198***	***90***
Apodemus sylvaticus				*84*		*56*	*27*
Myodes glareolus				*22*		*17*	*5*
Microtus agrestis				*13*		*13*	*0*
Rattus norvegicus				*13*		*3*	*10*
Apodemus flavicollis				*7*		*3*	*4*
Sciurus carolinensis				*0*		*1*	*0*
Unknown				*10*		*105*	*44*
Mollusc	**1**	**1**	**0**	**0**	**1**	**0**	**1**
Reptile	**2***	**8**	**6**	**3**	**14**	**8**	**6**
Total		**105**	**345**	**244**	**450**	**295**	**151**

* A grass snake was recorded by the owner but not verified.

these were not included in analysis (and hence our results are conservative). There were 22 organs and six blood stains leaving 450 recorded prey items from 46 cats (33 did not return any prey), 25 from the boundary and 21 from the non-boundary locations (Table 3). Overall mammals (69% of returns) were significantly more likely to be returned than birds, the second most returned category (25%, $G_1 = 99.99$, $p < 0.001$). Reptiles comprised 3% of returns, with amphibian, invertebrates and other at 1% each (Table 4). Boundary cats were significantly more likely to return prey compared to their non-boundary counterparts ($G_1 = 30.87$, $p < 0.001$), with mammals being significantly more likely to be returned ($G_1 = 36.89$, $p < 0.001$).

Although bird returns were not found to be significantly different between boundary and non-boundary cats, robins were significantly more likely to be returned by boundary cats ($G_1 = 5.52$, $p = 0.019$) and blackbirds by non-boundary cats ($G_1 = 4.21$, $p = 0.04$; Table 3). There was a significant difference in prey returns over the four seasons with total prey significantly higher in spring and summer than in winter and autumn ($G_1 = 43.34$, $p < 0.001$). Birds were significantly more likely to be returned during summer ($G_3 = 42.48$, $p < 0.001$) and mammals during spring ($G_3 = 32.18$, $p < 0.001$; Fig. 2). Total prey and mammal returns were found to be significantly higher with an increase in natural habitat and a decrease in cat age (Table 4). Wearing a bell was significantly associated with an increase in prey returns (Table 4), and there was a significant correlation with owner perceptions of how often prey was likely to be returned and prey numbers for mammal ($R_s = 0.60$, $p < 0.001$) and bird returns ($R_s = 0.33$, $p = 0.002$), suggesting owners were aware of their cat's predatory behaviour. The top two models for bird returns both showed decreasing age and bell wearing significantly affected predation rates, although the average model still contained these as the only significant factors, the intercept was not significant (Table 4).

3.4. Home range and habitat selection by cats returning prey

Of the 46 cats that returned prey, 27 cats were tracked for 96 of all (499) of the returns (15 cats from the boundary, and 12 non-boundary cats). Daily mean prey returns when cats were tracked and not tracked were not significantly different, suggesting that carrying a GPS device did not change cat behaviour. There was no difference between home-ranges calculated from fixes when prey were caught and not caught.

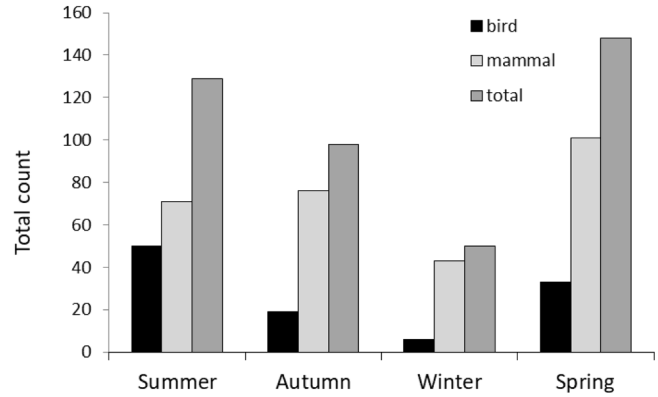

Fig. 2. Counts of total prey, mammal, and birds returned by owned cats (N = 46) over each season.

Cats which did not return prey were found to significantly avoid gardens (D = −0.47; 95% CI −0.47 and 0.55) and when prey was returned, they significantly avoided built-up surfaces (D = −0.27 95% CI −0.26 and 0.42). Preference was shown for natural habitat when prey was returned (D = 0.37) and not returned (D = 0.30). When location was considered separately, boundary cats not returning prey avoided gardens and showed some preference for built-up surfaces and a stronger preference for natural areas (Table 5). When prey was returned, boundary cats significantly avoided built-up surfaces and showed a similar preference for gardens and natural areas (Table 5). Non-boundary counterparts not returning prey showed a significant avoidance for gardens, but a strong preference for built-up surfaces and natural areas. When prey was returned, natural areas appeared to be preferred over gardens (Table 5).

3.5. Predation rates

The mean number of prey returned was 5.20 (S.E. ± 1.26, N = 79)

Table 4
Top generalised linear mixed models within 2Δ AICc of the top model with the lowest AICc and the averaged model containing significant variables for total prey, mammals and birds only returned by cats (N = 79).

Dependent variable	Top Models	*df*	AICc	Δ AICc	Wgt	Contributing variables to averaged model	Contributing weight to averaged model	Averaged model Independent Variables	Est.	SE	*p*
Total prey	A	7	380.66	0	0.29	1,2,3,4	0.46	**Intercept**	**1.93**	**0.55**	**<0.001**
								1.Age	**−0.22**	**0.06**	**<0.001**
	B	6	382.25	0.59	0.21	1,2,3	0.34	**2.Bell (Yes)**	**1.16**	**0.39**	**0.003**
	C	7	383.40	1.74	0.12	1.2.3,5	0.19	**3.Amount of natural habitat within 300 *m***	**0.06**	**0.02**	**0.002**
								4.Constant access to wet food (Yes)	−0.42	0.56	0.46
								5.Sex (Male)	0.09	0.25	0.73
Mammal only	A	7	321.06	0	0.25	1,2,3,5	0.42	**Intercept**	**1.55**	**0.57**	**0.007**
	B	6	321.59	0.53	0.19	1,2,3	0.32	**1.Age**	**−0.26**	**0.07**	**<0.001**
	C	7	321.98	0.92	0.16	1,2,3,4	0.26	**2.Bell (Yes)**	**1.02**	**0.42**	**0.02**
								3.Amount of natural habitat within 300 *m*	**0.07**	**0.02**	**<0.001**
								4.Constant access to wet food (Yes)	−0.21	0.45	0.64
								5.Sex (Male)	0.32	0.47	0.50
Birds only	A	5	228.65	0	0.20	1,2	0.28	Intercept	0.78	0.50	0.12
								1.Age	**−0.21**	**0.06**	**0.001**
	B	6	228.65	0	0.20	1,2,3	0.28	**2.Bell (Yes)**	**1.30**	**0.38**	**<0.001**
							0.18	3.Constant access to wet food (Yes)	−0.80	0.52	0.13
	C*	6	229.53	0.88	0.13	1,2,5	0.18	4. 95 KDE	0.02	0.04	0.51
	D*	7	229.68	1.03	0.12	1,2,3,5	0.16	5. Amount of natural habitat within 300 *m*	0.02	0.02	0.25
	E*	7	230.59	1.94	0.08	1,2,3,4	0.10				

*= Non-significant intercept

Table 5
Jacobs' index (D) results from the mean proportion of habitat type within 300 m of the house and mean proportion of overlap with habitat type within the 95% KDEs for cats that were tracked when they returned prey and did not return prey (N = 27). The 95% confidence intervals (CI) for prey returns and not at each location are included and numbers in bold denote significance of 0.05.

Location	Habitat type	D for prey not returned	D for prey returned
Boundary	Built-up	0.02	**−0.35**
	Gardens	−0.25	0.29
	Natural	0.33	0.26
	95% CI	−0.29 – 0.36	−0.34 – 0.48
Non-boundary	Built-up	0.48	−0.16
	Gardens	**−0.69**	0.07
	Natural	0.48	0.42
	95% CI	−0.67 – 0.85	−0.22 – 0.44

$cat^{-1}year^{-1}$. The mean for boundary cats was 7.91 (S.E ± 2.70) and 3.35 (S.E. ± 1.06) for non-boundary cats. Prey numbers were then extrapolated taking estimated return rates, resulting in an overall estimate 22.60 (17.12–28.07) prey cat^{-1} $year^{-1}$, for boundary 34.40 (22.66–46.15) and non-boundary residents 14.57 (9.95–19.18) $cat^{-1}year^{-1}$respectively.

4. Discussion

We examined how living next to natural areas affects the home-range size, habitat use and predation rate of pet domestic cats. Cats resident adjacent to natural areas incorporated these areas into their home ranges, which in turn were larger in area than those of cats resident in suburban areas. While there was no difference between boundary and non-boundary cats in the return rate for birds, cats living on urban boundaries killed significantly more mammals. Where the cats lived affected prey identity, with rabbits and field voles returned only by boundary cats, and blackbirds only returned by non-boundary cats. Young cats, and those with increased available natural habitat, killed more mammals, and unexpectedly, bell wearing was associated with increased overall predation.

4.1. Home range and habitat used

Our estimates of home ranges for non-boundary cats are similar to previous estimates from the large nearby conurbation of Reading (Hanmer, Thomas, & Fellowes, 2017; Thomas, Baker, & Fellowes, 2014). In contrast, the mean home range (95% KDE) of our boundary study cats was ~ 70% larger than that of our non-boundary cats (3.42 ha vs 2.01 ha). In addition, greater variation in range size was seen among boundary cats (boundary cats min–max: 1.14–27.06 ha; non-boundary cats: 0.75–6.23 ha). Critically, the mean furthest point from home that cats moved did not differ between non-boundary (669.9 m; individual maximum 1294 m) and boundary (649.9 m; individual maximum 1502 m) cats, suggesting that cats were equally *capable* of movement, but that their *likelihood* of movement differed. The influence of sex, with males having larger ranges, supports some studies (Kays et al., 2020) but not others (Thomas et al., 2014). While cat age was present in the home range model it was not significant, which mirrors Hanmer, Thomas, & Fellowes, 2017; but *c.f.* Hall et al., 2016).

4.2. Prey returned

Our mean cat prey returns (5.20 prey (±S.E 1.18) $cat^{-1}year^{-1}$), was similar to other UK studies (Baker et al., 2005; Thomas et al., 2012), but this masks considerable variation between our non-boundary (3.35 prey $cat^{-1}year^{-1}$) and boundary (7.91 prey $cat^{-1}year^{-1}$) cats and suggests that if we are to estimate the total prey killed per year by domestic cats, then cat location must be taken into consideration. Returns from this UK study were lower than studies in other countries, with 8.89 prey returned cat^{-1} $year^{-1}$ in Poland (Krauze-Gryz et al., 2017) and 13.4 and 21.6 prey returned cat^{-1} $year^{-1}$ in New Zealand (van Heezik et al., 2010; Gillies & Clout, 2003 respectively) which is not only likely to be a reflection of prey abundance (all) and naivety (New Zealand), but also prey type availability. Reptiles (mainly skinks in the New Zealand studies; 0.99 and 1.59 and lizards in Poland; 5.04, Krauze-Gryz et al., 2017) and invertebrates (2.40 and 9.84; New Zealand, van Heezik et al., 2010; Gillies & Clout, 2003 respectively) were returned in larger quantities per cat compared to the 0.18 reptiles and 0.09 invertebrates per cat in our study. The greater prey returns in spring and summer supports findings by Thomas et al. (2012), but differs in timing between taxa (mammals in spring, birds in summer). In Poland, a mammal peak was seen in autumn (Krauze-Gryz et al., 2017) and in New Zealand and Poland a bird peak was seen in spring (van Heezik et al., 2010; Krauze-Gryz et al., 2017) . These patterns are again likely to be a reflection of local availability of prey.

The decrease in rates of prey return associated with increasing cat age does support other studies (Barret 1998; van Heezik et al., 2010). Counterintuitively, returns were found to increase with bell wearing even though other studies have found them to be effective in reducing hunting success (Gordon et al., 2010; Ruxton, Thomas, & Wright, 2002). However, we speculate that bells were placed on cats that were already known to return high numbers of prey as we found a significant correlation with prey returns and owner perception of their predatory behaviour.

4.3. Home range and habitat selection by cats returning prey.

The lack of difference between boundary and non-boundary cats in bird prey returns, contrasts with mammal returns. This may reflect differences in prey availability, where birds are more abundant and/or more accessible in the habitat matrix provided by urban domestic gardens, and bird populations are supported by supplementary feeding (Orros & Fellowes, 2015) and provision of nest sites (Hanmer, Thomas, Beswick, Collins, & Fellowes, 2017). In New Zealand, van Heezik et al. (2010) had greater bird returns compared to mammals (37% and 34% respectively), with cats showing a preference for gardens over natural forest and scrub. In contrast, small mammal populations and diversity are greater in natural habitats such as rough grassland or heathland, than in urban domestic gardens. This hypothesis is supported by the range of prey species returned by boundary cats. Other studies from New Zealand (Gillies & Clout, 2003; Morgan et al., 2009), found that cats that not only had access to natural habitats but used them (reported by Morgan et al., 2009, but not monitored by Gillies & Clout, 2003), had significantly higher numbers of mammals returned. Therefore, prey availability associated with differences in the habitats our study cats hunted in is likely to be the ultimate explanation for why we see this difference.

It is not only direct predation which matters; the presence of a cat can have indirect implications on wildlife through sub-lethal fear effects. For instance, disturbance and predator avoidance can decrease breeding success and fitness due to adults being flushed from nests, leaving nests exposed to predators (Bonnington, Gaston, & Evans, 2013; Langston, Liley, Murison, Woodfield, & Clarke, 2007). Predator presence may cause the avoidance of suitable habitat (Cresswell, 1994) or produce an increase in vigilance consequently reducing foraging rates (MacLeod, Lind, Clark, & Cresswell, 2007). While such effects are likely to be a constant presence in domestic gardens, introducing cats to natural habitats through increased urbanisation may have additive negative effects on bird populations.

4.4. Predation rates

If we are to understand the effect of cat predation on wildlife populations, then we must consider the cumulative predation rate of cats, rather than the behaviour of individuals. While the estimated prey return (23%) and non-return rates (77%; Loyd et al., 2013) may vary with location, it is evident that if the cats and habitats in our study system are a reasonable reflection of what is found elsewhere in the country, then the annual predation rate of the 9.5 M domestic cats in Britain is likely to be substantial. As new residential developments are built on the edges of towns adjacent to areas of conservation value, it is likely that predation will increase as homeowners are often also owners of pet cats. Indeed, in 2018 the UK government suggested that 164,000 new households will be formed on average each year until 2028, a total number almost half as large as currently found in Greater London (Office for National Statistics, 2020). While some of these new homes will be built on brownfield sites, many will be on the edges of current conurbations. Separating housing built on the edges of towns and cities from areas of biodiversity value may well be effective for reducing predation. This in itself is not enough, as other approaches are also required, but data are limited on alternative habitat management approaches.

4.5. Conclusion and management

Here we show cats use natural areas when available, and cats with access to such habitats have larger home ranges and kill more prey. A simple extrapolation based on the predation rates found in this study suggests that the 9.5 M pet cats in Great Britain (Murray et al., 2015), may kill in the region of 160–270 million prey individuals per year. However, without a large scale, multi-site study, gaining a more precise understanding of national predation rates (and the possible consequences for prey populations) is challenging. Certainly, we find that location differentially affects predation, with cats on urban fringes posing a greater threat to small mammals, but there was no effect of location on rates of bird predation. Nevertheless, cat presence in conservation areas could have implications for conservation due to the potential for direct effects of predation and indirect effects of disturbance, particularly on more vulnerable species. Therefore, restricting cat access to such areas especially where sensitive wildlife is found should be considered.

A buffer zone > 300 m around natural areas (328 m, Thomas et al., 2014; 360 m, Lilith, Calver, & Garkaklis, 2008), outdoor cat enclosures (catios) and cat curfews have been suggested as management options, with the latter implemented by some Australian councils (Council, 2019). Although catios appear to be gaining popularity and confining cats or restricting access would help to reduce predation while benefiting cat welfare (Grayson & Calver, 2004), their introduction in the UK would be met with strong opposition due to the restricting of roaming behaviour being perceived as cruel (McDonald, Maclean, Evans, & Hodgson, 2015). In practical policy terms, assessing the possibility of a suitable buffer zone around developments (Metsers et al., 2010), combined with consideration of natural or artificial barriers that deter cats from entering conservation areas, may mitigate the potential indirect and direct negative effects increasing numbers of cats will have on wildlife living on our urban fringes.

Domestic cats bring great joy and companionship to their owners, with benefits for mental health and well-being (Endo et al., 2020, but see Islam & Towell, 2013). But they also cause the loss of tens of millions of animals each year through predation, which in some cases may go beyond animal welfare concerns and become conservation concerns. It is only by understanding the possible negative ecological effects pet cats may be exerting on their local biodiversity that we can begin to develop appropriate approaches to environmentally-sensitive cat ownership.

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Appendix 1. Site characteristics: Population, house numbers and area size for each ward within study site (ha; UK census data 2011), Site category; SPA (Thames basin heaths special protection area; Joint Nature Conservation Committee, 2005), SSSI (Site of special scientific interest; Defra 2019), species (Joint Nature Conservation Committee, 2005; Sussex Wildlife Trust, 2012).

Site N°	Site name	Ward	Coordinate	Category	Species	Pop.	House	Area ha
1	Reading	Loddon Coronation	51.447048 N, −0.886516 E	No		9,006 5,654	3,542 2,176	295 193
2	Tadley	Central South	51.346483 N, −1.128900 E	SPA / SSSI	Nightjar/ Occasionally Dartford Warbler	5,889 2,713	2,482 2,713	514 63
3	Crowthorne		51.377354 N, −0.790578 E	SPA / SSSI In vicinity	Nightjar/ Dartford Warbler	5,253	2,095	1,194
4	Bracknell	Crown wood and Harmans water E00081987 E00081988 Great Hollands Hanworth	51.398589 N, −0.725302 E	SPA / SSSI	Nightjar/ Dartford Warbler	7,736 337 249 5,721 8,059	3,381 124 113 2,188 3,476	138 6 4 307 173
5	Sandhurst	Owlsmoor College Town	51.352817 N, −0.772579 E	SPA / SSSI	Nightjar/ Dartford Warbler	5,116 6,300	1,997 2,055	394 406
6	Mortimer		51.377002 N, −1.077309 E	No		5,732	2,326	3,626
7	Burghfield		51.396893 N, −1.054893 E	No		5,955	2,272	1,711
8	Hook		51.284260 N, −0.972681 E	No		8,334	3,214	1,765
9	Farnborough	Blackwater and Hawley Westheath, Mayfield, Fernhill	51.309886 N, −0.780692 E	SPA / SSSI	Nightjar/ Dartford Warbler	4,473 5,547 6,635 5,598	1,833 2,182 2,344 2,121	1,165 119 94 141

Appendix 2. General characteristics of 79 cat participants.

Category	Yes	No	Total
Sex (male)	51	28	79
Neutered	78	1	79
Normally wore a collar	41	38	79
Normally wore a bell	27	52	79
Generally kept in at night	14	65	79
Rescue cat	31	48	79
Moved prior to study	19	60	79
	Min	Max	Mean
Weight	2 kg	8.2 kg	4.8 kg
Age	1yrs	16yrs	6.7yrs

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