

RH: Cats in Suburban Nature Preserves

1 **Title**

2 Anthropogenic factors influence the occupancy of an invasive carnivore in a suburban
3 preserve system

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20 **Abstract**

21 Domestic cats (*Felis catus*) are one of the world's most damaging invasive species. Free-
22 ranging cats kill billions of wild animals every year, spread parasites and diseases to both
23 wildlife and humans, and are responsible for the extinction or extirpation of at least 63
24 species. While the ecology and conservation implications of free-ranging cats have well
25 studied in some locations, relatively little is known about cats inhabiting urban nature
26 preserves in the United States. To address this knowledge gap, we used camera traps to
27 study the occupancy and activity patterns of free-ranging cats in 55 suburban nature pre-
28 serves in the Chicago, IL metropolitan area. From 2010–2018 (4,440 trap days), we rec-
29 orded 355 photos of free-ranging cats across 26 preserves ($\psi_{\text{naïve}} = 0.45$) and 41 randomly
30 distributed monitoring points ($\psi_{\text{naïve}} = 0.18$). Cats were detected every year, but rarely at
31 the same point or preserve, and cats were largely crepuscular/diurnal. Using single-sea-
32 son occupancy models and a “stacked” design, we found that cat occupancy increased with

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33 building density and detectability was highest near the urban/preserve boundary. Based
34 on our top-ranked model, predicted occupancy within individual preserves ranged from
35 0.09 to 0.28 ($\psi_{\text{mean}} = 0.11$) and was poorly correlated with preserve size or shape. Overall,
36 our results suggest that free-ranging cats are rare within suburban preserves in our study
37 area, and that these cats are most likely owned or heavily subsidized by people (which
38 pose different risks and management challenges than truly feral cats). We discuss the
39 conservation and management implications for urban natural areas.

40

41 **Keywords**

42 Chicago, detection probability, domestic cat, *Felis catus*, Illinois, modeling, urbanization,
43 wildlife

44

45 **Highlights**

- 46 • We surveyed for domestic cats across 55 suburban preserves from 2010-2018.
- 47 • We modeled occupancy and detectability as a function of urban covariates.
- 48 • Cat occupancy was low overall and best predicted by building density.
- 49 • The risk to native species is highest near preserve boundaries bordered by built envi-
50 ronments.

51

52

53 **1. Introduction**

54

55 Following a global trend of urbanization (Vitousek et al. 1997), most people in the
56 United States now live in urban areas (U.S. Department of Housing and Urban Develop-
57 ment and U.S. Census Department 2017). However, the area occupied by urban landcover
58 (indicative of suburban development), has greatly outpaced the rate of urban population
59 growth itself (Heimlich and Anderson 2001, Destefano et al. 2005). Suburban areas differ
60 from that of intensely urban city centers (e.g. Manhattan or downtown Chicago) and typ-
61 ically consist of single-family homes (single or double-storied) with lawns and backyards
62 spaced at a moderate to high density, interspersed with light industry, basic services, and
63 multi-family homes (Marzluff et al. 2001). This suburban expansion or “urban sprawl” is
64 a major threat to biodiversity, as it spreads the most pernicious threats of urbanization
65 (i.e. habitat loss, habitat fragmentation, and invasive species) outward from city centers
66 into the surrounding landscape (Czech et al. 2000, Marzluff et al. 2001, Marzluff 2002,
67 McKinney 2002, 2008).

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68 Domestic cats (*Felis catus*) are an invasive species common in urban and suburban
69 areas. Free-ranging domestic cats (i.e. cats that are outside direct supervision of a human
70 including pet cats that are allowed outside, barn cats, “community” cats, and feral or wild
71 cats) are one the world’s most damaging invasive species (Lowe et al. 2000, Doherty et al.
72 2016). Free-ranging cats kill billions of birds, mammals, and reptiles every year (Blancher
73 2013, Loss et al. 2013, Woinarski et al. 2017, 2018). Cats also spread parasites and dis-
74 eases to both humans and wildlife (Dubey and Jones 2008, Gerhold and Jessup 2013, Ma
75 et al. 2018), and are responsible for the extinction or extirpation of at least 63 species
76 (reviewed in Doherty et al. 2016). For example, cat depredation led to the extinction of
77 the Stephens Island Wren (*Traversia lyalli*) (Galbreath and Brown 2004) and the extir-
78 pation of the Estanque Island population of the Ángel de la Guarda Deer Mouse
79 (*Peromyscus guardia*) (Vázquez-Domínguez et al. 2004).

80 The ecological impacts of free-ranging cats are not limited to islands or wilderness
81 areas. Cats in urban areas prey on native species and can occur at densities much greater
82 than that of native carnivores (Churcher and Lawton 1987, Coleman and Temple 1993,
83 Burton and Doblár 2004, Lepczyk et al. 2004). For example, Balogh et al. (2011) reported
84 that domestic cats were responsible for 47% of known predation events on radio-tracked
85 fledglings, and Flockhart et al. (2016) estimated a free-ranging cat density of up to 49
86 cats/ha in Guelph, Canada. Cats in urban areas tend to have smaller home ranges than
87 those in rural or wild landscapes (Horn et al. 2011, Hall et al. 2016, Hanmer et al. 2017),
88 but they still venture into urban greenspaces, such as parks and nature preserves
89 (VanDruff and Rowse 1986, Kays and DeWan 2004, Morgan et al. 2009, Wierzbowska et
90 al. 2012, Gehrt et al. 2013), where potential impacts on biodiversity are likely larger. Hab-
91 itat selection of free-ranging cats, particularly in urban areas, is highly variable and likely
92 location specific. Studies from New Zealand to Illinois, USA have reported selection for
93 both urban and natural areas, avoidance of natural areas, and no habitat selection (Met-
94 sers et al. 2010, Horn et al. 2011, Gehrt et al. 2013, Kays et al. 2015, Elizondo and Loss
95 2016). Clearly, more research is necessary to better explain the habitat selection and space
96 use of free-ranging cats in urban areas.

97 In this paper, we describe the spatial ecology of free-ranging cats inhabiting 55
98 nature preserves in the suburbs of the third largest metropolitan area in the United States:
99 Chicago. While the demography and movements of free-ranging cats have been studied
100 extensively in dense urban areas, relatively few studies explore the ecology of cats inhab-
101 iting suburban nature preserves, and fewer still take a landscape-scale approach (Kays
102 and DeWan 2004, Morgan et al. 2009, Kays et al. 2015). Further, while anthropogenic
103 factors have been linked to cat population parameters (e.g. Flockhart et al. 2016), few
104 studies have compared the relative utility of different urban metrics (e.g. building density
105 versus percent impervious surfaces) as predictors of population parameters. To address
106 this deficit, we analyze nine years of systematic camera trapping data from a large-scale
107 and on-going suburban wildlife monitoring program. Specifically, we (1) use occupancy

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108 modeling to compare the relative importance of different urban covariates, (2) explore
109 temporal patterns of cat activity, and (3) examine the relationship between preserve de-
110 sign (e.g. size, shape, degree of urbanization) and cat occupancy.

111 To the best of our knowledge, this is the first study to generate detection-corrected,
112 spatially explicit estimates of free-ranging cat occupancy across a landscape of suburban
113 preserves. The results from this study can be used by land managers, conservation biolo-
114 gists, and urban planners to aid in the management of free-ranging cats, to help develop
115 conservation plans for cat-sensitive species, and to guide the design of suburban nature
116 preserves.

117

118 **2. Methods**

119 *2.1. Study Location*

120 Our study took place in Lake County, IL (land area = ~1150 km²). Lake County is a
121 highly urbanized suburb in the Chicago Metropolitan Area (Figure 1). Lake County is one
122 of the most densely populated counties in the United States with ~700,000 people and a
123 population density of 607 persons/km² (United States Census Bureau 2018), and the
124 greater metro area has >10,000,000 inhabitants. Prior to European settlement (pre
125 1830), Lake County was a mosaic of savanna (45%), prairie (30%), and woodland/forest
126 (15%) (Bowles and McBride 2005), but today is dominated by anthropogenic features
127 (Figure 1). Within this urban landscape, the Lake County Forest Preserve District
128 (LCFPD) manages 55 “forest preserves”, totaling 120 km² for multiple uses, including bi-
129 odiversity conservation and outdoor recreation. During our study, dominant plant com-
130 munities within LCFPD preserves included forest (28%), wetlands (17%), and old fields
131 (15%). Historically dominant communities such as prairie and savanna were uncommon
132 (8% and 5%, respectively). Developed land (including turf grasses) was rare (3%) within
133 the preserve boundaries themselves, although this excludes public roads and private in-
134 holdings. Other community types (e.g. crops, woody shrubs) make up the remaining 24%
135 (XX, unpublished data). The climate in Lake County is temperate with precipitation av-
136 eraging 93 cm/year (Illinois State Climatologist 2019). In this paper we refer to these
137 “forest” preserves as “preserves” or “nature preserves,” but point out we are not referring
138 to Illinois Nature Preserves as designated by the Illinois Nature Preserve Commission.

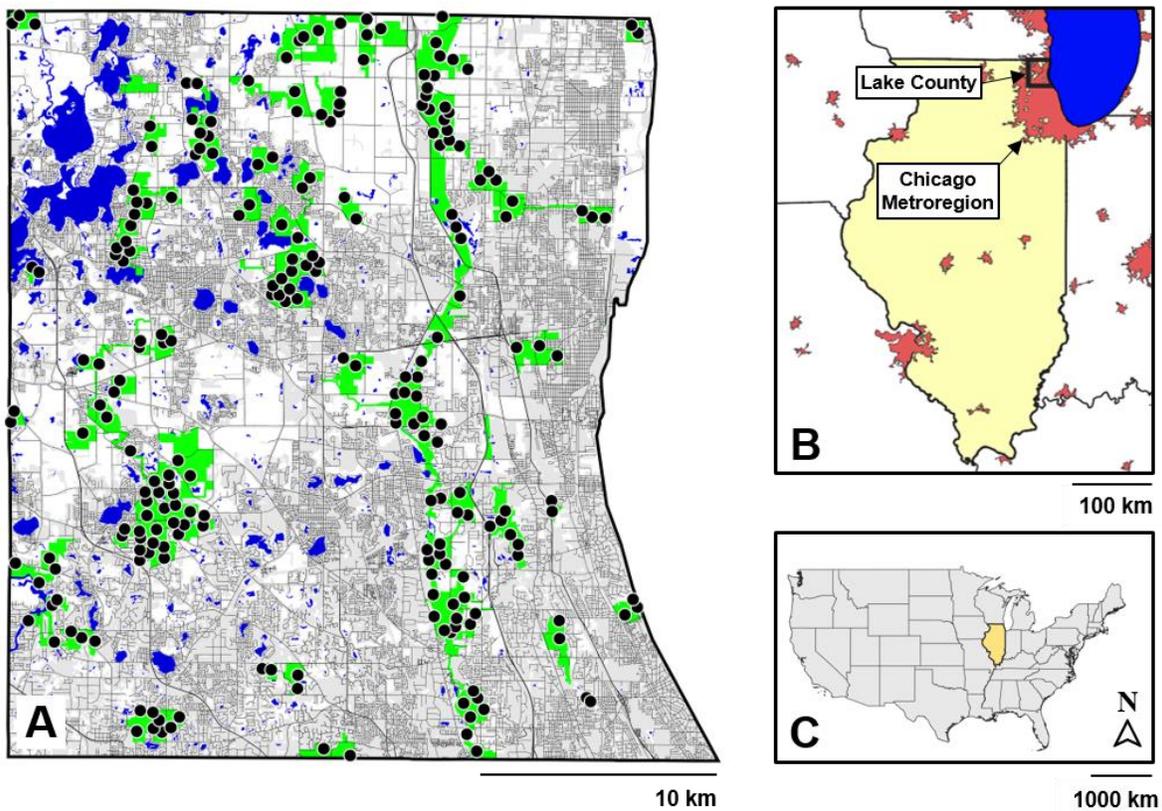
139 *2.2. Field Methods*

140 We used remote camera traps (Kelly et al. 2012) to monitor mesopredators, includ-
141 ing domestic cats, at 232 monitoring points across 55 Lake County preserves from 2009
142 to 2018 (Figure 1). As part of the long-term multi-taxa wildlife monitoring program (Cas-
143 sel 2014, Cassel et al. 2019, 2020, Vanek and Glowacki 2019, Vanek et al. 2019) preserves
144 were initially categorized into two groups (priority and non-priority) based on *a priori*

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145 restoration and management goals by LCFPD wildlife ecologists. We used a geographic
146 information system (GIS) to randomly distribute points at an average density of 0.5
147 points/ha in priority preserves and 0.2 points/ha in non-priority preserves with a mini-
148 mum of 2 points/preserve and a minimum distance of 400 m between points. Not all
149 preserves could be sampled every year due to the scale of the study, so we used a stag-
150 gered-entry design starting in 2010 with 18 preserves and 82 points (Table 1). We sampled
151 priority preserves (n = 26) every other year and non-priority preserves (n = 29) every four
152 years. Each year we sampled scheduled preserves (and all monitoring points within) for
153 4 nights (5 calendar days) over an 8-week period from mid-August through early Novem-
154 ber. These rapid biodiversity surveys took place in the autumn to maximize the detection
155 probability of native mesopredators as offspring mature and disperse.

156



157

158

159 **Figure 1.** Lake County is a highly urbanized suburb of Chicago, IL, USA. (A) Camera trap loca-
160 tions (black circles, n = 232) and preserves (green polygons, n = 55) monitored from 2009-2018
161 for mesopredators, along with roads (dark grey lines), open water (blue polygons), and urban land-
162 cover classes (light grey polygons) pooled from the from the 2011 National Landcover Database
163 (Homer et al. 2015). White space indicates other landcover classes which consist mostly of

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164 agriculture (center) and emergent wetlands (northwest and northeast corners). (B) Location of
165 Lake County within Illinois (beige) and in relation to the third largest metro region in the USA,
166 Chicago (labeled) and other major US Census designated urban areas (maroon). (C) Location of
167 Illinois (beige) within the United States.

168

169 During each sampling occasion, we deployed one camera (Leaf River® IR-3BU™,
170 Cuddeback® Ambush™, or Bushnell® Trophy Cam™) within a 100 m buffer of each
171 monitoring point at locations frequented by mesopredators (e.g. game trails or habitat
172 edges). We mounted cameras on trees or metal posts at a height of 0.5 m with a line-of-
173 sight parallel to the ground or slightly downward. We emptied one can of sardines (106
174 g) on the ground 5 m in front of each camera and cleared any vegetation or debris between
175 the camera and the bait. Cameras were deployed on Mondays and removed on Fridays
176 (thus totaling 4 trap nights over 5 calendar days per sampling occasion). We set cameras
177 to take 1 photo per trigger with a delay of 1 minute. Cameras were checked daily and we
178 replaced bait as needed.

179

180 **Table 1.** Camera trap effort used to sample mesopredators at 232 monitoring points across 55
181 preserves from 2010–2018 in Lake County, IL. Preserves were sampled using a staggered-entry
182 design entry and preserves were sampled either every two or four years depending on their priority
183 status. One camera was assigned to each monitoring point and set for 4 trap nights (Monday–
184 Friday; 5 calendar days) during each sampling period. The Trap Days column reflects missing
185 sampling periods due to malfunctioning cameras, theft, etc.

186

Year	Preserves Sampled	Points Sampled	Trap Nights	Trap Days
2010	20	105	420	515
2011	21	94	376	455
2012	21	108	432	540
2013	20	87	348	435
2014	20	105	420	445
2015	20	91	364	455
2016	20	106	424	530
2017	20	87	348	435
2018	20	105	420	525
Total	55	232	3552	4335

187

188 *2.3. Activity Patterns*

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189 We created circular kernel density estimates for free-ranging cats using the *over-*
190 *lap* package in the R Statistical Environment (R Core Team 2018), which uses a *von*
191 *Mises* kernel density function to accurately represent the circular distribution of time of
192 day (Rowcliffe et al. 2014). We excluded all detections at the same site if they were
193 within 10 minutes of a previous detection to avoid temporal autocorrelation of the same
194 animal triggering a camera repeatedly.

195 2.4. Occupancy Models

196 We used single-season occupancy models (MacKenzie et al. 2002, Tyre et al. 2003)
197 to investigate the occupancy and detectability of free-ranging cats. This method estimates
198 rates of site occupancy (the probability a site is occupied; ψ) and detectability (the prob-
199 ability a species is detected at a site *given a site is occupied*) based on repeated surveys at
200 a site. Estimates of ψ explicitly incorporate the uncertainty of detection probabilities < 1 .
201 Ignoring the biological reality of imperfect detectability can result in incorrect estimates
202 of wildlife parameter estimates (Gu and Swihart 2004). Occupancy models are useful
203 when surveying large areas because they do not rely on identifying individuals, require
204 only presence-absence data, and allow for both parameters to vary by both site- and sur-
205 vey-specific covariates (MacKenzie et al. 2002, 2017). The alternative for a multi-year
206 study like ours would be to use a dynamic occupancy model (MacKenzie et al. 2003), but
207 we were more interested in site-use and spatial patterns than rates of colonization and
208 extinction. See Bailey & Adams (2005) for an accessible overview of occupancy analysis.

209 2.5. Modeling Procedure

210 We considered four indices of urbanization we hypothesized would predict occu-
211 pancy and detectability of free-ranging cats: distance to nearest building, building den-
212 sity, % impervious surface, and area protected by preserves. We developed directional
213 predictions based on how they might influence these parameters (Table 2). The average
214 correlation coefficient between these covariates was $|0.48| \pm 0.05$. We used a GIS to cal-
215 culate the distance to nearest building, building density, and impervious surface indices
216 using high resolution (1 m) landcover data for Lake County (Chicago Metropolitan Agency
217 for Planning Data Hub 2018). We used a 400 m buffer from the center of each monitoring
218 point for the building density, impervious surface, and preserve area covariates based on
219 the minimum distance between monitoring points, which also corresponds to the recom-
220 mended buffer distance between houses and areas containing species vulnerable to cat
221 depredation (Hanmer et al. 2017). We used a preserve area covariate instead of a “dis-
222 tance to urban-edge” covariate as used in other studies because it is often arbitrary where
223 the “urban-edge” begins. We included sampling year as a site-specific covariate, along
224 with survey day and temperature as survey-specific covariates to control for any latent
225 heterogeneity in our sampling methodology. We created the temperature covariate using
226 historical data from weather station USCO0115961 in Lake County (Midwestern Regional
227 Climate Center 2019).

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228

229 **Table 2.** Site and survey covariates used to model the occupancy (ψ) and detectability (p) of do-
230 mestic cats in Lake County, IL preserves from 2010–2018. Hypotheses refer to the predicted rela-
231 tionship between urban covariates and model parameters. Site covariates were used to model oc-
232 cupancy and detectability, while survey covariates can only be used to model detectability. Sam-
233 pling year was modeled as a categorical covariate.

Covariate	Parameters and Hypotheses	Median (Range)	Description
Nearest Building (km)	ψ : decrease p : decrease	0.24 (0.08–0.98)	distance from monitoring point to nearest building
Building Density (buildings/ha)	ψ : increase p : increase	0.22 (0.00–4.66)	number of buildings within 400 m buffer (50.4 ha) around monitoring point
Impervious Surface (%)	ψ : increase p : increase	3.06 (0.00–24.2)	area impervious surface (roads, pavement, buildings) within 400 m buffer around monitoring point
Preserve Area (%)	ψ : decrease p : decrease	0.71 (0.15–1.00)	area within 400 m buffer of monitoring point within preserve boundaries
Sampling Year	ψ : n/a p : n/a	N/A (2010–2018)	year monitoring point was sampled
Temperature (°C)	p : n/a	14.4 (01.7–28.1)	mean daily temperature of survey period
Survey Date	p : n/a	275 (233–309)	ordinal day of year of survey period (275 = 2 Oct)

234

235 We compiled detection histories for each monitoring point-year combination and
236 considered each calendar day a camera was active to be a single survey. Thus, we had a
237 total of 5 survey periods for each point-year combination. We considered each monitoring
238 point-year combination to be a distinct site (i.e. a stacked design) (Fuller et al. 2016, Crum
239 et al. 2017, Goldspiel et al. 2019). We excluded data from the first year of the monitoring
240 program (2009) from our analysis due to low detections for all species and lower effort
241 relative to subsequent years.

242 We fit models using a maximum likelihood implementation of single-season occu-
243 pancy analysis within the *unmarked* R package (Fiske and Chandler 2011). This hierar-
244 chical model contains two submodels, one for the occupancy component (ecological pro-
245 cess; ψ), and the other for the detection component (observation process; p):

246

$$z_i \sim \text{Bernoulli}(\psi)$$

247

$$y_{ij} | z_i \sim \text{Bernoulli}(z_i * p)$$

248 where z_i is a latent variable representing the true occupancy state at site i , and y_{ij} is the
249 observed occupancy status at site i during survey j , conditional on the true occupancy
250 status z_i (Kéry and Royle 2016). Using a two-stage modeling approach, we first deter-
251 mined the best occupancy sub-model by ranking *a priori* candidate models using a highly
252 parameterized detection sub-model. We then used the most parsimonious occupancy

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253 sub-model to determine the best detectability sub-model (MacKenzie et al. 2017). We
254 used the *AICcmodavg* package to rank models with QAIC_c (quasi-Akaike's Information
255 Criterion corrected for small sample sizes) with an overdispersion modifier of 1.1 based
256 on 1000 simulations of the MacKenzie and Bailey Goodness-of-fit Test (MacKenzie and
257 Bailey 2004). We considered models with $\Delta\text{QAIC}_c < 2$ to have “substantial empirical sup-
258 port” (Burnham and Anderson 2002, Powell and Gale 2015). See the supplemental mate-
259 rials for yearly detection histories, site-specific covariate data, candidate model sets, and
260 R scripts.

261 *2.6 Overall Detection Probability*

262 To estimate the number of surveys needed to detect cats during a single 4 trap
263 night, 5 calendar day camera trap survey, we used values from top ranked, detection
264 corrected occupancy model and the formula

$$265 \quad d = 1 - (1 - p)^k$$

266 where p = the per-survey detection probability and k = the number of surveys (Powell
267 and Gale 2015).

268 *2.7 Landscape Scale Occupancy*

269 We used the top ranked, detection corrected occupancy model to generate spatially
270 explicit estimates of cat occupancy across all 55 preserves. First, we generated a grid of 25
271 m x 25 m squares across all preserves using a GIS, then estimated the occupancy value for
272 the centroid of each point using the *predict* function in R. We averaged these predicted
273 occupancy values to estimate mean occupancy for each preserve. In addition, because
274 preserves often consist of distinct geographic units, we also calculated predicted occu-
275 pancy for each preserve patch, which we defined as each separate polygon in our preserve
276 shapefile layer. For example, a preserve bisected completely by a paved road would con-
277 sist of two separate patches. In total, we were able to divide the 55 preserves into 159
278 distinct patches (mean area = 73.1 ha, median = 40.7 ha, SD = 89.5, range = 0.02 – 453.7
279 ha). We hypothesized that cat occupancy would be higher in smaller preserves and
280 patches (Crooks 2002).

281 Finally, we compared the estimated occupancy for each preserve against two com-
282 monly used landscape/design metrics: preserve size (log ha) and an index of preserve
283 shape (Patton 1975):

$$284 \quad \text{SHAPE} = \frac{\text{perimeter}}{2 * \sqrt{\pi * \text{area}}}$$

285 where *perimeter* is the perimeter of a preserve in m and *area* is the area of a preserve in
286 m². A perfectly compact preserve (a circle) would have a SHAPE index of 1, and values
287 larger than 1 indicate an increasingly irregular perimeter to area ratio. We hypothesized

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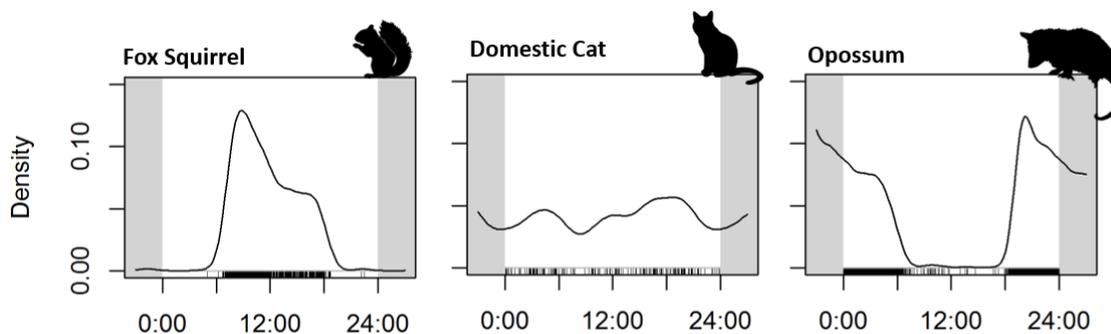
288 that cat occupancy would be lower in more compact preserves and patches (Crooks and
289 Soulé 1999).

290

291 3. Results

292 3.1 Camera Trapping

293 We detected cats during all 9 years of the study (Table 3) with the number of de-
294 tectations ranging from four in 2018 to nine in 2012 and 2014. We defined a detection as at
295 least one cat photo at a monitoring point during a survey day. We detected cats 94 times
296 across 45% of preserves ($n = 25$) and 18% of monitoring points ($n = 41$). Cats were most
297 often detected only once during a single survey week ($n = 37$), less frequently twice ($n =$
298 10), three times ($n = 8$), and four times ($n = 2$). Cats were only detected during all five
299 survey days once. We detected cats at the same monitoring point between years infre-
300 quently ($n = 11$ points) and we tentatively identified at least 16 unique cats at these 11
301 points (based on a visual assessment). Cats were active during the evening, night, and day
302 with slight peaks of activity before dawn, at noon, and after dusk (Figure 2).



303

304 **Figure 2.** Free-ranging cats (*Felis catus*) in Lake County preserves were active at all times of the
305 day and were not clearly diurnal. Examples of diurnal species, the fox squirrel (*Sciurus niger*), and
306 a nocturnal species, the Virginia opossum (*Didelphis virginiana*), are shown for comparison. Cam-
307 era trap detections are shown above each x-axis. Activity periods were created using the overlap
308 package in R, which uses a von Mises kernel density function to accurately represent the circular
309 distribution of time of day.

310

311 **Table 3.** Domestic cats and species of native terrestrial mesopredators detected in Lake County
312 Forest Preserves via camera traps surveys from 2010–2018. Naïve occupancy is calculated as the
313 number of locations where a species was detected at any point of the nine years divided by the
314 total number of preserves ($n = 55$) and permanent monitoring points ($n = 232$).

Species	Years detected	# photos	Naïve Occupancy
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			Preserve	Points
Raccoon	9	10,197	0.98	0.92
Opossum	9	13,522	0.96	0.85
Coyote	9	913	0.91	0.57
Striped Skunk	9	898	0.75	0.47
Domestic Cat	9	355	0.47	0.18
Red Fox	7	26	0.15	0.04

315

316 **3.2. Occupancy and Detection**

317 After removing models ($n = 5$) with uninformative parameters (Arnold, 2010), we
 318 found substantial support ($\Delta\text{QAIC}_c < 2$) for two occupancy sub-models: $\psi(\text{IMPERVIOUS}$
 319 $\text{SURFACE})$ and $\psi(\text{BUILDING DENSITY})$. These models had very similar levels of support and
 320 were essentially equivalent with comparable QAIC_c weight and a cumulative model weight
 321 of 0.79 (Table 4). These models were 4.1–5.0 times more likely to be the best model than
 322 the null model (model likelihood = 0.20), 4.9–6.0 times more likely than the $\psi(\text{NEAREST}$
 323 $\text{BUILDING})$ model, and 15.1–18.5 times more likely than the $\psi(\text{PRESERVE AREA})$ model.
 324 There was essentially no support ($\Delta\text{QAIC}_c > 12$) for models containing the year covariate
 325 (Table 4). Full model selection results, including identification of models with uninforma-
 326 tive parameters, are presented in the Supplementary Materials.

327

328 **Table 4.** Full model set used to evaluate occupancy (ψ) for domestic cats fitted to stacked detection
 329 history data from 232 monitoring points across 55 preserves in Lake County, IL from 2010-2018.
 330 We modeled occupancy while fixing detection to a sub-global model: $p(\text{DOY} + \text{TEMP} + \text{BDE} +$
 331 $\text{DNB} + \text{FPA} + \text{IMP})$.

332

Model ^a	K ^b	ΔQAIC_c ^c	QLL ^d	w_i ^e	Cumulative w_i
$p(\text{G}) \psi(\text{IMP})$	10	0.00	-330.97	0.21	0.21
$p(\text{G}) \psi(\text{BDE})$	10	0.40	-331.17	0.17	0.38
$p(\text{G}) \psi(\text{IMP} + \text{FPA})^*$	11	0.54	-330.14	0.16	0.54
$p(\text{G}) \psi(\text{BDE} + \text{FPA})^*$	11	1.20	-330.47	0.12	0.66
$p(\text{G}) \psi(\text{BDE} + \text{IMP})^*$	11	1.59	-330.67	0.09	0.75
$p(\text{G}) \psi(\text{BPR} + \text{IMP})^*$	11	2.08	-330.91	0.07	0.83
$p(\text{G}) \psi(\text{BDE} + \text{BPR})^*$	11	2.20	-330.97	0.07	0.90
$p(\text{G}) \psi(\cdot)$	9	3.22	-333.68	0.04	0.94
$p(\text{G}) \psi(\text{BPR})$	10	3.59	-332.77	0.04	0.98
$p(\text{G}) \psi(\text{BPR} + \text{FPA})$	11	5.71	-332.73	0.01	0.99

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$p(G) \psi(FPA)$	10	5.84	-333.89	0.01	1.00
$p(G) \psi(YEAR + IMP)$	18	12.43	-328.08	0.00	1.00
$p(G) \psi(YEAR + BPE)$	18	13.26	-328.50	0.00	1.00
$p(G) \psi(YEAR)$	17	15.46	-330.77	0.00	1.00
$p(G) \psi(YEAR + BPR)$	18	15.57	-329.65	0.00	1.00
$p(G) \psi(YEAR + FPA)$	18	17.81	-330.77	0.00	1.00

333

334 ^a G = sub-global model; DNB = distance to nearest building; FPA = preserve area; IMP = impervious surface; BDE =
 335 building density; (.) = null model (no covariates); * = model with uninformative parameter(s).

336 ^b number of model parameters.

337 ^c difference in quasi-Akaike's Information Criterion corrected for small sample sizes between current model and the
 338 top model.

339 ^d quasi-Log Likelihood

340 ^e model weight

341

342 Because there was a similar level of support for two occupancy covariates, we as-
 343 sessed detection sub-models containing both the building density and impervious surface
 344 occupancy covariates. Of these 16 models, only one model was competitive ($QAIC_c < 2$):
 345 $p(PRESERVE\ AREA) \psi(BUILDING\ DENSITY)$ (Table 5). This model was 4.4 times more likely to
 346 be the best model relative to the second highest ranked model $p(PRESERVE\ AREA) \psi(IMPER-$
 347 $VIOUS\ SURFACE)$, and > 600 times more likely than the null detection model. There was
 348 essentially no support ($\Delta QAIC_c > 10$) for detection models containing other urban covari-
 349 ates, the year covariate, or survey-specific covariates (e.g. temperature, survey day) (Table
 350 5). Full model selection results are presented in the Supplementary Materials.

351

352 **Table 5.** Full model set used to evaluate detectability (p) for domestic cats fitted to stacked detec-
 353 tion history data from 232 monitoring points across 55 preserves in Lake County, IL from 2010-
 354 2018. We modeled detectability using the two top-ranked occupancy submodels, $\psi(BDE)$ and
 355 $\psi(IMP)$. The top ranked model is bolded.

Model ^a	K ^b	$\Delta QAIC_c$ ^c	-2QLL ^d	w_i ^e	Cumulative w_i
$\psi(BDE) p(FPA)$	5.00	0.00	-334.41	0.81	0.81
$\psi(IMP) p(FPA)$	5.00	2.98	-335.90	0.18	0.99
$\psi(BDE) p(BPR)$	5.00	10.91	-339.87	0.00	0.99
$\psi(BDE) p(.)$	4.00	13.03	-341.97	0.00	1.00
$\psi(BDE) p(BDE)$	5.00	13.18	-341.00	0.00	1.00
$\psi(BDE) p(IMP)$	5.00	13.93	-341.38	0.00	1.00
$\psi(IMP) p(BPR)$	5.00	14.18	-341.50	0.00	1.00
$\psi(BDE) p(TEMP)$	5.00	14.67	-341.75	0.00	1.00

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$\psi(\text{BDE}) p(\text{DOY})$	5.00	15.11	-341.97	0.00	1.00
$\psi(\text{BDE}) p(\text{YEAR})$	12.00	15.38	-334.53	0.00	1.00
$\psi(\text{IMP}) p(\text{BDE})$	5.00	16.00	-342.41	0.00	1.00
$\psi(\text{IMP}) p(\cdot)$	4.00	17.46	-344.19	0.00	1.00
$\psi(\text{IMP}) p(\text{YEAR})$	12.00	17.56	-335.62	0.00	1.00
$\psi(\text{IMP}) p(\text{TEMP})$	5.00	18.96	-343.89	0.00	1.00
$\psi(\text{IMP}) p(\text{IMP})$	5.00	19.13	-343.98	0.00	1.00
$\psi(\text{IMP}) p(\text{DOY})$	5.00	19.48	-344.15	0.00	1.00

356

357 ^a DNB = distance to nearest building; FPA = preserve area; YEAR = sampling year; IMP = impervious surface; TEMP

358 = mean temperature °C on day of survey; DOY = ordinal day of year of survey; (·) = null model (no covariates).

359 ^b number of model parameters.

360 ^c difference in quasi-Akaike's Information Criterion corrected for small sample size between current model and the
361 top model.

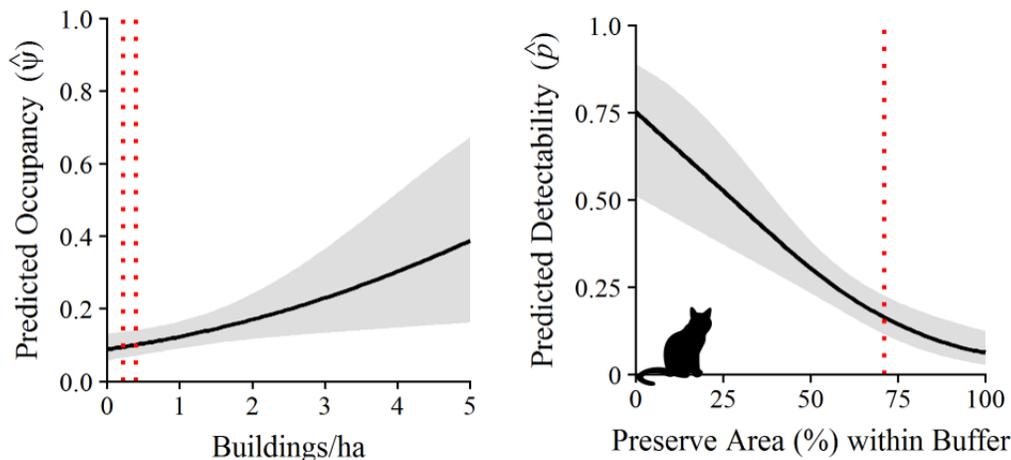
362 ^d quasi-Log Likelihood

363 ^e model weight

364

365 Based on our final detection-corrected model $p(\text{PRESERVE AREA}) \psi(\text{BUILDING DEN-}$
366 $\text{SITY})$, predicted detection probability decreased with increasing preserve area within the
367 400 m buffer ($\beta = -3.79 \pm 0.85 \text{ SE}$) and predicted occupancy increased with the number
368 of buildings within the 400 m buffer ($\beta = 0.38 \pm 0.15 \text{ SE}$) (Figure 3). Beta values are on
369 the logit scale.

370



371

372 **Figure 3.** Domestic cat occupancy increased with the number of buildings within a 400 m buffer
373 (50.2 ha) of each monitoring point. The dotted lines represent the median building density (build-
374 ings/ha) across all 232 monitoring points (building density_{point} = 0.22) and averaged across all
375 preserves (building density_{preserve} = 0.40). Free-ranging cat detectability decreased with increasing

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376 amounts of preserve area within 400 m (50.2 ha) of a monitoring point. The dotted line represents
377 the median preserve area across all 232 monitoring points (preserve area = 71%).

378

379 Using values from the final detection-corrected model, we estimated an overall de-
380 tection probability of 97.4% for a single 4 trap night, 5 calendar day, camera trapping
381 session if the monitoring locations with a 25% preserve area buffer. This overall detection
382 probability drops to 26% at locations that are 100% preserve, and it would take at least
383 four 5-day camera trapping sessions to reach 90% with a single baited camera.

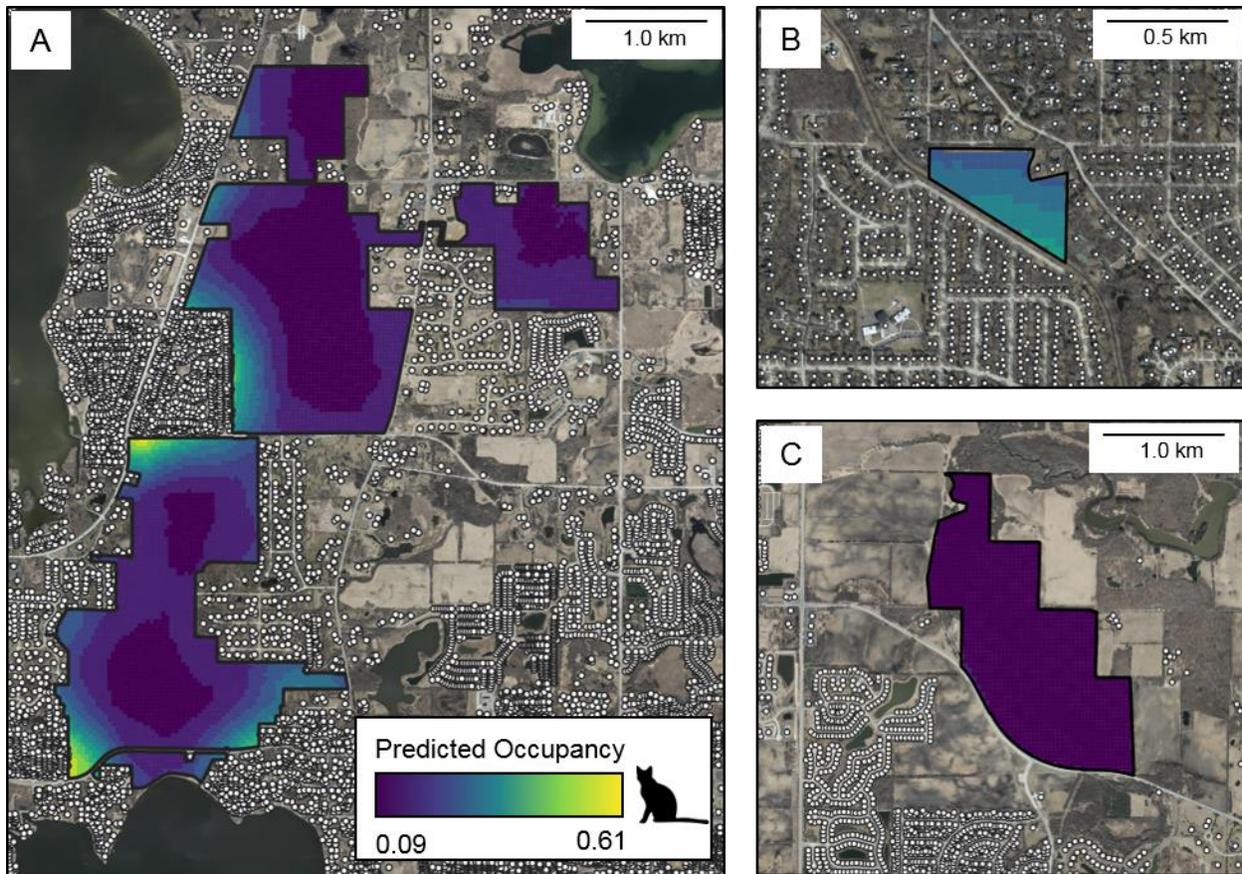
384 *3.3. Landscape Scale Patterns*

385 Preserve level building density averaged 0.57 buildings/ha (based on a 400 m
386 buffer around each 25 m x 25 m grid square centroid) and ranged from 0.04–3.68 build-
387 ings/ha. Correspondingly, preserve level occupancy was low and averaged 0.11 ± 0.03 SD
388 across all 55 preserves, ranging from 0.09 (95% CI = 0.06 – 0.13) at Mill Creek, Ethel's
389 Woods, and Gander Mountain to 0.28 (95% CI = 0.15 – 0.48) at Berkeley Prairie (Figure
390 3). Predicted occupancy across the 159 patches was 27% higher than preserve level occu-
391 pancy at 0.14 (± 0.07 SD) and ranged from 0.09 (95% CI = 0.06–0.13) to 0.60 (95% CI =
392 0.20–0.89). As expected, predicated cat occupancy was lower in larger preserves at both
393 the preserve ($R^2 = 0.159$, $F = 10.02$, $p = 0.003$) and patch level ($R^2 = 0.194$, $F = 39.2$, $p <$
394 0.001).

395

396

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397

398 **Figure 3.** Predicted occupancy for free-ranging cats across three preserves in Lake County, IL.
399 Predicted occupancy at Grant Woods (A) was 0.14 (95% CI 0.09–0.21) and there were pockets of
400 low and high occupancy. Berkeley Prairie (B) was the smallest preserve (7.6 ha) and had the high-
401 est predicted occupancy of the 55 preserves at 0.28 (95% CI = 0.15–0.48). C) Mill Creek (112 ha)
402 had the lowest predicted occupancy at 0.09 (95% CI = 0.06–0.13). Building centroids displayed
403 as white circles.

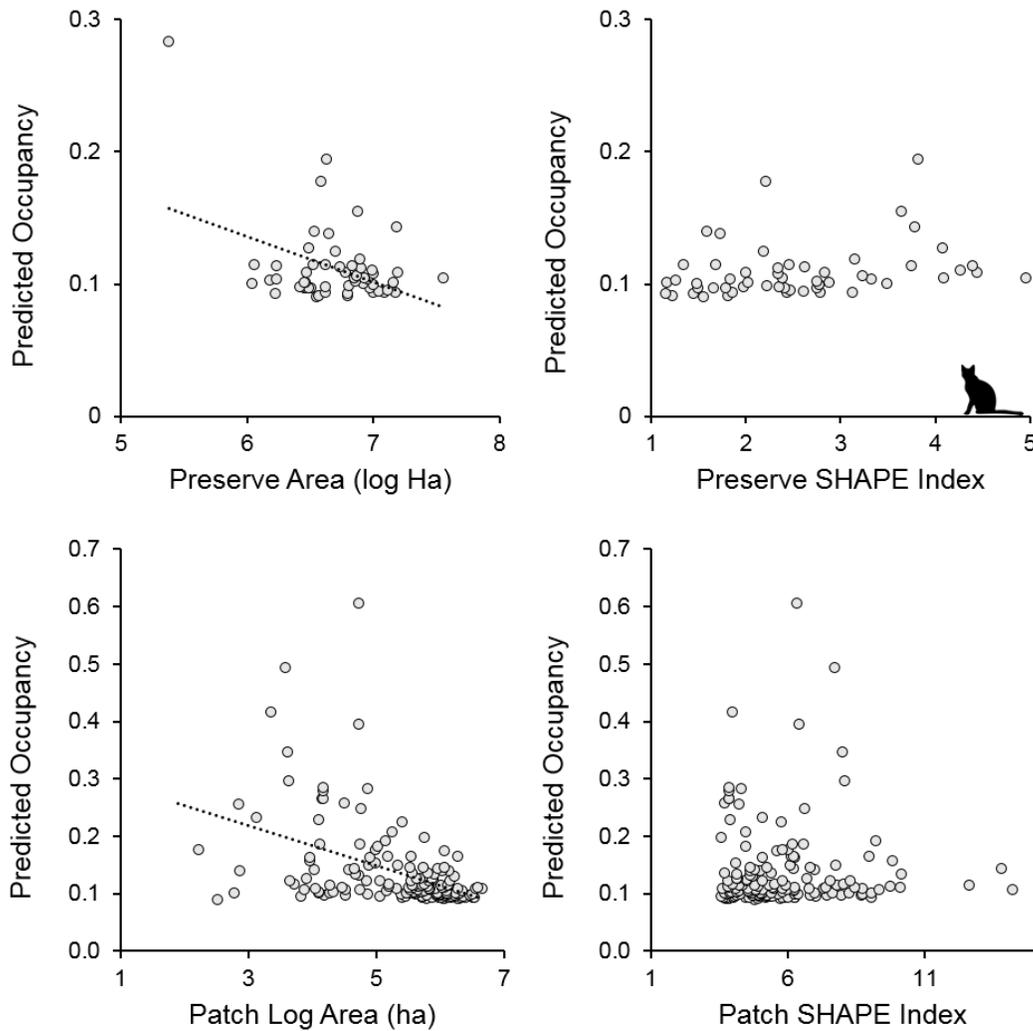
404

405 We found no relationship between the SHAPE index and predicted occupancy
406 (Figure 4) at either the preserve ($R^2 = 0.003$, $F = 0.174$, $p = 0.673$) or patch level ($R^2 = -$
407 0.006 , $F = 0.004$, $p = 0.948$). Larger preserves tended to be more irregular than smaller
408 preserves ($R^2 = 0.27$, $F = 19.56$, $p < 0.0001$), but larger patches did not tend to be more
409 irregular than smaller patches ($R^2 = -0.005$, $F = 0.151$, $p = 0.698$).

410

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413

414 **Figure 4.** Relationship between predicted occupancy of free-ranging cats, preserve area, and the
415 SHAPE index (a measure of compactness) for 55 sampled preserves in Lake County, IL. A per-
416 fectly compact preserve (a circle) would have a SHAPE index of 1, and values larger than 1 indi-
417 cate an increasingly irregular perimeter to area ratio.

418

419 **4. Discussion**

420 We used occupancy modeling and camera trap data from a long-term wildlife mon-
421 itoring program to explore the spatial ecology of free-ranging cats within a large network
422 of suburban natural areas. We detected cats in less than half of our preserves and at less
423 than 20% of monitoring points, although cats were likely to be present at more preserves

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424 due to the relatively low detection probability across much of the preserve network (see
425 section 4.2 below). In contrast, raccoons, opossums, skunks, and coyotes were widely dis-
426 tributed, and we documented their presence in nearly every preserve, consistent with re-
427 gional predictions (Gallo et al. 2017, Greenspan et al. 2018). There are few landscape level
428 reports of urban biodiversity (but see Gallo et al. 2017 and Magle et al. 2019), and our
429 work provides important baseline data for land managers and conservation planners.

430 Cats in our study area were not decidedly nocturnal or crepuscular, but active
431 around the clock (Figure 4). This is consistent with the activity patterns of owned cats
432 (Horn et al. 2011), where feral and unowned cats typically show a nocturnal or strongly
433 crepuscular mesopredators activity pattern (Konecny 1987, Horn et al. 2011, Wang et al.
434 2015, Cove et al. 2018). Most mesopredators native to the region are crepuscular or noc-
435 turnal (Lesmeister et al. 2015). Therefore, if cats are active in preserves during the day,
436 they likely pose an additional risk to diurnal prey species which may not be adapted to
437 diurnal mammalian mesopredators. In addition, free-ranging cats may compete with
438 other diurnal predators, such as raptors (George 1974, Monterroso et al. 2013).

439 Previous research clearly shows that urban areas can foster large cat populations
440 (Flockhart et al. 2016), and Lake County has a human population density greater than
441 >98% of all counties in the United States. Indeed, with over 240,000 households in Lake
442 County (Planning, Building, and Development Department 2019), there are likely to be
443 over 110,000 individual pet cats, based on the national average of 1.8 cats per household
444 at a cat ownership rate of 25% (American Veterinary Medical Association 2019). We hy-
445 pothesize that the large population of coyotes in the Chicago Metropolitan Area (Gehrt et
446 al. 2009, 2011) might be limiting cat occupancy of suburban nature preserves in Lake
447 County, as has been proposed in other areas (Crooks and Soulé 1999, Gehrt et al. 2013,
448 Kays et al. 2015). For example, in neighboring Cook County, IL, Gehrt et al. (2013) used
449 GPS collars on sympatric free-ranging cats and coyotes to show habitat partitioning, with
450 cats selecting areas of urban landcover types and avoiding natural areas, which they at-
451 tribute to predator avoidance. Our results are consistent with this interpretation, with cat
452 occupancy and detection probability lowest in areas further from urban infrastructure.

453 Free-ranging cat occupancy was influenced by the density of buildings and pre-
454 dicted occupancy more than tripled from points with no nearby buildings to points with
455 4.5 buildings/ha (Figure 2). This is consistent with the observed patterns of cat activity
456 and suggests that cats are selecting habitat near areas of denser human population, indic-
457 ative of a population of cats relying on people for subsidy. These results are also consistent
458 with landscape-scale studies linking free-ranging cats to building density. Flockhart et al.
459 (2016) found that cat density increased with building density in Guelph, Ontario, and
460 free-ranging cat occupancy was associated with the density of human-made structures
461 across rural southern Illinois (Morin et al. 2018). Similarly, Krauze-Gryz et al. (2012)
462 linked cat occupancy with distance to nearest building in an agricultural landscape in

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463 central Poland. However, our building proximity covariate was poorly ranked relative to
464 building density and even the null model, and the importance of building density was only
465 apparent after modeling detection probability. Moreover, we found relatively little corre-
466 lation between building density and building proximity ($r = -0.44$). In rural areas, build-
467 ing distance is likely to be important because that building might be the only one near a
468 monitoring location, whereas in urban areas, single buildings are rare, and thus the num-
469 ber of buildings provides more variation for modeling. Care must be taken when selecting
470 indices of urbanization, as indicated by our model selection results and the lack of a strong
471 correlation between our urban covariates.

472 In contrast to our occupancy results, we found building density to be a poor pre-
473 dictor of detection probability, ranking below the null model. Rather, the amount of pre-
474 serve within the monitoring area was the top-ranked detection model. That is, detection
475 probability was highest in areas with a greater proportion of non-preserve land (e.g. res-
476 idential neighborhoods or farm fields) increasing from less than 20% detection probabil-
477 ity at interior portions of preserves to more than 75% at the edges of preserves (Figure 3).
478 These results are consistent with our occupancy results, as both building density and the
479 preserve area around a monitoring point are associated with preserve boundaries. In an
480 urban reserve in New Zealand, Woolley and Hartley (2019) found that detection rates at
481 cameras near the preserve edge were 6 times greater than at cameras just 100 m into the
482 preserve. Similarly, in a suburban preserve in New York, Kays and DeWan (2004) found
483 that free-ranging cats were rarely detected at scent stations > 50 m from the neighbor-
484 hood/preserve edge. As detection probability can be influenced by abundance (Royle and
485 Nichols 2003), our occupancy and detection results strongly suggest that cat populations
486 are highest near the edges of suburban natural areas. Therefore, species vulnerable to cat
487 predation or competition along urban-natural edges are likely to be at higher risk in these
488 areas.

489 Our use of rapid biodiversity surveys was effective at detecting cats at areas near
490 preserve edges. In contrast, much greater survey effort was needed to detect cats at the
491 interior portions of most preserves (i.e. where occupancy is low). While a single week (5
492 calendar days) of camera trapping was effective for detecting cats near preserve edges, it
493 would take more than a month to reach a 90% detection probability with a single baited
494 camera. This echoes recent recommendations that up to 4 weeks of camera trapping may
495 be needed to obtain precise estimates of local detection probabilities (Kays et al. 2020).
496 Thus, free-ranging cats might go un-noticed in rapid biodiversity surveys in larger urban
497 natural areas. We suggest more than one camera be used in rapid biodiversity surveys of
498 large urban preserves.

499 Predicted occupancy across the preserve network was low and averaged less than
500 12%. Most areas of higher occupancy were located near the boundaries of preserves. For
501 example, one of our largest sampled preserves, Grant Woods, had areas of high predicted

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502 occupancy where preserve boundaries bordered densely populated neighborhoods. At the
503 same time, large portions of the preserve had low levels of occupancy, as building density
504 in these areas was near or at zero (Figure 4). Our predicted occupancy value is remarkably
505 similar to the predicted occupancy of free-ranging cats from a mosaic of public and private
506 land across 16 counties in rural southern Illinois, where cat occupancy was higher on private
507 land and also linked to anthropogenic features (structures/ha) (Morin et al. 2018).
508 Thus, cats are likely to be present across a small but consistent proportion of natural areas
509 in the Midwestern United States, with pockets of higher occupancy associated with built-
510 up areas.

511 We found a negative relationship between preserve/patch size and predicted occu-
512 pancy. This is consistent with our hypothesis and similar to the findings of Crooks (2002).
513 However, the relationship was weak, explaining no more than 20% of the variance at either
514 scale. For example, while the smallest preserve, Berkeley Prairie, had the highest levels
515 of predicted occupancy, it was an outlier in terms of size, at a fourth the size of the next
516 smallest preserve and 20 times smaller than the median preserve. In addition, the predicted
517 occupancy was 1.5 times higher than the preserve with the second highest predicted
518 occupancy. Further, removing Berkeley Prairie from the analysis renders the preserve-
519 scale regression non-significant. There were no obvious outliers at the patch scale. Except
520 for extremely small patches and preserves, we suggest that size alone is a poor predictor
521 of free-ranging cat occupancy in suburban nature areas, as cat occupancy can still be high
522 in portions of larger preserves adjacent to dense residential areas (Figure 4).

523 Contrary to our predictions, we found no relationship between the SHAPE index
524 and predicted cat occupancy at either the preserve or patch scale. That is, compact pre-
525 serves had similar levels of occupancy as to more irregularly shaped preserves. Crooks
526 and Soulé (1999) found that smaller habitat fragments had higher cat abundance, which
527 they attributed to smaller patches having “proportionately more urban edge and therefore
528 greater access by housecats bordering the fragment.” However, that study examined
529 mostly small linear fragments (mean area = 13.8 ha), and only one of the 37 fragments
530 was larger than 100 ha (Soule et al. 1988). In contrast, 73% of the preserves in our study
531 were greater than 100 ha, and our largest preserve, Lakewood had the highest SHAPE
532 index, equivalent to 400% more edge than a circular preserve of the same area. This ex-
533 emplifies the reality of urban preserves, which are rarely designed, but rather are often
534 obtained and expanded opportunistically. For example, since its inception in 1968, Lake-
535 wood has more than doubled in size through 39 individual acquisitions (XXX, un-
536 published data, masked for double-blind peer review). As with preserve size, highly irreg-
537 ular preserves and patches can occur in both areas of high and low building density, even
538 in urban areas. Thus, nearby building density should be the primary concern for suburban
539 land managers, not proxies like preserve size or irregularity.

540

541 **5. Conclusions**

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542

543 Free-ranging cats are a threat to biodiversity, but we have a limited understanding
544 of their ecology and distribution in urban preserves. Our results show that free-ranging
545 cats occur sporadically throughout nature preserves in Lake County. However, cat occu-
546 pancy was low relative to native mesopredators, possibly due to high coyote occupancy.
547 Cats were active during all times of the day and night, whereas native mesopredators were
548 mostly nocturnal. Overall, these results suggest that most free-ranging cats within the
549 preserves were not feral (e.g. living independent of humans) but were more likely pet cats
550 with access to the outdoors. This has important implications for the management of free-
551 ranging cats in Lake County, as the control of free-ranging cats is a contentious issue (Ash
552 and Adams 2003, Longcore et al. 2009, Loyd and Miller 2010a, b, McDonald et al. 2015,
553 Loss and Marra 2018, Loss et al. 2018, Woolley and Hartley 2019).

554 Traditional measures of preserve design (i.e. shape and size) may not accurately
555 predict the risk of free-ranging cats. We suggest that urban land managers interested in
556 the conservation and reintroduction of cat-sensitive species to urban natural areas con-
557 sider the surrounding urban matrix in their decision-making process. In addition, urban
558 ecologists should consider multiple indices of urbanization in their analyses instead of
559 assuming all urban metrics are all equivalent. Finally, while the cat occupancy may be low
560 in urban nature preserves, we caution against complacency as even low numbers of cats
561 can cause substantial harm to biodiversity and human health.

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