Prey selection and predation behavior of free-roaming domestic cats (*Felis catus*) in an urban ecosystem: Implications for urban cat management

D.J. Herrera [a,b,*], M.V. Cove [c], W.J. McShea [d], D.T. Flockhart [e], S. Decker [a], S.M. Moore [a], T. Gallo [b]

[a] *Humane Rescue Alliance, 71 Oglethorpe Street NW, Washington, DC 20011, United States of America*
[b] *Department of Environmental Science and Policy, College of Science, George Mason University, 4400 University Drive, Fairfax, VA 22030, United States of America*
[c] *North Carolina Museum of Natural Sciences, 11 W Jones Street, Raleigh, NC 27601, United States of America*
[d] *Smithsonian Conservation Biology Institute, 1500 Remount Road, Front Royal, VA 22630, United States of America*
[e] *Appalachian Laboratory, University of Maryland Center for Environmental Science, 301 Braddock Rd., Frostburg, MD 21532, United States of America*

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ABSTRACT

The ecological impact of free-roaming domestic cats (*Felis catus*) is well-studied. However, despite receiving considerable attention in both the scientific and popular literature, predation behavior is rarely an explicit consideration when developing cat population management plans. We used motion-activated wildlife cameras to document predation events by cats in Washington, D.C. (U.S.A), and assessed the relationships between predation and local environmental characteristics. Our analyses reveal that predation by cats is greatest where supplemental food is most abundant, and that the probability of a cat preying upon a native species increases closer to forest edges. Conversely, we found that the probability of a cat depredating a non-native brown rat increases with increasing distance from forest edges. Therefore, we recommend the implementation of cat exclusionary buffer zones around urban forests and that free-roaming domestic cat management policies explicitly consider the spatial location of cat-feeding sites. Our findings provide a data-driven approach to free-roaming cat management.

1. Introduction

Free-roaming domestic cats (*Felis catus*; hereafter 'cats') are both common and found at high densities in urban areas worldwide (Hansen et al., 2018; Legge et al., 2016; Gehrt et al., 2013). Cats with outdoor access are subjected to numerous risks, including possible vehicle collisions (Rochlitz, 2003), heightened exposure to zoonotic disease (Gehrt et al., 2013; Roseveare et al., 2009), exposure to toxins (Tan et al., 2020; Berny et al., 2010), increased potential for abuse (Bonela Gomes et al., 2021), and possible predation by native predator species (Larson et al., 2020; Tan et al., 2020; Kays et al., 2015). Similarly, cats pose a risk to wildlife through the transfer of zoonotic disease (Lehrer et al., 2010) and direct predation (Cove et al., 2018; Loss et al., 2013; Loyd et al., 2013). Despite these risks, the management of free-roaming cat populations is often controversial (e.g., Calver et al., 2020; Read et al., 2020; Crawford et al., 2019; Wolf et al., 2019).

Numerous stakeholders share an interest in free-roaming cats, resulting in a diverse and nuanced spectrum of proposed management solutions ranging from complete tolerance of outdoor cats to population control to euthanasia. Although sentiments vary internationally (Foreman-Worsley et al., 2021; Hall et al., 2016), organizations in the United States that advocate for the welfare of domestic animals largely prefer management options such as Trap-Neuter-Return (hereafter, 'TNR'; e.g., ACA, 2022; ASPCA, 2022; BF, 2022; HSUS, 2022; *but see also*: PETA, 2022) where cats are allowed to remain outdoors, but are surgically altered and unable to reproduce (Boone et al., 2019). Veterinary professionals also tend to favor TNR, but not overwhelmingly (Sherwood et al., 2019, *but see also*: Jessup, 2004). Some cat owners view cats' outdoor access as integral to the cat's welfare (Crowley et al., 2019), and similarly prefer management options like TNR that provide sterilized cats some degree of caretaking from humans while still living outdoors (Crowley et al., 2019; Parsons et al., 2018; Loyd and Hernandez, 2012). Conservationists and advocates for native animal welfare, on the other hand, argue that the ecological impact of predation by cats is too great to justify their outdoor access (Crawford et al., 2019; Loss et al., 2013, Calver et al., 2011; *see also*: ABC, 2014) and often recommend the

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complete banning of outdoor cats or fines for unrestrained cats (Loss and Marra, 2017; Calver et al., 2011). Given disagreements between stakeholders, comprehensive management decisions are often delayed or unrealized (Wald et al., 2013), and this may be, in part, because stakeholders tend to focus on all-or-nothing decisions rather than shared goals such as improved animal welfare and/or pest management (Wald et al., 2013). A multi-angled and collaborative approach to free-roaming cat management may circumvent these entrenchments and will likely be integral to reducing the impact of cats on native wildlife. Here we assess environmental factors that influence predation behavior of cats and recommend data-driven and achievable approaches to free-roaming cat management in an urban area.

As obligate carnivores, cats prove efficient hunters of small-bodied vertebrates (Bradshaw, 2006) and are often used as a biological control for pest management, especially against non-native rodents (Foreman-Worsley et al., 2021; Crowley et al., 2019). While cats may be known for their predation of non-native rats, most studies conclude that such predation is relatively rare and is unlikely to suppress rat populations (Glass et al., 2009; Parsons et al., 2018). Instead, cats prefer smaller (<250 g) prey items such as non-native house mice (*Mus musculus*) and other small-bodied species like native rodents, songbirds, butterflies, and reptiles (Fleming et al., 2020; Parsons et al., 2018; Loss et al., 2013; Loyd et al., 2013; Childs, 1986). In a comprehensive review, however, Loss et al. (2013) found that the predation of non-native mice and rats by domestic cats increased with urbanization. Since a cat's diet is proportional to local prey availability (Krauze-Gryz et al., 2017; Kutt, 2012; Van Heezik et al., 2010), it follows that cats within less biodiverse urban areas may prey more frequently on non-native species, and potentially provide a service by preying on non-native rodents to some extent (Van Heezik et al., 2010). If true, management approaches may benefit from focusing their efforts on reducing cat populations in more ecologically sensitive areas where the predation of native fauna is more prevalent (Loss and Marra, 2017). Such an approach would take into consideration a cat's potential to control non-native species, while reducing the probability of predation on native species.

The implementation of cat exclusion zones around areas of ecological concern has been one approach to location-specific cat management and has been implemented to reduce the risk of biodiversity loss (e.g., Lilith et al., 2008). This approach allows free-roaming cat programs (e. g., TNR programs and sanctioned cat care) to operate in areas with a low probability of impact on native species (Metsers et al., 2010; Lilith et al., 2008). Cat exclusion buffer zones have traditionally been drawn around nature reserves using only the average home range size for cats as a buffer distance (Metsers et al., 2010; Lilith et al., 2008). This approach assumes that native wildlife are constrained to the reserve boundaries, and that variation in cat roaming behavior is minimal. However, in urban areas, many native species are found beyond the borders of green spaces (Herrera et al., 2021), and variation in cat roaming behavior can be substantial (Kays et al., 2020; Metsers et al., 2010). Designating buffer zones based on biological aspects of cat predation rather than administrative boundaries may facilitate more impactful cat management policies.

The goal of this study was to investigate the spatial drivers of predation by free-roaming cats in Washington, D.C., USA, and propose location-specific management options based on our findings. Our specific research questions were (1) do habitat characteristics and supplemental feeding correlate with predation events by cats?, (2) do cats within a TNR program have lower predation rates?, and (3) what variables influence prey selection (native vs. non-native prey species)? Since cats are known to hunt regardless of whether or not they are sterilized (e. g. Castillo and Clarke, 2003), and cat populations tend to congregate where there is access to supplemental food (e.g. Cove et al., 2018; Kays and DeWan, 2006), we hypothesized that overall predation would not be impacted by a cat's inclusion in a TNR program, but that overall predation rates would be highest where supplemental food was most abundant. We also hypothesized that the composition of prey species

would reflect their availability across the landscape (e.g., Krauze-Gryz et al., 2017), with predation of native species being greatest near forested areas and predation of non-native species being greatest in more developed areas. We used our results to develop cat-exclusionary buffer zones that are based on the behavior of cats. Our findings provide biologically relevant information about cat predation that can inform free-roaming cat management in urban areas.

2. Methods

2.1. Study area

We conducted our study in Washington, D.C., which is the sixth largest metropolitan area (158 km^2 of land; U.S. Census Bureau, 2019) in the USA, with a population of approximately 705,750 residents ($\sim$4466 people/km^2; U.S. Census Bureau). The city boundary resides at the confluence of the Potomac and Anacostia Rivers (Ossi et al., 2015) in the ancestral homeland of the Nacochtank (also called Anacostan) people, and later the Piscataway people (Mooney, 1889). The climate is temperate/tropical with an average of 110 cm of annual precipitation and an average summer and winter temperature of 21.6 °C and 6.9 °C, respectively (NOAA, 2021). Despite intense development, the city maintains the highest proportion of parkland of any U.S. city (21.9%; Harnik et al., 2017). Approximately half of the parkland is forested and contains an assemblage of oaks (*Quercus* spp.), maples (*Acer* spp.), and American beech (*Fagus grandifolia*), consistent with Northeastern upland forests (Ossi et al., 2015).

2.2. Data collection

Reconyx HyperFire 2 remotely-triggered trail cameras (Reconyx Inc., 3828 Creekside Ln, Ste. 2, Holmen, WI 54636) were deployed at 1530 sampling sites across Washington, D.C. as part of the DC Cat Count project (Flockhart et al., 2022). Sampling site locations were distributed across the city and were roughly proportionate to the city's socioeconomic stratification (low, medium, and high median household income) and landcover classifications (forested, moderate development, high development). Sampling sites included private residences and institutions (n = 441), public greenspaces (n = 796), alleys (n = 265), and sidewalks (n = 28) within each income-landcover stratification (high income-forested = 11%, medium income-forested = 9%, low income-forested = 2%, high income-moderate development = 8%, medium income-moderate development = 30%, low income-moderate development = 12%, high income-high development = 1%, medium income-high development = 21%, low income-high development = 6%).

Camera deployments occurred between September–December 2018 (n = 192), April 2019–January 2020 (n = 867), and June–October 2020 (n = 471). At each sampling site one camera was continuously active for 15 consecutive days, after which the site was not sampled again (one sampling period per site). Cameras were affixed to a solid substrate at a height of $<$0.5-m using a nylon strap and lock and aimed at a probable corridor of animal movement (e.g. game trails, fence lines, alley). Cameras were set to take five consecutive photographs with no delay period between each camera trigger. See Herrera et al. (2021) for additional study design details.

2.3. Data processing

Photos collected from each camera underwent a multi-stage review process to identify each animal to species and were uploaded to the eMammal photo repository (McShea et al., 2016; *see also*: http://emammal.si.edu). Photos taken in rapid succession ($<$1 min apart) were considered a single observation. During photo review, animals were also inspected for prey items. If an animal was determined to be carrying a prey item, it was assumed to be a predation event and both the predator and prey species were recorded. We then classified each prey species

into native or non-native categories. Brown rat (*Rattus norvegicus*), house mouse (*Mus musculus*), and European starling (*Sturnus vulgaris*) were classified as non-native species. All other identifiable prey items were classified as native species. Prey that were not identifiable to species were recorded as 'unknown animal', 'unknown bird', or 'unknown rodent' and were included in analyses investigating overall predation rates, but excluded from analyses that considered whether a species was native or non-native. Our methods likely yield a conservative estimate of predation frequency since predators often consume their prey on-site rather than transport it (Windell et al., 2019; Parsons et al., 2018). Additionally, predation events from photographs may be biased towards larger species as smaller species are harder to see in the photos. It is also possible that prey were scavenged rather than predated, and the correlation between predation rates and carrying rates may vary across individuals, times, and locations. However, our method offers a non-invasive sampling method for predation events and has become increasingly common in recent years (e.g., Bowler et al., 2020; Fernandes Lima Luciano et al., 2020; Herrera and Cove, 2020; Keiter et al., 2020; Windell et al., 2019; Meek and Wishart, 2017).

Domestic cats were identified as having participated in a TNR program by the presence of a notched or flattened left ear-tip (here after an "ear-tip"). If the ear was not clearly visible, TNR status was recorded as 'unknown' unless the individual cat was otherwise identifiable and known to have been sterilized (e.g., previous photos of the same individual). Although an ear-tip is indicative that a cat has been sterilized, the lack of an ear-tip does not imply that sterilization has not taken place, as this is not standard practice for owned pet cats. We were not able to identify the sex or age of individuals, as sterilization often impacts physical development and sex-driven characteristics such that they often cannot be identified in photographs.

2.4. Predictor variables

2.4.1. Density of known cat feeding locations

Feeding location density was calculated based on responses to a city-wide household survey pertaining to owned cats, which was administered electronically as part of the DC Cat Count (Gramza, 2022). Any cat was considered to be owned if it was fed by someone at least once per week, regardless of indoor or outdoor status. Respondents were asked 'what type of outdoor access does your cat have?' To meet the survey's definition of being an owner of a free-roaming domestic cat, the respondent must feed at least one cat outdoors at least once per week. The number of respondents that answered 'outdoors always' were retained and considered to be a cat feeding location. These responses are not specific to managed colonies of free-roaming cats nor individual pets, but rather reflect any situation in which food is supplied for consumption by cats outside the home. To maintain survey participant anonymity, responses were aggregated to 400×400-m grid cells across the entire city. Cat feeding location density (feeding locations/km^2) was calculated by summing the cell values for each grid cell that fell within a 171-m fixed-radius site buffer based on the upper estimate of the average home range size of an urban cat (area = 0.092 km^2; Kays et al., 2020) and dividing that sum by the total area of the corresponding cells. Twelve predation events occurred at three sites within grid cells that did not contain survey responses, so were instead assigned the mean feeding location density from the most adjacent grid cells.

2.4.2. Distance to forest edge

Forest boundaries were created using a 1-m resolution landcover dataset (CCCIC, 2014) by isolating raster cells that were classified as 'tree canopy'. Continuous adjacent cells were considered a 'patch' and patches with continuous cover greater than 0.004 km^2 and a width of at least 37-m were considered a 'forest' per the U.S. Forest Service definition (USFS, 2016). Distance between the camera location and the nearest forest edge was calculated using the *near* tool in ArcMap 10.8 (*ESRI*, 380 New York Street, Redlands, CA 92373). Distance values were

considered negative if a camera was within a forest patch.

2.4.3. Impervious cover

Percent impervious surface was calculated by isolating cells from the above-mentioned 1-m resolution dataset (CCIC 2014) classified as 'structures,' 'impervious surfaces,' 'impervious roads,' 'tree canopy over structures,' 'tree canopy over impervious surfaces,' and 'tree canopy over impervious roads.' These cells were then reclassified as a single 'impervious surface' category. We calculated the proportion of impervious surface within the 171-m fixed-radius home range buffer around camera locations that contained predation events.

2.5. Data analysis

Prior to analysis, we standardized all numeric covariates by mean-centering each covariate and dividing by the standard deviation. Covariates were tested for collinearity using the Pearson correlation coefficient and found no evidence of collinearity ($r < 0.7$).

2.5.1. Overall predation

To assess whether predictor variables affected the overall predation rate of free-roaming cats, we used a negative-binomial model to assess the number of predation events as a function of each predictor variable. To account for differences in cat activity across the study area, we included the number of cat observations at each predation site as an offset term in our model. A global model with all covariates was fit and found to be over-dispersed ($\hat{c} = 1.72$); thus, justifying the negative-binomial distribution to account for overdispersion of the data. Competing models were built using all additive combinations of the four predictor variables, and a null model (n = 15 models). Models were ranked using Akaike information criterion corrected for small sample size (AIC$_c$) and models within 2 ΔAIC$_c$ were considered our top models. Models were fit using the MASS package (Venables and Ripley, 2002) and AIC$_c$ values were calculated using the AICcmodavg package (Mazerolle, 2020) in R version 4.0.0 (R Core Team, 2020; R Studio Team 2019).

2.5.2. Prey selection

We estimated the probability of a prey item being a native species using a binomial model (native species = 1; non-native species = 0). Due to a small sample size, our competing model set was limited to univariate models of each predictor variable, and a null model (n = 5 models). We also estimated the probability of a prey item being a brown rat using a binomial model (rat = 1; non-rat = 0). All possible additive combinations of the predictor variables, and a null model, were used as our model set (n = 15 models). Models were again ranked using AIC$_c$ and models within 2 ΔAIC$_C$ were considered our top models.

2.6. Formation of buffer zones

We overlaid a 30×30-m grid on the study area, and each predictor variable was calculated for each grid cell. The top model for the probability of a prey species being native was run to estimate a probability for each grid cell and used as a measure of relative risk across the study area. Four probability thresholds were selected to represent varying levels of risk: 0%, 10%, 25%, and 50% probability that a prey item would be a native species. At each threshold, cells with probabilities at or above the threshold level were considered part of the exclusionary buffer. A secondary 170-m buffer was added to the risk buffer to account for roaming distance of cats based on the average cat home range (Kays et al., 2020). The proportion of the city encompassed by each risk threshold's buffer was calculated by dividing the terrestrial area of the buffer by the total terrestrial area of the city.

3. Results

We captured 33,134 observations of cats (22% of all animal observations) over 22,268 trap nights. We documented 73 instances of cats carrying a prey item ($n_{ear\,tip} = 29$, $n_{no\,ear\,tip} = 44$) at 38 sites. Two additional predation events were documented in which it was not possible to determine if the cat had been ear-tipped; these records were not included in our analyses. Predation events by other species are reported in Appendix 1.

3.1. Total predation

The total number of cat predation events at a site was best predicted by a cat's prior participation in a TNR program (*ear-tipped* $\beta = -0.80$ [95% CI: -1.41 to -0.19]) and local feeding location density ($\beta = 0.46$ [95% CI: 0.17–0.75]; Table 1). While we did find a decrease in overall predation – on average – by a cat's prior participation in a TNR program, when predicted across covariate gradients we found the confidence intervals of ear-tipped (TNR) and non-ear-tipped cats largely overlapped each other (Fig. 1). Feeding location density alone was our second best model ($\Delta AIC_c = 1.72$; $\beta = 0.60$ [95% CI: 0.29–0.91]; Table 1) and our third ranked model ($\Delta AIC_c = 1.74$; Table 1) consisted of TNR (*ear-tipped* $\beta = -0.71$ [95% CI: -0.96 to -0.46]), feeding location density ($\beta = 0.45$ [95% CI: 0.18–0.72]), and distance to nearest forest ($\beta = -0.14$ [95% CI: -0.39–0.11]; Fig. 1).

Table 1
Model selection results for A) overall predation rates, B) probability of prey being a native species, and C) probability of prey being a brown rat. Models that received less support than the null model are not listed. Covariates are abbreviated as *food* (density of feeding locations within home range), *forest* (distance to forest edge), *TNR* (ear-tip visible), and *impervious* (percent impervious surface within home range).

Model	k	Log likelihood	AIC_c	ΔAIC_c	AIC_c weight
(A) Overall predation					
TNR + food	4	−75.06	159.23	0.00	0.33
Food	3	−77.15	160.95	1.72	0.14
TNR + food + forest	5	−74.62	160.96	1.74	0.14
forest + food	4	−76.27	161.65	2.42	0.10
TNR + impervious + food	5	−75.01	161.74	2.51	0.09
impervious + food	4	−77.12	163.34	4.12	0.04
TNR + impervious + food + forest	6	−74.56	163.59	4.36	0.04
TNR	3	−78.51	163.67	4.44	0.04
impervious + food + forest	5	−76.16	164.04	4.81	0.03
TNR + forest	4	−77.92	164.95	5.72	0.02
TNR + impervious	4	−78.36	165.83	6.60	0.01
TNR + impervious + forest	5	−77.69	167.09	7.87	0.01
null	2	−81.63	167.57	8.35	0.01
(B) Predation of native species					
forest	2	−15.41	35.06	0.00	0.98
impervious	2	−19.82	43.88	8.81	0.01
food	2	−20.95	46.15	11.08	0.00
null	1	−22.32	46.73	11.67	0.00
(C) Predation of brown rats					
forest + food + impervious	4	−37.22	83.03	0.00	0.22
forest + impervious	3	−38.36	83.06	0.04	0.22
forest	2	−39.47	83.11	0.08	0.21
forest + food	3	−38.71	83.77	0.75	0.15
forest + impervious + TNR	4	−38.33	85.24	2.21	0.07
forest + TNR	3	−39.47	85.28	2.26	0.07
forest + food + TNR	4	−38.65	85.90	2.87	0.05
food + impervious	3	−47.17	100.69	17.66	0.00
impervious	2	−48.37	100.90	17.87	0.00
TNR + impervious	3	−48.19	102.73	19.70	0.00
food + impervious + TNR	4	−47.12	102.84	19.81	0.00
null	1	−50.43	102.91	19.89	0.00

3.2. Probability of preying on native species

Cats were detected transporting 8 identifiable species. Of the 73 domestic cat predation events, 11% (n = 8) of prey items were native species, 60% (n = 44) were non-native, and the remaining 29% (n = 22) could not be identified to species (Table 2). An additional predation event of a 9th identifiable species by a cat whose TNR status could not be determined was not included in our models, but is listed in Table 2. Distance to forest edge received the greatest model support for predicting whether a prey species was native or non-native ($\beta = -2.27$ [95% CI: -3.81 to -0.73]; Table 1; Fig. 2).

3.3. Predation of non-native brown rats

Thirty four of the 44 (77%) predated non-native species were brown rats (Table 2). Predation of rats was best explained by distance to forest ($\beta = 1.52$ [95% CI: 0.66–2.38]; Fig. 2), percent impervious surface ($\beta = 0.58$ [95% CI: -0.11–1.27]) and feeding location density ($\beta = -0.46$ [95% CI: -1.08–0.16]; Table 1). Models containing distance to forest edge and impervious surface ($\Delta AIC_c = 0.04$; $\beta = 0.49$ [95% CI: -0.19–1.17]); distance to forest edge alone ($\Delta AIC_c = 0.08$; $\beta = 1.55$ [95% CI: 0.72–2.38]); and distance to forest edge ($\beta = 1.65$ [95% CI: 0.75–2.53]) and feeding location density ($\Delta AIC_c = 0.75$; $\beta = -0.37$ [95% CI: -0.97–0.23]) were all within 2 ΔAIC_c (Table 1). For all four top models, distance to forest edge was the only variable with 95% confidence intervals that did not overlap zero.

3.4. Buffer zones to reduce the probability that a prey species is native

We used the results of our top model explaining the predation risk for native species (distance to forest edge) to designate cat exclusion buffer zones based on 4 probability levels: 0% (808-m), 10% (416-m), 25% (254-m), and 50% (81-m), plus an additional 171-m to account for the average cat home range. The near-zero probability that a cat preys upon a native species (<1% probability threshold + home range buffer; 979-m buffer) would require excluding cats from 91.7% of the study area (Fig. 3). A 10% (587-m), 25% (425-m), and 50% (251-m) buffer would consist of 81.0%, 73.8%, and 62.1% of the total land area, respectively (Fig. 3).

4. Discussion

Biodiversity loss via predation by free-roaming domestic cats is well-documented (Doherty et al., 2016). Such loss can include the extirpation of ecosystem services and keystone species that are integral to the health of the ecosystem (Trouwborst et al., 2020; Cove et al., 2019; Mori et al., 2019; Doherty et al., 2016), especially in areas already subject to external stressors such as urban environments (Trouwborst et al., 2020; Francis and Chadwick, 2015). While predation by cats may be the motivation for many population management decisions (e.g., Calver et al., 2011), predatory behavior is often not an explicit consideration in the formation of such decisions (Longcore et al., 2009), possibly due to a scarcity of data pertaining to predatory behavior across urban landscapes. By implementing location-specific management decisions based on predation behavior, the impact of cats on native biodiversity could be notably reduced. Our study found that feeding location density and TNR status were the strongest predictors of local predation rates by cats. Furthermore, we found that the probability of a prey species being native increased closer to forest edges, and the probability of a prey species being a brown rat increased as distance to forest edge increased. These findings can inform free-roaming cat management that protects native wildlife without relying on policies that are unlikely to be implemented at a large scale such as total bans on cats.

Supplemental feeding of cats is often conducted to satiate a cat's drive to hunt (Cecchetti et al., 2021; Robertson, 2008). However, most studies conclude that cats receiving subsidized food continue to prey
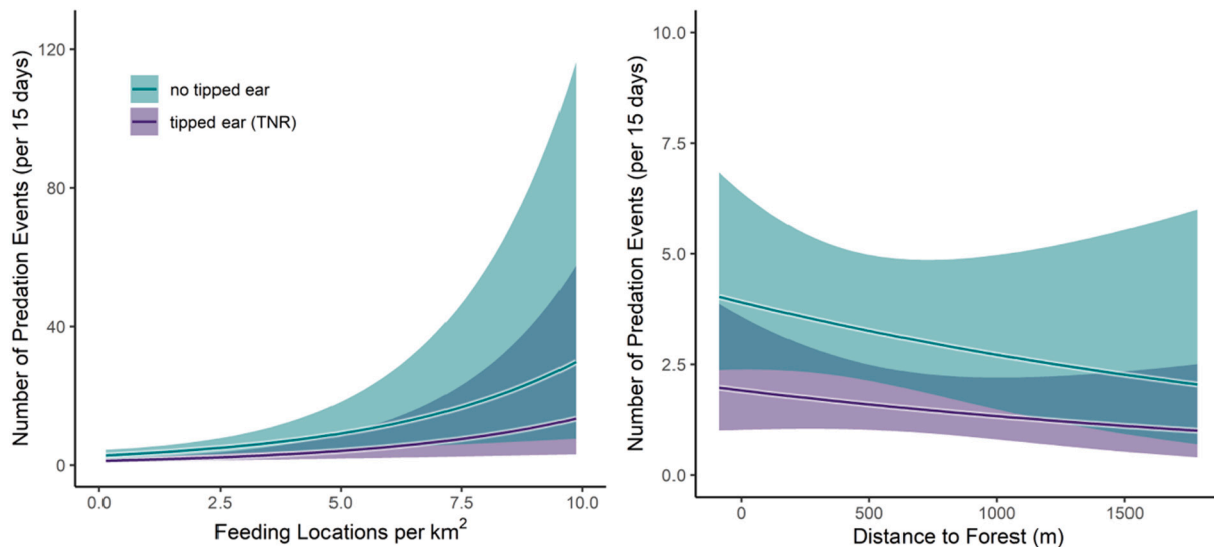
Fig. 1. Predicted number of total predation events (solid lines) and 95% confidence interval (shaded polygons) as a function of feeding location density predicted from our top model (left) and distance to forest edge predicted from our third top model (right). When predicting across distance to forest edge, density of feeding locations was held constant at the mean density. A tipped ear indicates participation in a TNR program.

Table 2

Tabulated documented predation events by domestic cats regardless of TNR status in Washington, D.C. (2018–2020). Predation events by other species can be found in Appendix 1.

Prey species		Class	Number of predation events
Brown rat	*Rattus norvegicus*	Mammal	34
House mouse	*Mus musculus*	Mammal	9
Unknown rodent species	NA	Mammal	6
White-footed mouse	*Peromyscus leucopus*	Mammal	3
Eastern gray squirrel	*Sciurus carolinensis*	Mammal	1
Southern flying squirrel	*Glaucomys volans*	Mammal	1
Unknown bird species	NA	Bird	4
European starling	*Sturnus vulgaris*	Bird	1
Northern cardinal	*Cardinalis cardinalis*	Bird	1
Mourning dove	*Zenaida macroura*	Bird	1
Yellow-throated warbler	*Setophaga dominica*	Bird	1
Unknown snake species	NA	Reptile	1
Unknown species	NA	Unknown	12

upon native wildlife (Cove et al., 2018; Loyd et al., 2013; Castillo and Clarke, 2003; Lepczyk et al., 2004; Hawkins et al., 1999). Furthermore, supplemental food reduces the territoriality of individual cats, allowing cat populations to persist at greater densities (Tennent and Downs, 2008; Kays and DeWan, 2006; Lepczyk et al., 2004; Warner, 1985), and presumably attracts rodents and other scavenging prey species (Hawkins et al., 1999). These unintended consequences of supplemental food potentially amplify population-level predation rates (Kays et al., 2020). Our analyses found that cat feeding location density had a positive relationship with the number of predation events (Table 1). Although TNR status was also included in two of the three top models, the 95% confidence intervals of ear-tipped and non-ear-tipped cats largely overlapped (Fig. 1), indicating a non-significant difference between the predation rates of these two sub-populations. Considered together, these findings support claims that subsidized populations of cats continue to have an adverse effect on local wildlife regardless of whether they are

sterilized or cared for (e.g., Cove et al., 2018; Longcore et al., 2009; Kays and DeWan, 2006; Castillo and Clarke, 2003).

Cat management decisions to preserve biodiversity would benefit from considering the spatial location of outdoor feeding sites. Currently, other municipalities may find it difficult to enact these management recommendations since feeding locations are often run by individuals and their locations are not readily known (Finkler et al., 2011). We recommend that stakeholders work together to document and share data on free-roaming cat feeding locations, while ensuring the privacy of individuals who feed cats. Such an initiative would provide practitioners with the data necessary to better manage cat populations and minimize their predation on native wildlife.

Despite their reputation for suppressing rat populations, cats often select smaller and easier-to-catch prey in lieu of rats when possible (Glass et al., 2009; Childs, 1986). However, cats are opportunistic generalists, and their prey composition is generally proportionate to local prey availability (Krauze-Gryz et al., 2017; Kutt, 2012). Our study found that the probability of rat predation increases with distance to the forest edge (Fig. 2), presumably as a function of greater rat availability in the more urbanized matrix (Herrera et al., 2021; Feng and Himsworth, 2014; Loss et al., 2013). Conversely, the probability of a prey species being native had an inverse relationship with distance to forest edge (Fig. 2). Since prey selection was greatly influenced by the degree of urbanization (i.e., impervious cover) and the distance to an urban forest, the predation of native species may be reduced by limiting free-roaming cats to developed areas where native species are less common (*but see also*: Van Heezik et al., 2010).

Our recommendations are based on the nature of predation rather than solely on administrative park boundaries, or the average roaming distance of cats, as previously reported (Metsers et al., 2010; Lilith et al., 2008). However, roaming distances are important to consider. For example, if the center of a cat's home range is located at the boundary of a risk threshold buffer, the cat's home range can extend roughly 170-m past this threshold and into areas that have a greater probability of native predation (Fig. 3). Therefore, we recommend adding the average home range of an urban cat to the risk threshold buffers (home range + buffer distance). Our analysis indicates that a buffer zone of 979-m (171-m home range + 808-m exclusion buffer) from forested areas would likely achieve near-zero probability (<1%) of predation of native species. Alternative buffer widths based on the probability of native predation and cat home range include 587-m (10% probability of preying
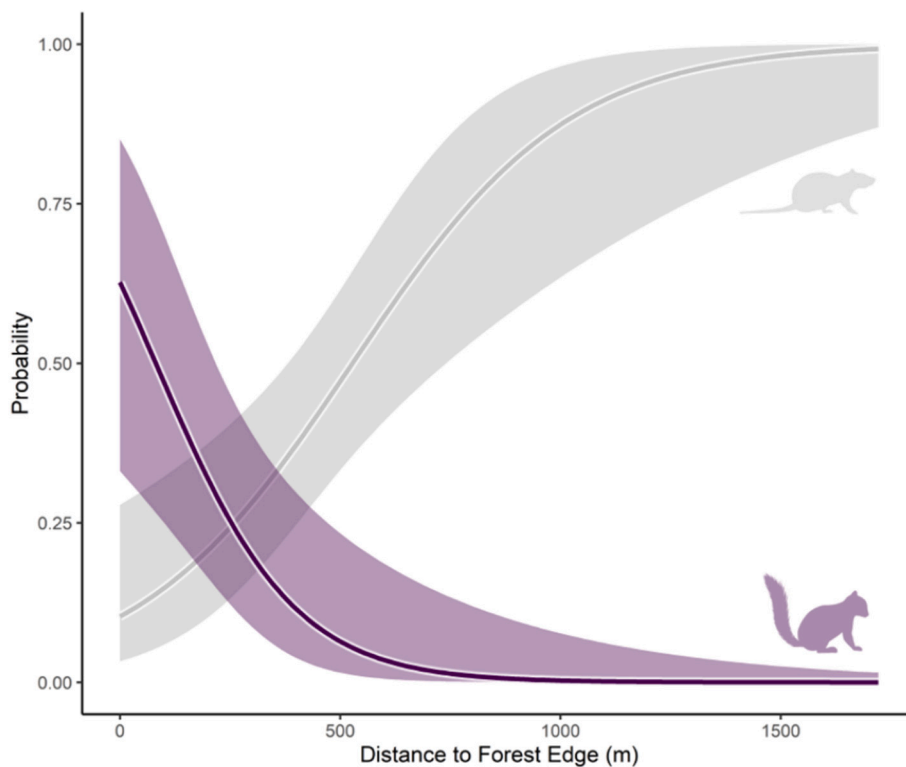
Fig. 2. Probability (solid line) and 95% confidence interval (shaded polygon) of a prey species being native (purple) or a non-native brown rat (gray) predicted as a function of distance to forest edge. Where applicable, other covariates within the model were held constant at their mean value. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
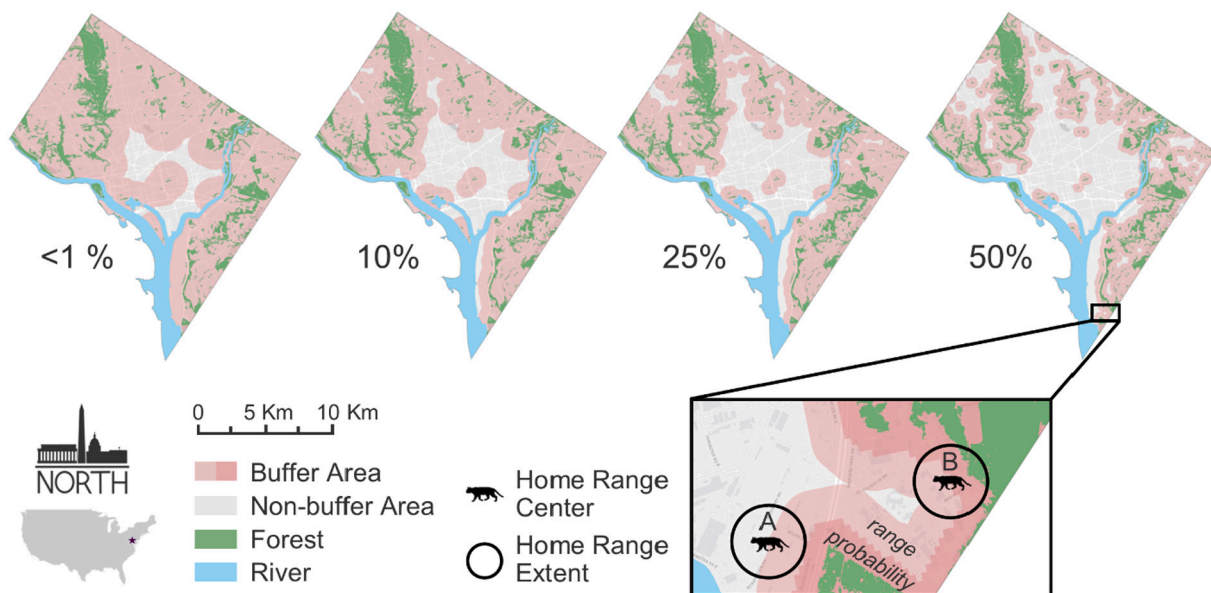

Fig. 3. Buffer zones in Washington, D.C. based on the probability of predation of native species and average cat home range. Within the inset, home range A illustrates how the additional range buffer positions the end of a cat's range at the probability threshold. Conversely, home range B does not utilize a home range buffer and the cat's range extends into the forest despite being centered at the cusp of the probability threshold.

on native species), 425-m (25% probability of preying on native species), and 251-m (50% probability of preying on native species) from forest edges (Fig. 3). We believe that a 25% probability risk threshold would be an attractive recommendation for multiple parties. This value is well below chance for prey being a native species and the threshold occurs at the approximate distance from the forest edge in which the probability of a cat preying upon a non-native brown rat becomes greater than the probability of a cat preying upon native wildlife (Fig. 2).

Once local stakeholders agree on an acceptable buffer size, we recommend communities use these buffers as the basis for location-specific management policies that will ultimately remove the local population. Examples of such policies include, but are not limited to, implementing any of the following within the buffer area: issuing fines to pet owners who allow their cats to roam (Lloyd et al., 1979),

prohibiting the feeding of outdoor cats (Hawkins et al., 1999), establishing a cat curfew (Lilith et al., 2010; Metsers et al., 2010), targeted removal of free-roaming cats (Boone et al., 2019), or banning cats altogether (Metsers et al., 2010). Because of differences in stakeholder perceptions, local geography and ecology, access to funding, and means of enforcement, a universal solution is not possible. As such, stakeholders should work together to determine the policies best suited for their community (e.g., ACT, 2021; NCMSG, 2020; G2Z, 2017; etc.). Additionally, we advocate that all stakeholders involved in the formation of these policies work to jointly communicate and implement policies to avoid polarization.

Biodiversity loss from non-native predators is a pressing environmental issue compounded by habitat loss and fragmentation (Doherty et al., 2016). The ecological loss inflicted by cats is well-documented (Loss et al., 2013). While some non-native species are relatively self-sufficient and are largely beyond human control, cats pose a unique situation in which their continued persistence on the landscape can be largely attributed to human actions (Doherty et al., 2014; Lepczyk et al., 2011; Finkler et al., 2011). Professionals across relevant fields largely agree that cats face and impose risks when outdoors, however proposed management actions differ (Foreman-Worsley et al., 2021; Leong et al., 2020; Sherwood et al., 2019; Wald et al., 2013). Here we present data-driven management recommendations with the goal of protecting areas of ecological concern rather than uniformly attempting to preserve the entire urban landscape. We believe that such a paradigm shift continues to satisfy the goals of most relevant stakeholders and offers a collaborative approach to free-roaming cat management.

5. Conclusions

Our analyses suggest that predation by free-roaming domestic cats is highest when supplemental food is abundant, and that the probability of a cat preying upon native species increases closer to forest edges. We contend that buffer zones based on a combination of probability of native species predation and cat home range will serve as a reasonable approach to urban free-roaming cat management. Since the probability of native predation increases with proximity to forest edges, and greater access to supplemental food increases local predation by populations of

free-roaming cats, we recommend (1) that acceptable probabilities of native predation be agreed upon by local stakeholders and (2) management that ultimately removes the local free-roaming cat population within a distance from forests that meet those probability thresholds. While these measures may reduce the risk of predation of native species, the risk to native species will only be eliminated by keeping cats indoors.

CRediT authorship contribution statement

D.J. Herrera: Investigation, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **M.V. Cove:** Methodology, Writing – review & editing. **W.J. McShea:** Methodology, Writing – review & editing. **D.T. Flockhart:** Methodology, Writing – review & editing. **S. Decker:** Writing – review & editing. **S.M. Moore:** Investigation, Data curation, Writing – review & editing. **T. Gallo:** Formal analysis, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix 1. Documented predation events by all predator species in Washington, D.C. (2018–2020)

Predator species	Prey species	Number of predation events detected
Domestic cat	Mammals	
Felis catus	Brown rat	34
	Rattus norvegicus	
	House mouse	9
	Mus musculus	
	Unknown rodent species	6
	White-footed mouse	3
	Peromyscus leucopus	
	Eastern gray squirrel	1
	Sciurus carolinensis	
	Southern flying squirrel	1
	Glaucomys volans	
	Birds	
	Unknown bird species	4
	European starling	1
	Sturnus vulgaris	
	Northern Cardinal	1
	Cardinalis cardinalis	
	Mourning dove	1
	Zenaida macroura	
	Yellow-throated warbler	1
	Setophaga dominica	
	Reptiles	
	Unknown snake species	1
	Other	

(*continued*)

Predator species	Prey species	Number of predation events detected
	Unknown species	12
Red fox	Mammals	
Vulpes vulpes	Virginia opossum	3
	Didelphis virginiana	
	Eastern gray squirrel	2
	Sciurus carolinensis	
	Eastern cottontail	1
	Sylvilagus floridanus	
	White-tailed deer	1
	Odocoileus virginianus	
	Unknown rodent species	1
	Birds	
	Black-crowned night heron	1
	Nycticorax nycticorax	
	Other	
	Unknown species	6
Red-tailed hawk	Mammals	
Buteo jamaicensis	Brown rat	1
	Rattus norvegicus	
	Birds	
	European starling	1
	Sturnus vulgaris	
	Rock dove	1
	Columba livia	
	Reptiles	
	Eastern worm snake	1
	Carphophis amoenus	
Virginia opossum	Mammals	
Didelphis virginiana	Eastern gray squirrel	2
	Sciurus carolinensis	
Gray fox	Other	
Urocyon cinereoargenteus	Unknown species	1

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Glossary

Free-roaming domestic cat   A domestic cat (Felis catus) with partial or total access to the outdoor environment without supervision or restraint, regardless of ownership or degree of sociability.:

Trap-Neuter-Return (TNR)   A population management strategy for free-roaming domestic cats in which cats are trapped, spayed or neutered, often vaccinated, and returned to the area from which they were trapped. Long-term care is generally provided via regular distribution of supplemental food and, in some cases, the provision of outdoor shelters.:

Feeding location   A location in which supplemental food is routinely provided for free-roaming domestic cats. Depending on the population of nearby cats and the frequency of food, this is also sometimes referred to as a 'feeding station.':

Ear-tip   A counterintuitive term that refers to the flattened end of a TNR'ed. cat's ear. Veterinarians surgically remove approximately one cm of the cat's left ear when spaying/neutering to ensure that future TNR practitioners can identify it as already sterilized.: