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Research article

Urbanisation influences range size of the domestic cat (*Felis catus*): consequences for conservation

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Abstract

Domestic cats (*Felis catus*) are the most abundant predator in many urban ecosystems, and their ranging behaviour will influence predation rates. To investigate how degree of urbanisation affects cat ranging behaviour, we used Global Positioning System trackers to follow 38 cats in 3 (urban, suburban and peri-urban) residential areas in the large town of Reading, UK. Median home range (95% KE) was 1.28 ha, but varied from 0.9 ha in the urban habitat, to 1.56 ha in the suburban habitat and 1.60 ha in the peri-urban region, with a maximum range size of 6.61 ha. The median maximum distance reached from home was 99 m, and again varied with level of urbanisation (urban: 79 m; suburban: 141 m; peri-urban: 148 m; maximum 278 m). For home and core (50% KE) ranges, there were no significant differences with respect to study areas, cat sexes, cats living in the same household or day/night range. A decreased proportion of constructed surfaces (a proxy for urbanisation) was associated with an increase in cat range size. As urban areas grow, many areas containing species of conservation importance are encroached upon by residential zones on urban fringes. To protect these species we suggest that boundary habitats should be managed to reduce rates of cat access to these areas, or that buffer zones of 300–400 m should be formed between housing and areas containing vulnerable species. These management options may help mitigate the ecological consequences of cat predation.

Key words: *Felis catus*, domestic cat, urban ecology, GPS, kernel contour estimates, exclusion zones

Introduction

As opportunistic, generalist predators (Barratt 1997a; Thomas et al. 2012; Loyd et al. 2013), domestic cats (*Felis catus*) are considered to be among the greatest threats to global biodiversity (Nogales et al. 2004; Medina et al. 2011; Loss et al. 2013; Doherty et al. 2016). It is thought that cats introduced to islands have caused the extinction of 63 animal species including 40 birds (Doherty et al. 2016) and domestic cats are the primary threat to over 8% of threatened reptiles, birds and mammals (Medina et al. 2011; Doherty et al. 2016). In many urbanised countries, domestic cats are commonly kept as companion animals, where they are fed and cared for. For example, the UK is home to more than 10 million pet cats (Murray et al. 2010) and >800 000 feral cats, making them the most common mammalian predator, outnumbering all others combined (Harris et al. 1995; Battersby 2005). In the USA and Canada, it is estimated that there are 84 million and 8.5 million owned cats, respectively, a number that may be almost matched by national feral cat populations (Blancher 2013; Loss et al. 2013).

Levels of cat ownership are highest in urban areas, resulting in extremely large local cat populations ($\gg$100 individuals km^{-2}; Baker et al. 2008; Thomas et al. 2012). Predation studies suggest that more than 180 million prey individuals (55 million birds, 119 million mammals) are killed annually by domestic cats in the UK (Thomas et al. 2012). Estimates of annual numbers of prey taken in the USA (>1 billion birds and 6 billion mammals;

Loss et al. 2013) and Canada (100–350 million birds, ~2–7% of all birds in southern Canada; Blancher 2013) implicate cats as one of the most important anthropogenic causes of bird mortality (Loss et al. 2015). In addition, cats need not actively hunt to have a negative effect on wild birds, as their presence alone may further depress wild bird populations (Beckerman et al. 2007; Bonnington et al. 2013). Despite such losses, whether such direct and indirect effects have population-level consequences for their prey is a topic of considerable debate (Baker et al. 2005, 2008; McDonald et al. 2015), but given the enormity of the estimated losses the precautionary principle suggests that we should act to mitigate cat predation (Lilith et al. 2006).

As the world becomes increasingly urbanised (UN 2011), biodiverse areas are increasingly encroached upon by development (McKinney 2002, 2008). Typically, suburban areas grow in the peripheral zones of urban areas, potentially resulting in increased numbers of domestic cats accessing areas of conservation concern (Morgan et al. 2009; McDonald et al. 2015). Town planners and conservation biologists have suggested that one possible mechanism to reduce potential cat predation is to introduce buffer zones around areas of greater conservation value, where either housing development would be prevented or through prohibiting the ownership of domestic cats for people choosing to live within a set distance of the protected area (Lilith et al. 2006, 2008; Metsers et al. 2010; Thomas et al. 2014).

Such buffer zones around protected areas have been proposed to keep cats away (Metsers et al. 2010) particularly for new housing developments (Thomas et al. 2014), although how enforceable such restrictions are is open to question (Hall et al. 2016a). A cat-free buffer zone of 300–400 m between housing developments and areas of higher biodiversity value has been suggested for Australia (Lilith et al. 2008) and the UK (Thomas et al. 2014), but in rural New Zealand a distance as great as 2.4 km has been proposed (Metsers et al. 2010). Such cat exclusion zones could be incorporated into the planning of developments near protected areas but must also be scaled appropriately to the landscape for effective management (Hall et al. 2016b). Night-time curfews are also a potentially useful cat management technique as cats have sometimes been found to range further at night than during the day (Metsers et al. 2010; Thomas et al. 2014). Some prey types, such as small mammals, are more active then (Woods et al. 2003) and make up a significant proportion of domestic cat prey (Thomas et al. 2012).

Monitoring the ranging behaviour of domestic cats using conventional telemetry radio tracking approaches has proved challenging to conduct in some habitats such as urban areas (Schmutz and White 1990) and combined Global Positioning System (GPS) and radio setups can be relatively heavy and expensive (Coughlin and van Heezik 2014). More recently, the development of lightweight, relatively inexpensive GPS trackers for human use such as iGotU GPS tags (Hervías et al. 2014; Coughlin and van Heezik 2014; Thomas et al. 2014; this study) or similar devices (Kitts-Morgan et al. 2015) has changed how cat ranging behaviour is studied. While such cheaper GPS trackers may sacrifice some accuracy and precision compared with specialised GPS trackers from wildlife telemetry suppliers, they make large-scale simultaneous tracking studies feasible (Adams et al. 2013; Coughlin and van Heezik 2014; Forin-Wiart et al. 2015).

The landscapes and countries in which tracking studies have taken place have varied, resulting in a wide range of domestic cat home ranges being calculated (Hall et al. 2016b), in part confounded by the use of differing methods and time scales (e.g. Morgan et al. 2009; Metsers et al. 2010; van Heezik et al. 2010; Wierzbowska et al. 2012; Coughlin and van Heezik 2014; Hervías et al. 2014; Thomas et al. 2014; Kitts-Morgan et al. 2015). Generally, rural cats (Wierzbowska et al. 2012; Kitts-Morgan et al. 2015) appear to range further than urban cats (Morgan et al. 2009; van Heezik et al. 2010; Thomas et al. 2014; Hall et al. 2016b) but studies directly comparing them in the same general geographical area are few in number (Metsers et al. 2010; Thomas et al. 2014) and the applicability of studies from one distinct biogeographic area such as New Zealand (Metsers et al. 2010; van Heezik et al. 2010) to another such as the UK is debatable even without considerations of local landscape structure. In the UK, the only previous published study considered only suburban domestic cats (Thomas et al. 2014), and it is not clear to what extent their findings are relevant to more or less urbanised areas. In particular, while domestic cats living on the edge of farmland, parkland or nature reserves in the urban environment may have the opportunity to extend their ranges into these areas to hunt, it is unclear if such areas are preferred by domestic cats (van Heezik et al. 2010).

If we are to develop appropriate management and planning recommendations then understanding how urbanisation level affects cat roaming behaviour is critical. Here, we address this using GPS tracking of free-ranging domestic cats in a large UK town, asking if the range size of cats was affected by level of urbanisation, habitat availability, cat sex and wearing a collar. In addition, we also explored if there were any differences between day and night ranging, and if the ranging behaviour of cats living in the same household differed since many domestic cats live in multi-cat households, and this may have implications for approaches to management.

Methods

Study areas

The study took place in and around Greater Reading (Fig. 1), south east UK (51°27'N, 0°58'W) during May 2016. The area is ~40 km west of London and has an overall population of around 230 000 people (Office for National Statistics 2013). Three sites were chosen to represent typical areas of housing present in the UK in terms of households/ha and build cover (all constructed impervious surfaces); core urban terraced housing with small gardens and little nearby green space (the inner town district of Katesgrove, ~27.8 households/ha, build cover >50%) surrounded entirely by similar housing and within 400 m of the town centre; suburban, primarily detached and semi-detached housing with generally large gardens, some of which are adjacent to an urban local nature reserve (Maiden Erlegh, in the district of Earley, ~10.7 households/ha, build cover 30–50%) surrounded entirely by similar housing; and a peri-urban area (Shinfield village south of Reading, ~7.3 households/ha) similar to the suburban area in terms of housing type and build cover within the settlement, but with open farmland and natural habitats within 200 m of the majority of the housing including the homes of all recruited cats. The households per hectare information is for the entire settlement area (Office for National Statistics 2013) and build cover derived from the Ordnance Survey Mastermap collection (EDINA, University of Edinburgh).

Cat recruitment

Recruitment was carried out primarily through leaflets posted through letter boxes, and door-knocking was carried out when necessary. Volunteers were asked to encourage friends and

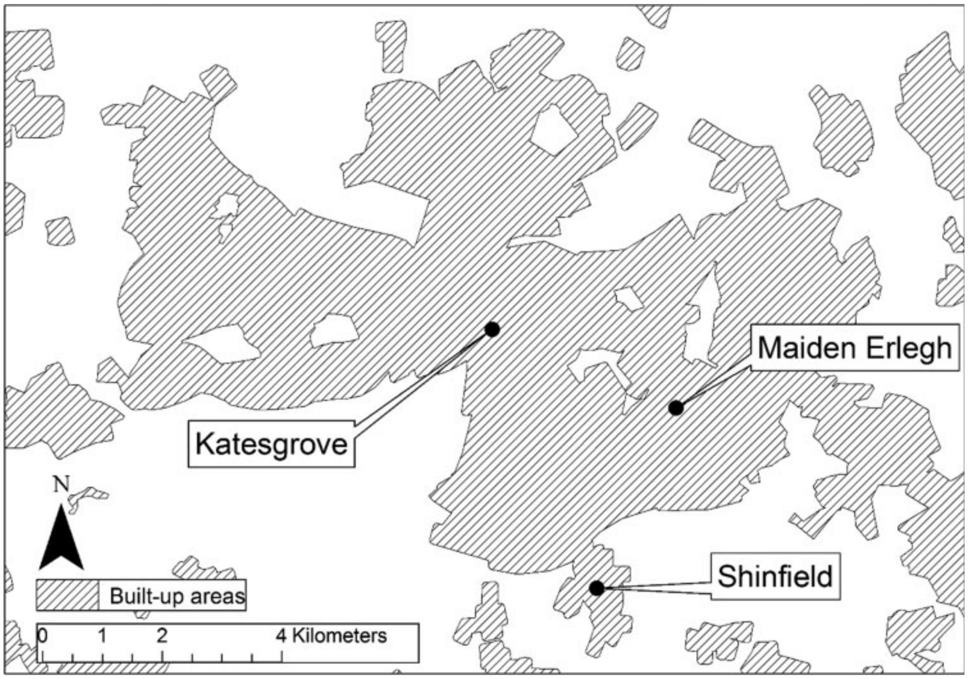

Figure 1: The three study sites within the general Greater Reading area, UK; the non-built up area consists primarily of mixed agricultural land and small scattered woodlands.

neighbours to take part. The study was approved by the School of Biological Sciences ethical review panel.

Just over half of the successfully tracked cats (53%) came from households with more than one cat participating in the study, which may violate the assumption of spatial independence due to cats ranging in identical habitat (Millspaugh et al. 1998). However, cats are independent animals and those residing in homes with two or more other cats live in a socially complex society where access to resources and behaviour vary (Crowell-Davis et al. 2004).

All cats were at least 1-year-old (fully grown) and in good health. The following information was recorded for each cat: age (to the nearest year with estimates for several former rescue cats), neutered status, sex, weight (on last veterinary visit if not more recently) and whether they had previously worn a collar on a regular basis prior to the study. Owners were asked to monitor the health of their cats throughout the study and record any prey items brought home during the tracking period. All cats generally had unrestricted access to the outdoors and were fed daily by their owners.

All cats not already usually wearing collars (29 of the 49 cats recruited) were provided with standard collars (Ancol Safety Buckle Cat Collar, Ancol, UK) ~2 weeks beforehand to attempt to get cats accustomed to them and to reduce the probability of tracker loss or rejection during the actual tracking period.

The GPS units

The GPS units were iGotU GT-120 USB GPS Travel Loggers ($4.4 \times 2.7 \times 1.3$ cm; Mobile Action Technology, Taiwan), set to acquire a fix once every 15 min, which theoretically enabled 10 days of recording battery life. The weight of the GPS unit including its gel cover was 26 g. Volunteers were provided with standard quick release collars weighing 7.2 g to attach them to, though a number of volunteers/cats preferred to use their current collars weighing up to 10 g. For standardisation provided collars were not fitted with bells. GPS fixes from the first hour of tracking were removed to allow time for the cats to get used to the trackers. The tracking period was intended to last approximately 7 days, effectively simultaneously across all cats though due to tracker losses and owner commitments two cats started and finished early and three cats started and finished late, while another ran for 9 days due to the unit being accidently left on the cat.

The collars with the GPS units were not counter-weighted for simplicity and to increase recruitment and reduce rejection by cats. This is likely to have increased the number of erroneous and missing GPS fixes (Coughlin and van Heezik 2014). Prior to analysis, the data were conservatively filtered to remove incorrect fixes on the basis of unrealistic distance/speed travelled. The number of filtered apparently erroneous fixes was used as a measure of logging errors in the analysis.

Trackers lost in the first half of the study period were replaced on the first loss instance within eight hours of it being reported by the owners. Several lost trackers were found and returned by members of the public allowing the data to be retrieved. The GPS tracks from these returned trackers were either added to the tracks taken by replacements if lost in the first half of the study period or treated as a full track if retrieved with more than 100 fixes spanning more than three full days of tracking (after filtering).

Accuracy and precision of GPS fixes can be influenced by the habitat the cat is in. Signal strength is reduced under dense foliage (D'Eon 2003) and within buildings so cat use of these areas is likely to be under-estimated (Coughlin and van Heezik 2014). The proximity to buildings can also influence GPS satellite signal acquisition and location precision is affected by the position and number of satellites available (van Heezik et al. 2010). Past studies using these same devices utilised in this study have found positional errors in the order of 10.03 m when placed upright with direct line of sight to the satellites, increasing to 29.96 m when placed under a mature tree with an open canopy

(Coughlin and van Heezik 2014). Such errors are likely to be increased in more highly urbanised areas or within thick vegetation due to interference with the GPS signal and therefore should be treated as a minimum possible error (Coughlin and van Heezik 2014).

Data analysis

Home range size

All home range estimation analysis was carried out in program R (R Core Team 2017) using the 'adehabitatHR' package (Calenge 2016; version 0.4.14). We used 95% kernel contour estimates (isopleth) to calculate cat home ranges and 50% kernel contour estimates to calculate cat core ranges (referred to as home range and core range respectively in this paper). To allow for direct comparisons between this study and older studies we have also included 95% minimum convex polygon (MCP) home range estimations using the default settings within package 'adehabitatHR'. In addition, each fix was classified as being during the day or night, calculated using local daily sunrise and sunset times. These were then split and used to calculate overall 95 and 50% kernel density estimates to examine any differences between night and day ranging.

Proportional range overlaps of cats living in the same household were calculated by estimating the proportion of animal i's home range that is overlapped by animal j's home range to create a median overlap value with interquartile ranges (Calenge 2016; Katajisto and Moilanen 2006; Walter and Fischer 2017). Polygons of the kernel estimate home and core ranges were then projected into ArcGIS 10 (ESRI 2011) via the R 'maptools' package (Bivand and Lewin-Koh 2016; version 0.8-39) on to Ordnance Survey Mastermap collection (EDINA, University of Edinburgh) land use data to determine habitat usage. Each projected kernel polygon was cut from the Mastermap layer, and the resulting areas for each habitat category extracted for each range. Fifteen habitat/land use categories occurred within cat ranges which were combined to form three broad categories: all constructed surfaces (buildings, roads etc.), natural surfaces (grassland, trees and scrub) and private gardens (mixed surfaces). Of these, constructed surfaces was included in further analyses as a measure of the level of urbanisation as it was present in all cat ranges, unlike natural surfaces which were not present in some urban areas. Incremental analyses using isopleth range increments of five in chronologically ordered location data were used to determine whether all home ranges (95% KDE) were fully revealed within the study timeframe. A cat range was considered to be fully revealed if the 90% KDE isopleth was within 10% of their total estimated home (95% KDE) range size (i.e. approaching the asymptote) (Harris et al. 1990; Barg et al. 2004; Plotz et al. 2016).

Maximum distance travelled from home was measured from the cat owner's home to the furthest point in their 95% Kernel home range estimates and recorded to the nearest metre. A recommended exclusion zone was calculated for each site by taking the cat with the maximum recorded distance from home in each site and incorporating a 20% increase as a safety margin for protecting wildlife sites and to allow a margin of error when ranges were not fully revealed (following Lilith et al. 2008). Habitat selection was evaluated for all cats and specifically for cats living adjacent to green spaces and natural habitat fragments (within 50 m) using selection ratios (Manly et al. 2002): both habitat use (based on location fixes) and availability were measured within 100% MCPs to better account for the available habitat in the local area.

Statistical analyses

As the data were not normally distributed, Kruskal–Wallis tests were used to compare across all three sites together, while unpaired Wilcoxon tests were used to compare between individual sites for logging errors (in the form of number of apparently erroneous fixes filtered from the data as detailed above), ranges (home and core) and maximum distance from home. To allow for potential Type II error from multiple comparisons P was adjusted for the false discovery rate where appropriate (Benjamini and Hochberg 1995). Day and night effects on home and core range area were analysed using separate paired sample Wilcoxon tests to first test for differences in the recorded ranges directly and then compare the proportional difference in range size when accounting for day length. Sex effects were analysed using unpaired Wilcoxon tests. The size and proportion of overlap in ranges for cats within the same household were compared using paired sample T-test or Wilcoxon tests as appropriate to their distribution.

To normalise data for linear mixed-effects model analysis, kernel home and core range estimates along with maximum distance from home were log transformed prior to analysis, with individual cat identity as a random factor to account for individual variation. We used R with the 'nlme' package (Pinheiro et al. 2016; version 3.1-127) to separately evaluate effectors on these three different measures of cat roaming. Factors considered in the range size models were: proportion of constructed surfaces (as a measure of the level of urbanisation) within the appropriate kernel estimate, cat age (rounded to the nearest year), cat sex and whether the cat usually wore a collar prior to the study. Cat age, sex and whether they usually wore a collar has been found to be associated with cat ranging behaviour in past studies and hence were included here (Coughlin and van Heezik 2014; Hall et al. 2016b). The same factors were used in models investigating effectors of the maximum distance reached from home. Model selection was carried out using an information theory approach based on the models' associated AICc values and model weights (Burnham and Anderson 2002). We chose a set of candidate models on the basis of a ΔAICc of 2. As multiple models were found within 2 ΔAICc of all AICc selected models, model averaging was used to produce a conditional average model with adjusted standard errors in the R package MuMin (version 1.15.6; Barton 2016). For these average models, the relative importance of each term (including interactions) was automatically calculated as a sum of the Akaike weights over all of the models in which the term appears (Barton 2016). Study site was not included in any of these models due to its high correlation with the proportion of constructed surfaces used as a measure of urbanisation.

Results

Tracking

Of the 49 cats originally recruited for the study, 2 were withdrawn due to unrelated health concerns and 4 were too uncooperative to fit with collars. Of the remaining 43 cats, 9 lost trackers at some point during the study but 6 of those were retrieved or replaced. Overall 5 cats produced fewer than 100 fixes in total due to tracker loses or malfunctions and were excluded from the analyses as incremental analysis showed they were poorly revealed compared with cats with longer tracks. This left 38 individual cats (14 females and 24 males; all neutered) ranging in weight from 2.0 to 7.5 kg (mean = 4.9 kg, median = 4.8 kg), varying in age from 1 to 15 years (mean = 6.6 years, median = 7)

Table 1: Mean and median home and core range (ha) for cats across three levels of urbanisation along with maximum straight-line distance from home (m) and sample sizes

Area	Mean home range area ± SE *Median* (min–max) 95% KE	 95% MCP	Mean 50% KE (core area) ± SE *Median* (min–max)	Mean maximum distance ranged ± SE *Median* (min–max)	Number of cats (female, male)
Urban	1.05±0.13 *0.90* (0.32–1.92)	0.75±0.10 *0.62* (0.22–1.42)	0.18±0.03 *0.15* (0.05–0.36)	85±5 *79* (58–122)	14 (6, 8)
Suburban	1.79±0.24 *1.56* (0.73–3.90)	1.31±0.17 *1.16* (0.51–2.67)	0.25±0.04 *0.18* (0.07–0.58)	127±8 *141* (81–170)	15 (4, 11)
Peri-urban	2.41±0.73 *1.60* (0.40–6.61)	1.63±0.42 *1.32* (0.27–3.96)	0.28±0.09 *0.17* (0.06–0.75)	153±27 *148* (62–278)	9 (4, 5)
Overall	1.66±0.21 *1.28* (0.32–6.61)	1.18±0.13 *0.95* (0.22–3.96)	0.23±0.03 *0.17* (0.05–0.75)	118±8 *99* (58–278)	38 (14, 24)

Areas determined by kernel density (KE) and minimum convex polygon (MCP) estimation.

and 19 had worn a collar prior to the study. There was some variation in the number of valid GPS points (median = 230, range = 143–527). The median tracking period was 7.1 days (mean = 6.8, SE = 0.2, range = 3.3–9.4). Owners reported four cats bringing back five individual prey items during the tracking period: three mice (*Mus*/*Apodemus* spp.), one rat (*Rattus norvegicus*) and one robin (*Erithacus rubecula*). This suggests the GPS trackers did not restrict normal predatory behaviour.

Logging errors

There were no significant differences in numbers of unfiltered, filtered or numbers of GPS fixes between study areas. However, there was a significant difference in the number of erroneous GPS fixes filtered from the data ($H = 16.9$, $P < 0.001$) among study areas. Significantly more GPS fixes were removed from the urban area (median = 23.5) compared to the suburban and peri-urban areas (median = 8.0, $W = 12$, $P < 0.001$ and median = 6.0, $W = 20.5$, $P = 0.012$ respectively) whereas there was no significant difference between the suburban and peri-urban areas ($W = 53$, $P = 0.4$).

Ranging characteristics

The median 95% kernel density estimate for home range size was 1.28 ha (mean = 1.66 ha, median 95% MCP = 0.95 ha; Table 1). The median core range estimate (50% kernel density estimate) was 0.17 ha (mean = 0.23 ha). Repeated incremental analysis utilising 90% KDE as the maximum home range showed fully revealed ranges, but at 95% KDE this was not so, suggesting that ranges were not fully revealed due to the influence of extreme locations on the range size estimates (Supplementary Fig. S1). Therefore we consider that there is no habitat bias in our study, and that our range size estimates should be considered to be conservative.

Home range size was only borderline significantly different between study sites overall ($H = 5.604$, $P = 0.061$) and pairwise comparisons found a borderline significant difference between the urban and suburban site ($W = 159$, $P = 0.054$, corrected for the false discovery rate) but not in other comparisons between sites. There was no significant difference between core range sizes, either overall or between individual sites ($P > 0.1$). The maximum estimated distance ranged was 278.0 m (with a high degree of variation between individual cats; Table 1). Cats in the peri-urban area ranged the furthest on average, and also showed the greatest degree of variation in maximum distance travelled, followed by cats dwelling in the suburban, then the urban area (Table 1). Overall there was a significant degree of variation across the different sites ($H = 10.7$, $P = 0.005$) and in individual comparisons between sites there was a significant difference between both the suburban and peri-urban (borderline) sites with the urban site but not with each other ($W = 182$, $P = 0.003$ and $P = 0.053$, respectively, corrected for the false discovery rate). Recommended exclusion zones based on maximum distance from home were 146 m for the urban area, 204 m for the suburban area and 334 m for the peri-urban area.

While male cats showed greater variation in their ranging areas and higher median range sizes than females, there was no overall significant difference between the sexes in home range ($W = 209$, $P = 0.224$), core range size ($W = 220$, $P = 0.12$; Fig. 2), or maximum distance ranged ($W = 187$, $P = 0.586$). The wearing of a collar did not affect home range ($W = 134$, $P = 0.181$) or maximum distance ranged ($W = 137$, $P = 0.204$), but there was a significant difference at the core range level ($W = 113$, $P = 0.05$; Fig. 3) with collarless cats having a larger core range size. There was no significant difference between the age ranges of male and female cats in the study ($P > 0.1$).

Samples were limited due to loses/insufficient data being generated by some cats among multiple cat households but no significant difference was found between the size of cat home or core ranges within households ($t = 0.468$, $P = 0.652$ and $W = 34$, $P = 0.192$, respectively, $n = 15$ cats, 7 households). The median proportional range overlap between cats living in the same household was 0.824 for home ranges (IQR = 0.460–0.861) and 0.821 for core ranges (IQR = 0.500–0.977) indicating that ranges overlapped considerably both around their homes and further afield.

Habitat selection

For cats living adjacent to large greenspaces and natural habitat fragments ($n = 11$) standardised average habitat selection ratios were 0.553 for garden habitat, 0.311 for anthropogenic surfaces and

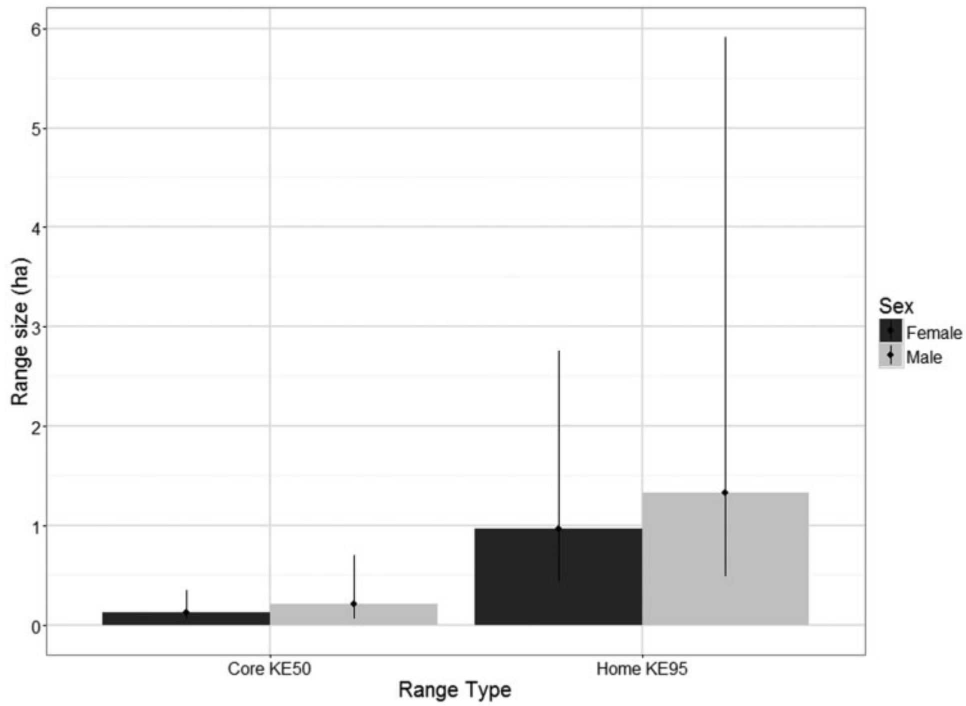

Figure 2: Median (±IQR) core 50% kernel contour estimates (KE50) and home 95% kernel contour estimates (KE95) domestic cat range sizes grouped by sex.

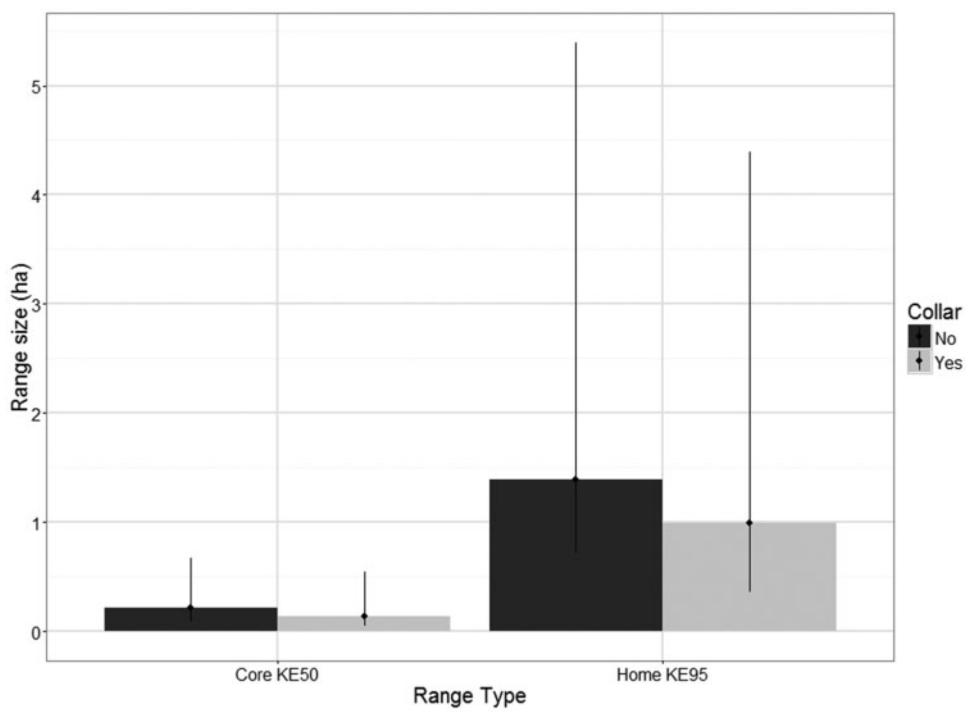

Figure 3: Median (±IQR) core 50% kernel contour estimates (KE50) and home 95% kernel contour estimates (KE95) range sizes grouped by whether a domestic cat normally wore a collar.

0.136 for natural habitat. Cats further away from these large greenspaces and natural habitat fragments ($n = 27$) had standardised average habitat selection ratios of 0.599 for garden habitat, 0.345 for anthropogenic surfaces and 0.056 for natural habitat. Despite these differences and their proximity to more natural habitat border cats still showed a clear selection preference for garden habitat.

Daytime/night time roaming

There was no difference between cat ranging during the day and night for home and core ranges ($P > 0.1$ for both, Table 2). Incremental analysis suggested that day and night home ranges had not been fully revealed.

Table 2: Mean and median day and night home and core ranges (ha) for cats across three levels of urbanisation determined by kernel density estimation (KE)

Area	Mean 95% KE home range area ± SE *Median* (min–max)		Mean 50% KE core area ± SE *Median* (min–max)	
	Day	Night	Day	Night
Urban	1.00±0.13 *0.82* (0.32–1.85)	1.10±0.15 *0.98* (0.32–2.58)	0.11±0.02 *0.06* (0.03–0.27)	0.09±0.01 *0.10* (0.03–0.16)
Suburban	1.65±0.20 *1.30* (0.63–2.98)	1.76±0.29 *1.29* (0.64–3.93)	0.16±0.04 *0.11* (0.04–0.61)	0.16±0.04 *0.10* (0.03–0.48)
Peri-urban	1.84±0.51 *1.02* (0.38–4.48)	3.11±1.12 *2.50* (0.46–10.64)	0.16±0.06 *0.07* (0.03–0.56)	0.12±0.03 *0.08* (0.03–0.29)
Overall	1.46±0.13 *1.12* (0.32–4.48)	1.84±0.31 *1.14* (0.32–10.64)	0.12±0.02 *0.09* (0.03–0.61)	0.12±0.02 *0.10* (0.03–0.48)

Factors influencing cat ranging

In the average model for the home range size the proportion of constructed habitat was found to be of high relative importance and significantly negatively associated with territory size ($P < 0.001$, relative importance = 1; Table 3). Males and cats that did not normally wear collars were associated with increased ranging but both were of low relative importance and non-significant in the average model ($P > 0.1$, relative importance < 0.5; Table 3).

The same predictors featured in cat core range AICc selected model. Proportion of constructed habitat and wearing a collar normally were both borderline negatively significant predictors in the average model ($P = 0.053$, relative importance = 0.85 and $P = 0.057$, relative importance = 0.71, respectively; Table 3). Males ranged further but sex was of low importance ($P > 0.1$, relative importance = 0.34; Table 3).

For the maximum distance reached from home the proportion of constructed habitat was significantly negatively associated with territory size ($P < 0.001$, relative importance = 1; Table 3). Not normally wearing a collar was again associated with increase ranging but was of low significance and importance ($P > 0.1$, relative importance = 0.4; Table 3).

Discussion

We find strong evidence for an effect of urbanisation on cat roaming behaviour. Cats residing in areas with a smaller proportion of constructed surfaces (buildings, artificial surfaces etc., i.e. less urban) ranged further than those in more urbanised habitats. Although some of the home ranges produced in this study are smaller than those reported in previous studies, which have generally taken place in entirely separate biogeographical areas, they are still broadly comparable. Here we provide one of the largest cat tracking samples to date and one of the few across different levels of urbanisation within the same local landscape. Unlike some previous studies we found that although males ranged further sex was not a significant predictor of range size and there was no significant difference between day and night ranging. We also found indications that cats that wore collars typically had smaller range sizes. Overall, our results suggest a buffer zone of ~335 m between peri-urban housing and areas of conservation concern would be appropriate. This finding may also help urban planners and conservation biologists consider the possible local effect of cat predation at different levels of urbanisation. In suburban areas, similar ‘effect’ zones would be ~200 m and in urban areas ~145 m in radius.

Cat ranges in the peri-urban area were particularly variable, although this sample had the fewest cats. Some of the peri-urban cats came from similar habitats to those found in the suburban areas (large gardens and semidetached/detached housing), whereas others lived on or close to the edge of the housing areas bordering on farmland habitats. Among the latter were the cats with the largest ranges, and they therefore, may represent the greatest risk to wildlife though some research suggests this may not always be the case (Metsers et al. 2010). In turn, cats in more rural landscapes are likely to range significantly further than those tested in this study (Metsers et al. 2010; Wierzbowska et al. 2012; Kitts-Morgan et al. 2015; Hall et al. 2016b). Given the potential biogeographical differences between such areas as New Zealand and North America compared with the UK, further comparable tracking studies to the present study would be necessary to determine the effect of further reduced urbanisation and its significance to inform additional management recommendations applicable to the UK. For example, comparing ranging behaviour of UK cats to that of cats in other countries where large predators may be present in the same habitat such as coyotes (*Canis latrans*) in North America (Gehrt et al. 2013) and dingoes (*Canis dingo*) in Australia (Johnson et al. 2007; Allen et al. 2013) may be inappropriate as domestic cat behaviour may be influenced by their presence (Ritchie and Johnson 2009). Likewise, the different prey (Barratt 1997a; Lilith et al. 2008) and/or habitats (Morgan et al. 2009; Kitts-Morgan et al. 2015; Wood et al. 2016) may also influence cat ranging behaviour both within and between general biogeographical areas. However, the dominant habitat selection of cats living on the edge of green spaces was still for garden habitat, indicating that they did not necessarily exploit these areas in relation to their availability despite bordering them (Kays and DeWan 2004; Metsers et al. 2010). This further reinforces the importance of understanding variation in ranging behaviour among individual cats (Dickman and Newsome 2015).

Table 3: Set of candidate and average models for 95% (home) and 50% (core) KDE home ranges and maximum distance reached from home of domestic cats using linear mixed-model analysis showing all variable contrasts with model weights and Delta AICc values

Dependent variable	Candidate model	Variables	Estimate	SE	P	Delta AICc	Model weight	Relative importance	n models
95% KDE	**Average Model**	**%constructed**	**−2.153**	**0.606**	**< 0.001***		**N/A**	**1.00**	**4**
		Sex	**0.265**	**0.201**	**0.187**			**0.41**	**2**
		Collar	**−0.293**	**0.192**	**0.128**			**0.49**	**2**
	AICc Selected Model	%constructed	−2.187	0.580	< 0.001*	0.00	0.253	N/A	
		Collar	−0.310	0.183	0.099				
	Model 1	%constructed	−2.149	0.593	< 0.001*	0.33	0.215		
	Model 2	%constructed	−2.112	0.584	< 0.001*	0.57	0.190		
		Sex	0.290	0.191	0.139				
	Model 3	%constructed	−2.152	0.577	< 0.001*	1.28	0.133		
		Sex	0.230	0.193	0.2421				
		Collar	−0.261	0.187	0.1710				
50% KDE	**Average Model**	**%constructed**	**−1.136**	**0.587**	**0.053**		**N/A**	**0.85**	**4**
		Sex	**0.301**	**0.231**	**0.057**			**0.34**	**2**
		Collar	**−0.416**	**0.218**	**0.191**			**0.71**	**3**
	AICc Selected Model	%constructed	−1.150	0.560	0.047*	0.00	0.222	N/A	
		Collar	−0.430	0.206	0.044*				
	Model 1	%constructed	−1.112	0.557	0.054	1.22	0.120		
		Sex	0.265	0.218	0.234				
		Collar	−0.375	0.210	0.083				
Maximum distance from home	**Average Model**	**%constructed**	**−1.588**	**0.328**	**< 0.001***		**N/A**	**1.0**	**2**
		Collar	**−0.130**	**0.103**	**0.207**			**0.4**	**1**
	AICc Selected Model	%constructed	−1.581	0.318	< 0.001*	0.00	0.352	N/A	
	Model 1	%constructed	−1.597	0.315	< 0.001*	0.85	0.230		
		Collar	−0.130	0.099	0.200				

'%constructed' refers to the proportion of constructed surfaces within a cat's range, 'Sex' refers to cat sex (female set to intercept) and 'Collar' refers to whether the cat normally wore a collar (no set to intercept). All other models had ΔAICc > 2. Standard errors were adjusted in averaged models. Relative importance indicates the relative importance of the covariate across the models within Δ2 AICc of the AICc selected model, as a sum of the Akaike weights over all of the models in which the term appears and *n* indicates the number of models the covariate featured in.

*indicates significance at the 95% alpha level.

Understanding the range size of domestic cats provides insights into where they are likely to be a threat to wildlife (Hall et al. 2016b). The concept of a buffer zone between housing and areas of conservation value is quite straight-forward (Lilith et al. 2008), but data on range size also allow us to consider the issue of cat ranging in two other ways. First, for reserve and park mangers in more urban areas, habitat and cat access could potentially be managed (e.g. through the use of fencing, or other barriers) in order to keep roaming cats apart from vulnerable species of interest (Kays and DeWan 2004; Metsers et al. 2010). Second, we suggest that cat roaming behaviour extends the ecological footprint of urbanisation out into the surrounding countryside beyond direct changes to habitats and resources (Thompson and Jones 1999; Marzluff 2001; McKinney 2006). Most simplistically, consider a hypothetical town with a periurban periphery comprised of dwellings. The incidence of predation by domestic cats on surrounding wildlife may be considerable (Barratt 1997b; Metsers et al. 2010; Hall et al. 2016b), and is evidently not confined to the urban area *senso strictu*; in a town 40 km^2 in area, cat predation and other indirect negative effects may extend to cover an additional area of ~8 km^2.

It is important to note that incremental analyses suggested that these ranges had not been fully revealed, though 90% KDEs were fully revealed, indicating the effect of extreme location fixes on the home range estimates (Harris et al. 1990). Therefore, the home range estimates presented here should be treated as a conservative estimate. However, they are in keeping with past studies in similar habitats (e.g. Kays and DeWan 2004; van Heezik et al. 2010; Coughlin and van Heezik 2014; Thomas et al. 2014) suggesting that they are still of relevance for comparisons between studies.

A curfew keeping cats inside at night may be considered a more acceptable form of cat management than exclusion zones by owners to reduce their effect on some vulnerable prey populations (Grayson et al. 2002; Lilith et al. 2006) with nocturnally active mammals likely to be the main beneficiary (Woods et al. 2003; Galsworthy et al. 2005; Thomas et al. 2014) rather than birds. In addition to conservation concerns there are clear welfare advantages to keeping cats indoors at night (Lilith et al. 2006; Toukhsati et al. 2012; McDonald et al. 2015). Such advantages include lowering the risk of road traffic accidents, infectious disease transmission and reducing injures from fighting with both other cats and wildlife, which may undermine cat welfare and contribute to cat mortality (Moreau et al. 2003; Rochlitz 2004; Egenvall et al. 2010; Calver et al. 2013).

We found no difference between the ranging behaviours of male and female domestic cats, supporting several broadly comparable studies (Metsers et al. 2010; van Heezik et al. 2010; Coughlin and van Heezik 2014; Thomas et al. 2014), and unlike the meta-analysis carried out by Hall et al. (2016b) which considered 24 separate studies. All study cats were neutered, which reflects typical cat fertility status in the UK where over 91% of domestic cats are believed to be sterilised (Murray et al. 2009; Thomas et al. 2012). Unneutered individuals, particularly males, have been suggested to range further though Hall et al. (2016b) did not find any overall significant influence on domestic cat ranging due to desexing considering data across seven separate studies featuring both neutered and unneutered individuals. Domestic cats generally show reduced territoriality due to the ready availability of supplementary food (Liberg 1984), which combined with neutering may reduce behaviours associated with roaming and territory defence.

Perhaps surprisingly age was not a significant predictor of cat ranging behaviour, in contrast to findings by other authors (Morgan et al. 2009; Hervías et al. 2014; Hall et al. 2016b). However, only three cats in the study were under 2 years old.

Similarly to Coughlin and van Heezik (2014), we found that cats which did not usually wear a collar had borderline significantly larger core ranges than those that did, though there was no difference between home ranges or maximum distance reached from home. In an attempt to counter this known effect (Coughlin and van Heezik 2014) and reduce the number of tracker losses, collars were provided beforehand in an attempt to get cats used to them. This difference is most likely due to cats adjusting differently to the presence of the added weight of the collar even though it made up <2% of their body mass in all cats as recommended in previous studies (e.g. Casper 2009; Coughlin and van Heezik 2014). The effect of wearing collars may disappear if cats wore them for longer. However, this difference in roaming behaviour between cats which normally wear a collar and those which do not may be a result of differences in cat personality (Dickman and Newsome 2015), with bolder individuals that may range more (Barratt 1997b) being less likely to accept collars. Further work is required to elucidate this. Nevertheless, collars with bells have been found to reduce cat predation success (Ruxton et al. 2006; Gordon et al. 2010) so from a conservation and animal welfare perspective it is advisable to fit free ranging cats with belled collars. Some cat owners remain concerned about potential health impacts collars may have on their cats (Harrod et al. 2016) but the risks appear to be minimal compared to the many other hazards present in their environment (Calver et al. 2013).

We found no significant difference between cat ranges for those living in the same house and unsurprisingly in all cases their home ranges overlapped considerably. It is interesting to note that the cats whose home ranges that lay entirely within another cat living in the same house's range were all female within related male ranges, suggesting at least for these households males ranged further than their female kin. Although tracking cats from the same household may violate spatial independence assumptions (Millspaugh et al. 1998) this represents the reality for many domestic cats (Metsers et al. 2010) with many households having multiple cats (Hall et al. 2016a). Due to the distribution of tracked cats and shortcomings of the GPS devices it is difficult to directly look at overlaps between cats in separate households in this study. However, how domestic cats interact in local areas may affect their ranging and predatory habitats and is worthy of future consideration. At higher housing densities cats are more likely to encounter other cats, dogs or other deterrents to widespread roaming. Therefore, housing density can be considered a surrogate for cat density and likely the real cause of changes in cat ranging behaviour with urbanisation (Hall et al. 2016a,b).

Understanding cat behaviour is central to reducing their predation rates, particularly in areas of higher conservation value. Insights into ranging behaviour are a first step towards developing recommendations for the provision of buffer zones, and other means of limiting the consequences of cat predation at a local scale (Hall et al. 2016b). From our study, we find that the level of urbanisation was a significant predictor of cat range size and suggest minimum exclusion zone distances between houses and areas of conservation concern (Lilith et al. 2008; Metsers et al. 2010) could be adjusted to the level of urbanisation in the landscape. The minimum exclusion zone distance for the most urbanised area was less than half the size of the peri-urban area (distances of 146, 204 and 334 m for urban, suburban and peri-urban sites, respectively). The exclusion zone calculated for the peri-urban area is similar to that found by Thomas et al. (2014). Exclusion zones for protected areas within urbanised areas could be tailored to the level of urbanisation in the local landscape. These may be both easier to enforce and increase cat owner collaboration, as cat management for conservation which can be problematic (Thomas et al. 2012; McDonald et al. 2015; Gramza et al. 2016; Hall et al. 2016a). Irrespective of management implications, such data also provide helpful insights into how estimates of the likely assemblages of prey taken by cats are calculated as the habitat will determine the possible prey species exposed to cats.

Cat exclusion zones could be incorporated into planning requirements for new residential developments and possibly into existing ones near protected areas with vulnerable species of conservation concern. In addition, management actions could be taken to restrict cat ranging at night as reduced nocturnal roaming may reduce predation pressure on some vulnerable prey types. However, only exclusion zones could fully reduce both the direct and indirect negative effects of cats on prey populations. Further studies should consider cat use of nature reserves and adjacent areas in the UK at different levels of urbanisation and with different habitats to inform these potential management actions. Furthermore, it is important to consider how cats adjacent to exclusion zones respond to the presence of cat-free areas. If cat density is the driver of range size (Hall et al. 2016b) then creating cat-free areas may encourage them to enter the exclusion zones and potentially range further into the areas they are meant to be excluded from. Therefore, we must err on the side of caution and consider larger exclusion zones than the tracking data may suggest (Lilith et al. 2008). It would be valuable to explore cat behaviour around fenced and unfenced exclusion zones to see not only how cats respond to these zones but also to see how potential prey populations respond. This would not only help confirm the effectiveness of unfenced exclusion zones but also help confirm if cats are an important predation threat in these areas.

Domestic cats occur at exceptionally high densities in the UK, particularly in urban areas. This introduced predator represents a high predation risk to many species living in and around urban areas. Buffer zones where free-ranging cat ownership is limited or night-time cat curfews represent potentially important management tools that could be used to limit their effect on species inhabiting protected areas. In this study, the second GPS tracking study in the UK, and the first to look at cat ranging across different levels of urbanisation within the same geographical area, we find cat ranges are larger in less urbanised habitats. We suggest cat management measures such as buffer zones should be scaled with the level of urbanisation in the local landscape which may increase their effectiveness for protecting wildlife.

Supplementary data

Supplementary data are available at *JUECOL* online.

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References

Adams, A. L., et al. (2013) 'An Evaluation of the Accuracy and Performance of Lightweight GPS Collars in a Suburban Environment', *PLoS One*, **8**: e68496.

Allen, B. L., et al. (2013) 'Dingoes at the Doorstep: Preliminary Data on the Ecology of Dingoes in Urban Areas', *Landscape and Urban Planning*, **119**: 131–5.

Baker, P. J. et al. (2005) 'Impact of Predation by Domestic Cats *Felis catus* in an Urban Area', *Mammal Review*, **35**: 302–12.

——, et al. (2008) 'Cats About Town: Is Predation by Free-Ranging Pet Cats *Felis catus* Likely to Affect Urban Bird Populations?' *IBIS*, **150**: 86–99.

Barg, J. J., et al. (2004) 'Describing Breeding Territories of Migratory Passerines: Suggestions for Sampling, Choice of Estimator, and Delineation of Core Areas', *Journal of Animal Ecology*, **74**: 139–49.

Barratt, D. G. (1997a) 'Predation by House Cats, *Felis catus* (L.), in Canberra, Australia. I. Prey Composition and Preference', *Wildlife Research*, **24**: 263–77.

—— (1997b) 'Home Range Size, Habitat Utilisation and Movement Patterns of Suburban and Farm Cats *Felis catus*', *Ecography*, **20**: 271–80.

Barton, K. (2016) MuMIn: Multi-Model Inference. R package version 1.15.6.

Battersby, J. (2005) *UK Mammals: Species Status and Population Trends*. Peterborough, UK: JNCC/Tracking Mammals Partnership.

Beckerman, A. P., et al. (2007) 'Urban Bird Declines and the Fear of Cats', *Animal Conservation*, **10**: 320–5.

Benjamini, Y., and Hochberg, Y. (1995) ' Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing', *Journal of the Royal Statistical Society. Series B (Methodological)*, **57**: 289–300.

Bivand, R., and Lewin-Koh, N. (2016) maptools: Tools for Reading and Handling Spatial Objects. R Package Version 0.8-39.

Blancher, P. (2013) 'Estimated Number of Birds Killed by House Cats (*Felis catus*) in Canada', *Avian Conservation and Ecology*, **8**: 20.

Bonnington, C., et al. (2013) 'Fearing the Feline: Domestic Cats Reduce Avian Fecundity Through Trait-Mediated Indirect Effects That Increase Nest Predation by Other Species', *Journal of Applied Ecology*, **50**: 15–24.

Burnham, K. P., and Anderson, D. R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York, USA: Springer.

Calenge, C. (2016) 'The Package Adehabitat for the R software: A Tool for the Analysis of Space and Habitat Use by Animals', *Ecological Modelling*, **197**: 516–9.

Calver, M. C., et al. (2013) 'Assessing the Safety of Collars Used to Attach Predation Deterrent Devices and ID Tags to Pet Cats', *Animal Welfare*, **22**: 95–105.

Casper, R. M. (2009) 'Guidelines for the Instrumentation of Wild Birds and Mammals', *Animal Behaviour*, **78**: 1477–83.

Coughlin, C. E., and van Heezik, Y. (2014) 'Weighed Down by Science: Do Collar-Mounted Devices Affect Domestic Cat Behaviour and Movement?' *Wildlife Research*, **41**: 606–14.

Crowell-Davis, S. L., et al. (2004) 'Social Organization in the Cat: A Modern Understanding', *Journal of Feline Medicine and Surgery*, **6**: 19–28.

D'Eon, R. G. (2003) 'Effects of a Stationary GPS Fix-Rate Bias on Habitat Selection Analyses', *Journal of Wildlife Management*, **67**: 858–63.

Dickman, C. R., and Newsome, T. M. (2015) 'Individual Hunting Behaviour and Prey Specialisation in the House Cat *Felis catus*: Implications for Conservation and Management', *Applied Animal Behaviour Science*, **173**: 76–87.

Doherty, T. S., et al. (2016) 'Invasive Predators and Global Biodiversity Loss', *Proceedings of the National Academy of Sciences USA*, **113**: 11261–5.

Egenvall, A., et al. (2010) 'Morbidity of Insured Swedish Cats During 1999–2006 by Age, Breed, Sex, and Diagnosis', *Journal of Feline Medicine and Surgery*, **12**: 948–59.

ESRI. (2011) *ArcGIS Desktop: Release 10*. Redlands, CA: Environmental Systems Research Institute.

Forin-Wiart, M.-A., et al. (2015) 'Performance and Accuracy of Lightweight and Low-Cost GPS Data Loggers According to Antenna Positions, Fix Intervals, Habitats and Animal Movements', *PLoS One*, **10**: e0129271.

Galsworthy, M. J., et al. (2005) 'A Comparison of Wild-Caught Wood Mice and Bank Voles in the Intellicage: Assessing Exploration, Daily Activity Patterns and Place Learning Paradigms', *Behavioural Brain Research*, **157**: 211–7.

Gehrt, S. D., et al. (2013) 'Population Ecology of Free-Roaming Cats and Interference Competition by Coyotes in Urban Parks', *PLoS One*, **8**: e75718.

Gordon, J. K., et al. (2010) 'Belled Collars Reduce Catch of Domestic Cats in New Zealand by Half', *Wildlife Research*, **37**: 372–8.

Gramza, A., et al. (2016) 'Understanding Public Perceptions of Risk Regarding Outdoor Pet Cats to Inform Conservation Action', *Conservation Biology*, **30**: 276–86.

Grayson, J., et al. (2002) 'Attitudes of Suburban Western Australians to Proposed Cat Control Legislation', *Australian Veterinary Journal*, **80**: 536–43.

Hall, C. M., et al. (2016a) 'Community Attitudes and Practices of Urban Residents Regarding Predation by Pet Cats on Wildlife: An International Comparison', *PLoS One*, **11**: e0151962.

——, et al. (2016b) 'Factors Determining the Home Ranges of Pet Cats: A Meta-Analysis', *Biological Conservation*, **203**: 313–20.

Harris, S., et al. (1990) 'Home-Range Analysis Using Radio-Tracking Data—A Review of Problems and Techniques Particularly as Applied to the Study of Mammals', *Mammal Review*, **20**: 97–123.

——, et al. (1995) *A review of British Mammals: Population Estimates and Conservation Status of British Mammals Other Than Cetaceans*. Peterborough, UK: The Joint Nature Conservation Committee (JNCC).

Harrod, M., et al. (2016) 'Use and Perception of Collars for Companion Cats in New Zealand', *New Zealand Veterinary Journal*, **64**: 121–4.

Hervías, S., et al. (2014) 'Assessing the Impact of Introduced Cats on Island Biodiversity by Combining Dietary and Movement Analysis', *Journal of Zoology*, **292**: 39–47.

Johnson, C. N., et al. (2007) 'Rarity of a Top Predator Triggers Continent-Wide Collapse of Mammal Prey: Dingoes and Marsupials in Australia', *Proceedings of the Royal Society B-Biological Sciences*, **274**: 341–6.

Katajisto, J., and Moilanen, A. (2006) 'Kernel-Based Home Range Method for Data With Irregular Sampling Intervals', *Ecological Modelling*, **194**: 405–13.

Kays, R. W., and DeWan, A. A. (2004) 'Ecological Impact of Inside/Outside House Cats Around a Suburban Nature Preserve', *Animal Conservation*, **7**: 273–83.

Kitts-Morgan, S. E., et al. (2015) 'Free-Ranging Farm Cats: Home Range Size and Predation on a Livestock Unit in Northwest Georgia', *PLoS One*, **10**: e0120513.

Liberg, O. (1984) 'Home Range and Territoriality in Free Ranging House Cats', *Acta Zoologica Fennica*, **171**: 283–5.

Lilith, M., et al. (2008) 'Roaming Habits of Pet Cats on the Suburban Fringe in Perth, Western Australia: What Size Buffer Zone is Needed to Protect Wildlife in Reserves?' in D. Lunney, et al. (eds) *Too Close for Comfort: Contentious Issues in Human–Wildlife Encounters*, pp. 65–72. Sydney: Royal Zoological Society New South Wales.

——,et al. (2006) 'Protecting Wildlife From Predation by Owned Domestic Cats: Application of a Precautionary Approach to the Acceptability of Proposed Cat Regulations', *Austral Ecology*, **31**: 176–89.

Loss, S. R., et al. (2015) 'Direct Mortality of Birds From Anthropogenic Causes', *Annual Review of Ecology, Evolution, and Systematics*, **46**: 99–120.

——, et al. (2013) 'The Impact of Free-Ranging Domestic Cats on Wildlife of the United States', *Nature Communications*, **4**: 1396.

Loyd, K. A. T., et al. (2013) 'Quantifying Free-Roaming Domestic Cat Predation Using Animal-Borne Video Cameras', *Biological Conservation*, **160**: 183–9.

Manly, B. F. J., et al. (2002) *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Dordrecht, Netherlands, Kluwer Academic Publisher.

Marzluff, J. M. (2001) 'Worldwide Urbanization and Its Effects on Birds', in J. M. Marzluff, et al. (eds) *Avian Ecology and Conservation in an Urbanizing World*, pp. 19–48. New York, USA: Springer.

McDonald, J. L., et al. (2015) 'Reconciling Actual and Perceived Rates of Predation by Domestic Cats', *Ecology and Evolution*, **5**: 2745–53.

McKinney, M. L. (2002) 'Urbanization, Biodiversity, and Conservation', *Bioscience*, **52**: 883–90.

—— (2006) 'Urbanization as a Major Cause of Biotic Homogenization', *Biological Conservation*, **127**: 247–60.

—— (2008) 'Effects of Urbanization on Species Richness: A Review of Plants and Animals', *Urban Ecosystems*, **11**: 161–76.

Medina, F. M., et al. (2011) 'A Global Review of the Impacts of Invasive Cats on Island Endangered Vertebrates', *Global Change Biology*, **17**: 3503–10.

Metsers, E. M., et al. (2010) 'Cat-Exclusion Zones in Rural and Urban-Fringe Landscapes: How Large Would They Have To Be?' *Wildlife Research*, **37**: 47–56.

Millspaugh, J. J., et al. (1998) 'Some Comments on Spatial Independence in Studies of Resource Selection', *Wildlife Society Bulletin*, **26**: 232–6.

Moreau, D., et al. (2003) 'Comparative Study of Causes of Death and Life Expectancy in Carnivorous Pets (II)', *Revue De Medecine Veterinaire*, **154**: 127–32.

Morgan, S. A., et al. (2009) 'Urban Cat (*Felis catus*) Movement and Predation Activity Associated With a Wetland Reserve in New Zealand', *Wildlife Research*, **36**: 574–80.

Murray, J. K., et al. (2010) 'Number and Ownership Profiles of Cats and Dogs in the UK', *Veterinary Record*, **166**: 163–8.

——, et al. (2009) 'Survey of the Characteristics of Cats Owned by Households in the UK and Factors Affecting Their Neutered Status', *Veterinary Record*, **164**: 137–41.

Nogales, M., et al. (2004) 'A Review of Feral Cat Eradication on Islands', *Conservation Biology*, **18**: 310–9.

Office for National Statistics. (2013) *Neighbourhood Statistics. 2011 Census Data. HM Government*. [Online]. HM Government. Crown Copyright. http://www.neighbourhood.statistics.gov.uk/ accessed 3 Aug 2016.

Pinheiro, J., et al. (2016) nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-127.

Plotz, R. D., et al. (2016) 'Standardising Home Range Studies for Improved Management of the Critically Endangered Black Rhinoceros', *PLoS One*, **11**: e0150571.

R Core Team. (2017) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ritchie, E. G., and Johnson, C. N. (2009) 'Predator Interactions, Mesopredator Release and Biodiversity Conservation', *Ecology Letters*, **12**: 982–98.

Rochlitz, I. (2004) 'The Effects of Road Traffic Accidents on Domestic Cats and Their Owners', *Animal Welfare*, **13**: 51–5.

Ruxton, G. D., et al. (2006) 'Bells Reduce Predation of Wildlife by Domestic Cats (*Felis catus*)', *Journal of Zoology*, **256**: 81–3.

Schmutz, J. A., and White, G. C. (1990) 'Error in Telemetry Studies: Effects of Animal Movement on Triangulation', *Journal of Wildlife Management*, **54**: 506–10.

Thomas, R. L., et al. (2014) 'Ranging Characteristics of the Domestic Cat (*Felis catus*) in an Urban Environment', *Urban Ecosystems*, **17**: 911–21.

——, et al. (2012) 'Spatio-Temporal Variation in Predation by Urban Domestic Cats (*Felis catus*) and the Acceptability of Possible Management Actions in the UK', *PLoS One*, **7**: e49369.

Thompson, K., and Jones, A. (1999) 'Human Population Density and Prediction of Local Plant Extinction in Britain', *Conservation Biology*, **13**: 185–9.

Toukhsati, S. R., et al. (2012) 'Wandering Cats: Attitudes and Behaviors Towards Cat Containment in Australia', *Anthrozoös*, **25**: 61–74.

UN (2011) *World Population Prospects: The 2010 Revision*. New York, United Nations: Department of Economic and Social Affairs, Population Division.

van Heezik, Y., et al. (2010) 'Do Domestic Cats Impose an Unsustainable Harvest on Urban Bird Populations?' *Biological Conservation*, **143**: 121–30.

Walter, W. D., and Fischer, J. W. (2017) *Manual of Applied Spatial Ecology [Online]*. Pennsylvania, USA: Walter Applied Spatial Ecology Lab, Pennsylvania State University. <http://ecosystems.psu.edu/research/labs/walter-lab/manual/preface> accessed 15 June 2017.

Wierzbowska, I. A., et al. (2012) 'Free-Ranging Domestic Cats Reduce the Effective Protected Area of a Polish National Park', *Mammalian Biology*, **77**: 204–10.

Wood, V., et al. (2016) 'Movement and Diet of Domestic Cats on Stewart Island/Rakiura, New Zealand', *New Zealand Journal of Ecology*, **40**: 186–90.

Woods, M., et al. (2003) 'Predation of Wildlife by Domestic Cats *Felis catus* in Great Britain', *Mammal Review*, **33**: 174–88.