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Spatial behavior of domestic cats and the effects of outdoor access restrictions and interventions to reduce predation of wildlife

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Abstract

Domestic cats (*Felis catus*) that roam outdoors have increased exposure to hazards to their health and welfare. Outdoor cats can themselves present a hazard to biodiversity conservation and wild animal welfare. Approaches to reducing predation of wildlife by cats might also bring benefits to cats by reducing their roaming and associated risks. We investigated ranging behaviors of domestic cats that regularly captured wild prey, and that had restricted or unrestricted outdoor access. We tested whether interventions aimed at reducing predation also affected their spatial behavior. We evaluated cat bells, Birdsbesafe collar covers, using a "puzzle feeder", provision of meat-rich food, object play, and a control group. Seventy-two cats in 48 households in England completed the 12-week trial in spring 2019. Home ranges were small (median $AKDE_{95}$ = 1.51 ha). Cats with unrestricted outdoor access had 75% larger home ranges, 31% greater daily distances traveled, and reached 46% greater maximum distances from home, than cats with restricted outdoor access. None of the treatments intended to reduce predation affected cat ranges or distances traveled. While owners might use interventions to reduce predation, the only effective means of reducing cat roaming and associated exposure to outdoor hazards was restriction of outdoor access.

KEYWORDS
domestic cats, GPS, home range, predation, tracking, welfare, wildlife

1 | INTRODUCTION

Owned domestic cats (*Felis catus*) that live as companion animals in human households, but which can range outdoors, are exposed to multiple hazards to their health and welfare. Roaming behaviors increase the risks to cats of contracting viral (e.g., FeLV) and parasitic (e.g., *Toxoplasma gondii*) infections (Chalkowski, Wilson, Lepczyk, & Zohdy, 2019), aggressive interactions with other cats (Loyd, Hernandez, Abernathy, Shock, & Marshall, 2013), being injured or killed in road traffic (Olsen & Allen, 2001; Rochlitz, De Wit, & Broom, 2001), and being attacked by wildlife (Lukasik & Alexander, 2011) or dogs (Olsen & Allen, 2001). Owned cats with unregulated access to roam

freely and unsupervised outdoors are at greater risk of getting lost and contributing to feral cat populations (Tan, Stellato, & Niel, 2020). Moreover, outdoor cats can be considered a nuisance to human residents (Toukhsati, Young, Bennett, & Coleman, 2012) and can acquire and transmit a variety of zoonotic infections (Gerhold & Jessup, 2013).

There were estimated to be 10–11 million pet cats in the United Kingdom in 2011 (Murray, Gruffydd-Jones, Roberts, & Browne, 2015) and 90 million cats in the United States in 2013 (Loss, Will, & Marra, 2013). Some, but not all, domestic cats kill wild animals (Baker, Bentley, Ansell, & Harris, 2005; Thomas, Fellowes, & Baker, 2012; Woods, McDonald, & Harris, 2003). Because cats live at high densities around human settlements, estimates of the total numbers of wild animals that might be killed by domestic cats tend also to be very high (Blancher, 2013; Lepczyk, Mertig, & Liu, 2003; Murphy et al., 2019; Woods et al., 2003). This leads to cumulative adverse effects on prey populations at local (Baker et al., 2005; Baker, Molony, Stone, Cuthill, & Harris, 2008; Sims, Evans, Newson, Tratalos, & Gaston, 2008; Thomas et al., 2012) up to continental scales (Blancher, 2013; Loss et al., 2013; Murphy et al., 2019; Woinarski et al., 2017). In many ecological contexts, the direct (Medina, Bonnaud, Vidal, & Nogales, 2014) and indirect (Beckerman, Boots, & Gaston, 2007; Bonnington, Gaston, Evans, & Whittingham, 2013) effects of cats can be detrimental to biodiversity conservation (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016), as well as to wild animal welfare (Baker, Thompson, & Grogan, 2018).

Assessments of the relationships between cat spatial behavior and wildlife depredation have produced ambiguous results. Variation in home range size has been found not to influence numbers of prey caught (van Heezik, Smyth, Adams, & Gordon, 2010), though cats with larger home ranges have been found to bring home a greater diversity of prey items (Morgan et al., 2009). Kays et al. (2020) found that pet cats generally had small home ranges (mean = 3.6 ha, $n = 876$), but estimated the numbers of prey animals killed to be 14.2–38.9 prey items per hectare per year per cat. The patterns and extent of roaming in domestic cats are influenced by a variety of factors: sex, with male cats having larger home ranges than females (Hall et al., 2016; Kays et al., 2020); reproductive status, with intact male cats having larger home ranges than neutered males (Ferreira, Machado, Nakano-Oliveira, Andriolo, & Genaro, 2020; Kays et al., 2020); age, older cats having smaller ranges than younger cats (Hall, Bryant, Haskard, et al., 2016; Hervías et al., 2014; Kays et al., 2020); and urbanization, with urban cats having smaller ranges than rural cats (Hall, Bryant, Haskard, et al., 2016; Hanmer, Thomas, & Fellowes, 2017; Kays et al., 2020; Kitts-Morgan, Caires, Bohannon, Parsons, &

Hilburn, 2015; Wierzbowska, Olko, Hędrzak, & Crooks, 2012).

Owners regularly express concern about the hazards to which outdoor roaming exposes their pets, and some are also concerned about their cats' impacts on wildlife (Crowley, Cecchetti, & McDonald, 2019, 2020a). To limit these risks, approaches like keeping cats indoors, or using enclosures such as cat patios ("catios"), have been advocated by groups promoting conservation, for example, American Bird Conservancy, and cat welfare, for example, American Society for the Prevention of Cruelty to Animals, alike. Complete confinement effectively eliminates predation of wildlife by cats, as well as their exposure to outdoor hazards. However, cat owners may perceive permanent confinement as impeding what they see as natural feline behaviors (Crowley et al., 2019; Tan, Rand, & Morton, 2017), though such perceptions are highly variable among human societies (Foreman-Worsley, Finka, Ward, & Farnworth, 2021). Partial curfews tend to be more acceptable to owners, with nocturnal mammals being the main beneficiaries of night-time confinement of cats (Woods et al., 2003), while night-time or crepuscular confinement, particularly in warmer months, is recommended when most wild species are active and in their reproductive periods (Mori et al., 2019). Some studies have shown that cats with unrestricted outdoor access roam significantly further at night than during the day (Metsers, Seddon, & van Heezik, 2010; Thomas, Baker, & Fellowes, 2014), while others found no differences (Hanmer et al., 2017; van Heezik et al., 2010). Similarly, whether a cat was kept indoors at night or allowed unregulated access to the outdoors has previously been found to have no impact on home range size (Hall, Bryant, Fontaine, & Calver, 2016).

Other potential strategies for reducing the numbers of wild animals killed by cats include collar-mounted devices, such as bells, collar covers, and bibs, that inhibit or impede the cat's hunting behavior. These devices have each been shown to be at least partly effective in reducing numbers of prey brought home (Calver, Thomas, Bradley, & McCutcheon, 2007; Cecchetti, Crowley, Goodwin, & McDonald, 2021; Nelson, Evans, & Bradbury, 2005; Ruxton, Thomas, & Wright, 2002). However, the collar-mounted pounce protector CatBib (Cat Goods Inc.) and the Birdsbesafe collar cover (Birdsbesafe LLC) have been found not to reduce cat home range size (Hall, Bryant, Fontaine, & Calver, 2016). Again, cat owners vary in their acceptance or application of such measures for several reasons and uptake may be low if purported benefits do not align with owners' priorities for their cats' welfare (Calver, Adams, Clark, & Pollock, 2013; Crowley et al., 2019, 2020a; Hall et al., 2016; Harrod, Keown, & Farnworth, 2016). Finding

noninvasive interventions that both reduce the exposure of wildlife to the hazards presented by cats, and the exposure of cats to environmental hazards encountered while roaming, might offer opportunities to increase owner action to reduce depredation of wildlife, even where this is not their primary motivation.

Cats are obligate carnivores with strict nutritional requirements (Macdonald & Rogers, 1984). Some commercial pet foods have been found not to provide some essential elements (Gosper, Raubenheimer, Machovsky-Capuska, & Chaves, 2016; Zafalon et al., 2020) and macronutrients (Hewson-Hughes et al., 2011). Furthermore, the proteins in pet foods can be derived from both animal and plant sources, but plant proteins have lower digestibility (Kanakubo, Fascetti, & Larsen, 2015; Neirinck, Istasse, Gabriel, Van Eenaeme, & Bienfait, 1991), lower bioavailability (Zafalon et al., 2020) and a less complete amino acid profile (Donadelli, Aldrich, Jones, & Beyer, 2019) than animal proteins. Cats also have specific behavioral needs, and encouragement of physical activity and reproduction of natural feline behavior in the home environment is important for preventing negative states such as boredom and frustration (Tan et al., 2020). Behavioral enrichment strategies include object play with toys that engages cats in a pseudo-predatory activity (Ellis, 2009; Ellis et al., 2013) and use of "puzzle feeders" (Dantas, Delgado, Johnson, & Buffington, 2016) that require cats to be more engaged in food acquisition. The nutritional and behavioral needs of cats prompted our testing of novel management strategies intended to reduce cats' motivation for hunting, rather than impede their hunting success. We have previously shown (Cecchetti, Crowley, Goodwin, & McDonald, 2021) that provision of food with high meat protein content, and object play, decreased numbers of prey brought home by cats by 36 and 25%, respectively, while puzzle feeders increased numbers of prey returned by 33%.

The extent of roaming behavior by domestic cats is therefore relevant to both cat safety and welfare, and to their predation of wildlife. We studied variation in the spatial behaviors of owned domestic cats that were living as companion animals in human households. We tracked them with collar-mounted GPS loggers, both before and after the introduction of interventions that are primarily intended to reduce predation. We evaluated the effects of two conventional measures (bells and Birdsbesafe collar covers) and three novel interventions (providing high meat content food, providing food in a puzzle feeder, and object play). If these management approaches could also be shown to reduce the extent of cats' roaming behaviors, they might offer options for cat owners seeking to reduce their cats' exposure to outdoor hazards, while also reducing the exposure of wildlife to the direct and indirect hazards presented by cats.

2 | METHODS

This study was conducted alongside a larger experimental study that aimed to test the efficacy of measures to reduce predation of wildlife by cats (Cecchetti, Crowley, Goodwin, & McDonald, 2021). Owners whose cats regularly killed wild animals and brought them back to the house were recruited through social, broadcast and print media. Recruited households were all located in southwest England (Figure 1), in diverse human settlements that we categorized as rural or urban, according to human population density in the local postcode sector (Nomis, 2013, KS101EW: rural ≤2.0 usual resident persons per ha, urban >2.0). Participants completed an online questionnaire regarding their cat's sex, age, and breed, health and behavioral status, feeding habits, outdoor access (restricted or unrestricted), frequency of hunting, and any ongoing management strategies adopted for reducing hunting. Not all owners were able to report their cats' exact age and so age class was recorded (<6 months; 6 months–1 year; 1–5 years; 6–10 years; 11–15 years; >15 years was included in the questionnaire, though these were merged to ≤5 years and >5 years for more even representation across age classes in our analyses). Cat owners recorded all animals that were captured and brought home to the household. They recorded the date of finding the prey item and the animal taxon (mammal, bird, reptile, amphibian, insect, or unidentified in case of indistinct remains). Where possible, they recorded the cat responsible for the returned prey item, otherwise entering "unknown" in case of uncertainty in a multiple cat household.

To test owner willingness to participate, and continuity in recording, we asked them to submit records for two initial surveillance weeks. For participation in the wider experimental study, we selected households in which at least one prey item had been brought home and recorded during these 2 weeks. The experimental trial of interventions to reduce cats' hunting behavior was carried out from 20th March to 23rd June 2019, comprising a pretreatment period of 7 weeks (including the initial two surveillance weeks), followed by a transition week during which owners introduced their cats to the intervention to which they were assigned, and then a treatment period of 5 weeks. The six treatment groups were: *Bell*, with cats fitted with a quick-release reflective collar (Kittygo, Wink Brands UK) and a bell attached; *Safe*, where the same quick-release collar was fitted with a rainbow-patterned Birdsbesafe (www.birdsbesafe.com) collar cover; *Food*, where owners provided cats with a food in which protein
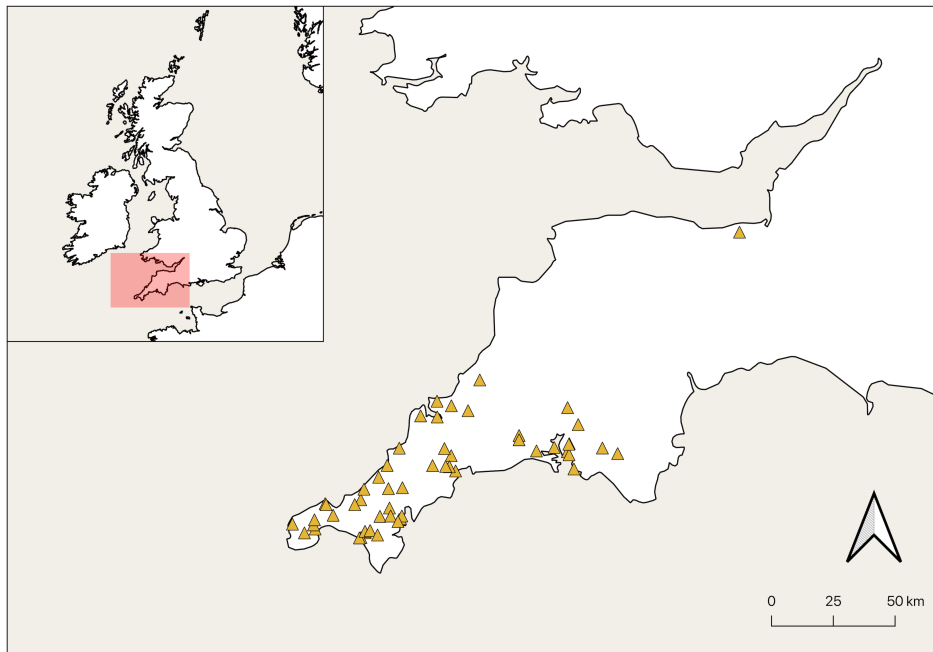
FIGURE 1 Locations of the households in southwest England in which domestic cats were tracked

was predominantly derived from meat sources (Lily's Kitchen Everyday Favourites paté as wet food; and Lily's Kitchen Delicious Chicken as dry food); *Puzzle*, in which owners provided their cats with dry food in puzzle feeders (PetSafe SlimCat interactive toy and food dispenser); *Play*, in which owners spent at least 5 min per day dedicated time playing with their cats, with a "fishing" toy (Cat Dangler Pole Bird) and a "mouse" toy (Kong refillable feather mouse toy, with the catnip replaced with bubble wrap); and *Control* with no intervention (owners were required to not make any changes to management of their cats). Details of the wider experimental trial are reported in full in Cecchetti, Crowley, Goodwin, and McDonald (2021). From an experimental sample of ~70 cats in each of the six treatment groups, we selected a subset of 10–20 cats per treatment group for detailed analysis of their spatial movements, based on owners' willingness to track their cats and household proximity to the university campus to enable frequent welfare checks and the possibility of replacing collars in case of loss (Figure 1).

Cats were fitted with a quick release collar to which we attached a GPS logging unit (iGotU GT120, Mobile Action Technology, Taiwan) with a schedule of 1 fix per 15 min. The GPS unit was $4.4 \times 2.7 \times 1.3$ cm, and weight with its gel cover was 26 g. We used heat shrink to make each unit waterproof and to attach it to a quick release collar, making a total unit weight of 41 g, comprising <2% body mass (Coughlin & van Heezik, 2015). The location accuracy of this GPS was considered sufficient for this study, with an average location error of approximately 10 m (Morris & Conner, 2017).

2.1 | Analytical methods

All statistical analyses were conducted in R (R Development Core Team, 2018).

2.2 | Range size

Prior to analysis, erroneous locations were identified, based on improbable travel distances given time between locations, and were removed (Hanmer et al., 2017; Kays et al., 2020; Morris & Conner, 2017). The threshold value for maximum speed/distance traveled was 100 m/min corresponding to 1.5 km/15 min and for removing "spike" locations, the speed angle threshold was set to 15 m/min (225 m in 15 min; Recio & Seddon, 2013). Home and core ranges were calculated using autocorrelated kernel density estimates (AKDE) from continuous-time movement models (Fleming et al., 2015). Models were fitted using the "ctmm" package (v0.5.10) following procedures set out by Calabrese, Fleming, Gurarie, and Freckleton (2016). Variograms were used to check the autocorrelation structure of each individual's movement data. Individuals were excluded from home range analyses if there was no asymptote in the variogram, suggesting the individual had not been monitored for long enough, or was exhibiting non-range-resident behaviors. Movement models were fitted using maximum likelihood, and model selection was determined on the basis of the Akaike information criterion (AIC). Once the models were selected, the 95% AKDE ($AKDE_{95}$) and the 50% AKDE ($AKDE_{50}$) were calculated to represent the home and core ranges, respectively.

Variation in the range sizes of cats in the pretreatment period was analyzed using a linear model. We only used $AKDE_{95}$ in this analysis as $AKDE_{50}$ was highly correlated (rho = 0.94, $p < .01$). Log_e-transformed $AKDE_{95}$ was the response variable and age class, sex, human settlement type (rural/urban) and number of tracking days, to control for sampling effort, were explanatory variables. We did not distinguish between diurnal and nocturnal fixes as some of the cats were confined at night. Instead, we included outdoor access as a binary variable in the analysis (unrestricted or restricted). To explore any relationships between numbers of prey brought home and home range size, we used a generalized linear model with a negative binomial structure. Explanatory variables were $AKDE_{95}$, age class, outdoor access, sex, and settlement type, while number of days of prey recording was set as an offset to account for sampling effort. Cats living in households with more than one cat, where owners were not able reliably to attribute prey records to an individual were excluded, as were cats with no prey return records in the pretreatment period.

Model selection adopted an information theoretic approach based on the value of AIC (Burnham & Anderson, 2002). A difference in AIC (ΔAIC) of <2 was used to select the top model set and to obtain the model-averaged coefficients of predictor variables, and to rank them according to their predictive importance ($\sum w$). Correlations between explanatory variables were investigated prior to all analyses using Spearman's rank correlation tests, and correlated variables were precluded from appearing in the same models. To check for collinearity in the final models, we calculated the variance inflation factors (VIF; Zuur, Ieno, & Elphick, 2010).

In order to understand if any treatment had an effect on home range size ($Llog_e$-transformed $AKDE_{95}$), we fitted a general linear mixed model (GLMM) using package lme4 (v1.1.20). Fixed factors were treatment (six levels), and period (pretreatment and treatment) and the effect of the treatment was tested by the treatment*period interaction term. Other explanatory variables: sex, age class, outdoor access, and settlement type, were included, based on the model averaging results of the model run in the pretreatment period. Individual cat was fitted as a random term. Because we were interested in the effect of the interaction term, the model was compared to a model with no interaction term using ANOVA. The proportion of variance explained by the selected model was expressed as conditional R^2 (R_c^2).

2.3 | Total distance traveled and maximum distance from home

In addition to size of home and core ranges, we evaluated two further measures of cat spatial behavior: daily total distance traveled and daily maximum distance from the house. Daily total distance traveled was calculated as the sum of distances from one fix to the next, over a 24-hr period from midnight to midnight. Daily maximum distance from home was measured from the edge of the home polygon, vectorized in QGIS (v3.10) (Figure 2), to the furthest point at which a cat was detected on each day.
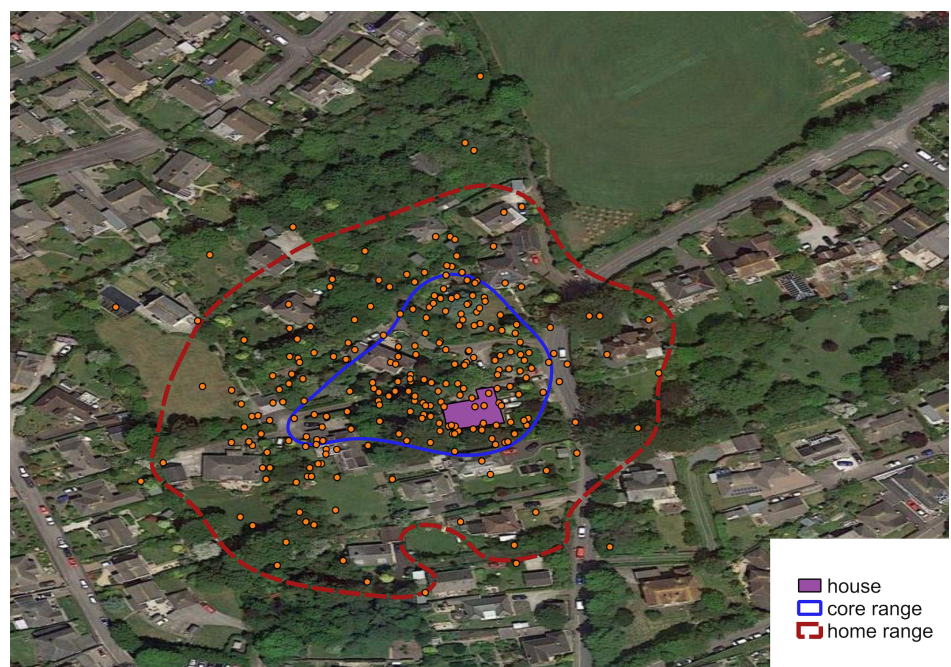

FIGURE 2 Representative map showing the house polygon, core range ($AKDE_{50}$), home range ($AKDE_{95}$), and the fixes recorded by the GPS unit for one of the cats in the trial

TABLE 1 Summary of domestic cat ranging behavior and measures of roaming in relation to cat and household characteristics

Variable	Category	Number of cats	Home range AKDE$_{95}$ (ha)	Core range AKDE$_{50}$ (ha)	Daily maximum distance from home (m)	Daily total distance traveled (m)
Sex	Female	30	1.13 (0.68–2.17)	0.17 (0.09–0.29)	76 (52–114)	828 (528–1205)
	Male	42	1.79 (1.02–2.71)	0.22 (0.13–0.36)	98 (59–158)	937 (565–1438)
Age class	≤5 years	38	1.80 (0.87–2.58)	0.21 (0.12–0.31)	95 (62–145)	985 (640–1415)
	>5 years	34	1.47 (0.67–2.33)	0.18 (0.09–0.33)	81 (47–129)	755 (458–1220)
Settlement type	Rural	53	1.69 (0.70–2.67)	0.21 (0.10–0.36)	89 (54–146)	904 (544–1355)
	Urban	19	1.28 (0.80–1.82)	0.19 (0.10–0.26)	87 (57–123)	831 (537–1323)
Outdoor access	Unrestricted	59	1.76 (0.99–2.58)	0.23 (0.12–0.36)	93 (60–145)	925 (560–1379)
	Restricted	13	0.75 (0.44–1.37)	0.10 (0.05–0.19)	59 (43–105)	792 (504–1104)
All cats		72	1.51 (0.76–2.38)	0.20 (0.10–0.33)	89 (55–138)	884 (543–1353)

Note: Home range is the 95% autocorrelated kernel density estimate (AKDE$_{95}$). Core range is the 50% autocorrelated kernel density estimate (AKDE$_{50}$). Median and interquartile ranges (25–75%) are provided for each parameter.

Variations in the spatial variables in the pretreatment period were analyzed using two separate models. In all models, age class, sex, outdoor access, and settlement type were explanatory variables. Individual cat was a random factor to account for repeated daily observations. Specifically, we ran two GLMMs with a Gaussian error structure with log$_e$-transformed daily total distance traveled and log$_e$-transformed maximum distance from home as the response variables. The model of daily total distance traveled included the log$_e$-transformed number of daily fixes as an offset to account for logger recording success. Checks for correlations among variables, and model selection and averaging were carried out following the same procedures as described above.

The effects of treatments on variation in these spatial variables was evaluated by running two separate models with the same error structure as above, in which the main effects were: treatment (six levels) and period (pretreatment and treatment). The effect of treatment was tested by the interaction term (treatment*period). Other explanatory variables: sex, age class, outdoor access, and settlement type were included based on the model averaging results of the model run in the pretreatment period. Checks for correlations among variables, and model selection were carried out as described above, with comparison of models with and without interaction terms by ANOVA. The proportion of variance explained by the selected model was expressed as conditional R^2 (R_c^2).

3 | RESULTS

Eighty-two cats completed the 12-week trial and generated usable tracking data. Ten cats were excluded from analyses; nine because they had variograms that did not level off (in one or both periods), and one with an exceptionally large home range (AKDE$_{95}$ = 17.3 ha) that had particular influence on the analyses, thus a total of 72 cats (30F:42M) were included in analyses (Table 1). All cats had been neutered. Thirty-eight cats were less than 5 years old and 34 were >5 years old. Fifty-three cats lived in rural settlements and 19 in urban settlements. Fifty-nine of the 72 cats (82%) had unrestricted access to the outdoors, and 13 (18%) had their outdoor access restricted. Owners reported that restrictions were primarily by confinement at night, though the exact form and duration of restrictions varied among households.

In the pretreatment period, the mean duration of deployment was 8.9 days (*SE* mean = 0.2 days, range = 5–13 days), while in the treatment period mean duration was 7.5 days (*SE* = 0.1 days, range = 6–11 days). The median number of daily fixes was 33 (IQR = 22–42). Overall, the median home range (AKDE$_{95}$) was 1.51 ha (interquartile range = 0.76–2.38 ha), median core range (AKDE$_{50}$) was 0.20 ha (IQR = 0.10–0.33 ha), median daily maximum distance from home was 89 m (IQR = 55–138 m) and the median daily total distance traveled was 884 m (IQR = 543–1353 m, Table 1).

Outdoor access had the greatest, and a significant, influence on variation in home range size. Cats that had unrestricted outdoor access had ranges that were 75% (95% confidence interval 5–191%) larger than those with restricted outdoor access (Table 2). Age class, sex, and days of tracking had some influence, but the estimated confidence intervals suggested that there was no discernible effect of these variables on home range size (Table 2). Human settlement type had no influence on cat home range size.

TABLE 2 Summaries of analyses of variation in domestic cat home range size, daily maximum distance from home and daily distance traveled

	Estimates	SE	Effect size (95% CI)	VIF	$\sum w$	N
Home range size (AKDE$_{95}$)						
Outdoor access	0.56	0.25	1.75 (1.05–2.91)	1.04	1	4
Age class	−0.07	0.15	0.93 (0.69–1.26)	1.03	0.28	1
Sex	0.03	0.11	1.04 (0.83–1.29)	1.01	0.19	1
Days of tracking	0.02	0.09	1.02 (0.86–1.21)	1.02	0.15	1
Daily maximum distance from home						
Outdoor access	0.38	0.15	1.46 (1.09–1.94)	1.04	1	3
Age class	−0.23	0.11	0.79 (0.63–0.99)	1.03	1	3
Sex	0.15	0.13	1.16 (0.90–1.51)	1.04	0.73	2
Settlement type	−0.03	0.08	0.97 (0.83–1.14)	1.06	0.25	1
Daily total distance traveled						
Outdoor access	0.27	0.09	1.31 (1.09–1.56)	1.04	1	3
Age class	−0.20	0.07	0.82 (0.72–0.94)	1.03	1	3
Sex	0.09	0.08	1.09 (0.93–1.28)	1.04	0.71	2
Settlement type	−0.03	0.06	0.97 (0.87–1.09)	1.06	0.29	1

Note: Categorical explanatory variables originally included in all the models, and their baseline levels in parentheses, were outdoor access (restricted), age class (≤5 years), sex (female), and settlement type (rural). Estimates, full model-averaged coefficients for explanatory variables; *N*, number of models containing the explanatory variable; *SE*, standard error of the coefficient; $\sum w$, sum of Akaike's weights; VIF, variance inflation factors. Variables were log$_e$-transformed for analysis. Effect sizes (95% CI) are proportional changes in the response variables, derived by exponentiating the estimates and 95% confidence interval.

TABLE 3 Summaries of analyses of variation in prey returned home by domestic cats and recorded by householders

	Estimates	SE	Odds ratio (95% CI)	VIF	$\sum w$	N
AKDE$_{95}$	0.06	0.09	1.06 (0.88–1.28)	1.13	0.42	3
Outdoor access	0.11	0.24	1.12 (0.65–1.92)	1.06	0.34	3
Age class	−0.13	0.27	0.88 (0.55–1.41)	1.04	0.27	3
Settlement type	−0.02	0.12	0.98 (0.77–1.24)	1.07	0.08	1

Note: Number of prey brought home is the number of individual items brought home and recorded by owners. Categorical explanatory variables originally included in both models were outdoor access (baseline-restricted), age class (≤5 years), and settlement type (rural). Estimates, full model-averaged coefficients for explanatory variables; *N*, number of models containing the explanatory variable; *SE*, standard error of the coefficient; $\sum w$, sum of Akaike's weights; odds ratio (95% CI), exponential of estimates and 95% confidence intervals, applied to negative binomial model; VIF, variance inflation factors.

Outdoor access had a strong and significant influence on variation in the daily maximum distance from home; cats that had unrestricted outdoor access tended to reach maximum distances 46% further from home than those with restricted outdoor access (Table 2). Older cats reached maximum distances 21% less far from home than younger cats (Table 2). Sex and human settlement type had some influence, but the estimated confidence intervals suggested that there was no discernible effect.

For daily total distance traveled, outdoor access and age class had the greatest effects. Cats with unrestricted outdoor access had daily total distances traveled that were 31% greater than those with restricted outdoor access. Older cats had daily total distances traveled that

were 18% less than younger cats. Sex and human settlement type had some influence, but the estimated confidence intervals suggested that there was no discernible effect.

None of the experimental treatments aimed at reducing predation had a significant effect on cat home range (AKDE$_{95}$) (ANOVA comparison of models, $\chi^2 = 4.26$, $p = 0.51$, R_c^2 for the model with no interaction term was 0.76), daily maximum distance from home ($\chi^2 = 7.97$, $p = 0.16$, $R_c^2 = 0.40$) or daily total distance traveled ($\chi^2 = 4.30$, $p = 0.51$, $R_c^2 = 0.44$).

In the pretreatment period, six cats were not recorded to bring home any prey, and so were excluded from the analysis investigating the relationship between prey

returned and home range size. In households owning multiple cats, few owners could unequivocally attribute prey records to a specific individual cat and so the number of cats in this analysis dropped to 34 individuals. None of the variables had a strong effect (Table 3). Sex did not influence the numbers of prey brought home by cats.

4 | DISCUSSION

Partial confinement of domestic cats, primarily by confinement at night, substantially reduced their roaming. Cats that were allowed unrestricted outdoor access had 75% larger home ranges, reached 46% greater maximum distances from home, and showed 31% greater daily total distances traveled than cats with partially restricted outdoor access. The greater extents of ranging displayed by the cats that were free to roam by day and night, likely stem from significant differences between day and night in cat ranging areas (Thomas et al., 2014). The number of prey brought home was not related to the extent of home ranges, suggesting that cats tend to roam, at least in part, to fulfill behaviors unrelated to hunting.

In terms of the spatial extent of domestic cat ranging, home ranges and core ranges were small and broadly consistent with those of domestic cats in other studies (Castañeda et al., 2019; Hall, Bryant, Haskard, et al., 2016; Kays et al., 2020). In contrast to other studies, which have found that older cats had smaller home ranges than younger ones (Castañeda et al., 2019; Hall, Bryant, Haskard, et al., 2016; Kays et al., 2020), and males tended to have bigger home ranges than females (Kays & DeWan, 2004; Thomas et al., 2014), our model did not find significant effects of these variables on home ranges, though older cats did tend to stay closer to home and travel less far on a daily basis. Cats living in households in rural or urban settlements, with a wide range of human population densities, showed similar spatial behavior in this study.

Our study indicates that, other than restricting access to the outdoors, neither existing management approaches to reducing predation (bells, Birdsbesafe collar covers), nor novel approaches (changing food, object play, puzzle feeders), were effective in reducing cat home range size, maximum distance from home, or daily distance traveled. In our associated experimental study (Cecchetti, Crowley, Goodwin, & McDonald, 2021), cats subjected to the food and object play treatments brought home significantly fewer prey items, while the use of the puzzle feeders resulted in an increase in number of prey brought home by cats. Cats are obligate carnivores, with a requirement for high levels of protein and no requirement for carbohydrates (Macdonald & Rogers, 1984). Our recent study (Cecchetti et al., 2021) has shown that cats that regularly hunt wild prey nevertheless rely almost exclusively on food provided by their owners. While it might be the case that fulfillment of physiological needs afforded by the provision of a new food with high meat-protein content reduced the motivation for hunting (Cecchetti, Crowley, Goodwin, & McDonald, 2021), it evidently did not affect the tendency to roam when outdoors, and consequently does not reduce the exposure of cats to outdoor hazards. Similarly, during hunting, play behaviors are commonly observed (Biben, 1979) and hunger increases both predation rate and play motivation in cats (Hall & Bradshaw, 1998). Because cats are "ambush predators" and spend large parts of their hunting excursions watching and stalking their prey, it might be that increasing the frequency and regularity of time spent in object play and opportunities for exercising natural behaviors in the home environment can reduce motivation to hunt (Cecchetti, Crowley, Goodwin, & McDonald, 2021), but again, this intervention appeared not to affect roaming. Roaming and maintaining a specific range might be driven by domestic cats' evolutionary heritage, manifest in establishing, patrolling and defending territories, and hence outdoor roaming might be intrinsically rewarding (Abbate, 2020; Cecchetti, Crowley, & McDonald, 2021; Crowley, Cecchetti, & McDonald, 2020b).

While owners have multiple options for reducing predation of wildlife, owners wishing to mitigate any risks to their cats associated with their roaming behavior therefore have fewer options. Keeping their cats indoors, particularly at night, is the best way to reduce the extent of their roaming. Owners are able to enrich the home environment if they are concerned about cat aversion to confinement or about restricting cat natural behaviors. Ellis et al. (2013) provide detailed guidance on feline environmental needs and lay out a framework for a healthy environment, ranging from providing hiding places (e.g., cardboard boxes) to opportunities for play and predatory behavior (e.g., hiding food). Nevertheless, cats that are used to having unrestricted outdoor access may experience problems in adapting to a life of even partial confinement indoors (Hubrecht & Turner, 1997). A pragmatic solution in such cases might be the use of outdoor enclosures, with enrichment by objects that enable the cat to hide, play and exercise (Ellis et al., 2013).

AUTHOR CONTRIBUTIONS

The study was conceived by M.C., S.L.C., and R.A.M. M.C. and S.L.C. conducted the experiment. M.C. collected and analyzed data and wrote the initial manuscript. L.N. and J.W-A. supported data analyses. All authors contributed to revision of the manuscript and agreed to the submission.

DATA AVAILABILITY STATEMENT

All data used in this study are available via the Dryad data repository at https://doi.org/10.5061/dryad.vx0k6djsx

ETHICS STATEMENT

The study protocol was approved by the ethics committee of the University of Exeter College of Life and Environmental Sciences (Reference 000181). The project also received specialist veterinary guidance and the protocols was approved by an independent Project Advisory Group, comprising feline veterinary, behavioral and welfare specialists. Cat owners provided informed written consent.

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