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Cats are rare where coyotes roam

Roland Kays,* Robert Costello, Tavis Forrester, Megan C. Baker, Arielle W. Parsons, Elizabeth L. Kalies, George Hess, Joshua J. Millspaugh, and William McShea

North Carolina Museum of Natural Sciences, 11 W. Jones St., Raleigh, NC 27601, USA (RK, AWP)
Department of Forestry & Environmental Resources, North Carolina State University, Campus Box 7646, Raleigh, NC 27695, USA (RK, GH)
Smithsonian National Museum of Natural History, 10th and Constitution Ave. NW, Washington, DC 20560, USA (RK, RC)
Smithsonian Conservation Biology Institute, 1500 Remount Rd., Front Royal, VA 22630, USA (TF, MCB, WM)
Department of Fisheries and Wildlife Sciences, 302 Anheuser-Busch Natural Resources Building, University of Missouri, Columbia, MO 65211, USA (ELK, JJM)

* *Correspondent:* *Roland.Kays@NCSU.edu*

Domestic cats (*Felis catus*) have caused the extinction of many island species and are thought to kill many billions of birds and mammals in the continental United States each year. However, the spatial distribution and abundance of cats and their risk to our protected areas remains unknown. We worked with citizen scientists to survey the mammals at 2,117 sites in 32 protected areas and one urban area across 6 states in the eastern United States using camera traps. We found that most protected areas had high levels of coyote (*Canis latrans*) activity, but few or no domestic cats. The relative abundance of domestic cats in residential yards, where coyotes were rare, was 300 times higher than in the protected areas. Our spatial models of cat distribution show the amount of coyote activity and housing density are the best predictors of cat activity, and that coyotes and cats overlap the most in small urban forests. Coyotes were nocturnal at all sites, while cats were nocturnal in protected areas, but significantly more diurnal in urban sites. We suggest that the ecological impact of free-ranging cats in the region is concentrated in urban areas or other sites, such as islands, with few coyotes. Our study also shows the value of citizen science for conducting broadscale mammal surveys using photo-vouchered locations that ensure high data quality.

Key words: camera trap, *Canis latrans*, citizen science, *Felis catus*, invasive species, protected areas

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Free ranging domestic cats (*Felis catus*) are a major conservation concern because of their predation on native wildlife (Loss et al. 2013). This situation is worse on oceanic islands, where prey species typically evolve without mammalian predators and have little innate ability to avoid cats. Cats have caused the extinction of 18 small terrestrial island vertebrates and are the primary extinction risk for another 36 island vertebrates that are now critically endangered (Medina et al. 2011). In island systems with simple food web structure, the addition of a predator species can severely shift community dynamics.

A recent review of cat predation in the United States also highlighted the conservation problems they pose to continental ecosystems. By combining typical kill rates and country-wide cat population estimates, Loss et al. (2013) estimated that domestic cats kill 1.4–3.7 billion birds and 6.9–20.7 billion mammals annually. Free-ranging, un-owned cats, as opposed to pet cats, are thought to cause the majority (69% for birds and 89% for mammals) of this mortality.

However, the spatial extent and ecological significance of this predation on native species remains unknown. Exactly where the more than 74 million pet cats (Shepherd 2012), and additional un-owned cats, hunt in the United States is a critical question. We might expect cats using residential areas to hunt primarily common prey species that are of lower conservation concern. However, if they penetrate public lands designed to protect native biodiversity, management action may be needed to reduce their impact. Two tracking studies of urban cats found them to avoid nature preserves, presumably because of abundant predators populations (Kays and DeWan 2004; Gehrt et al. 2013). Less is known about cats outside of developed areas, where most important protected natural areas are, although one tracking study found that

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un-owned rural cats frequently used natural habitats (Horn et al. 2011).

We worked with citizen scientists to use camera traps to survey cats and native wildlife in 32 protected areas across 6 states in the eastern United States and in residential yards and small urban forests (some along greenway trails) in Raleigh, North Carolina. If coyotes in protected areas are negatively influencing cats, as seen in urban areas (Kays and DeWan 2004; Gehrt et al. 2013), then we expect to find a negative relationship between coyote and cat detections. The intensity of this competition between predators is not only interesting ecologically, but also important for conservation managers concerned about the potential negative impacts of cats on native prey.

Materials and Methods

Citizen science camera trap surveys.—From 2012 to 2014, we recruited and trained 486 volunteer citizen scientists, undergraduate students, and middle school students to deploy camera traps across the study area. Most protected area cameras were run from April to November, while the Raleigh area cameras were run year-round. Camera traps set in protected areas were deployed in groups of 3, with one camera placed on a hiking trail, one 50 m from the trail, and one 100–200 m from the trail. Camera traps along Raleigh's greenways were set in pairs with one camera on the trail and one approximately 25 m off-trail in nearby wooded areas. Backyard camera traps were set to minimize pictures of resident humans, typically along the edge or towards the back of the yard, as described in our earlier work (Kays and Parsons 2014). Volunteers used Reconyx (RC55, PC800, and PC900; Reconyx, Inc. Holmen, Wisconsin) and Bushnell (Trophy Cam HD, Bushnell Outdoor Products, Overland Park, Kansas) camera traps that were equipped with an infrared flash. These cameras all function similarly in having highly sensitive triggers and quick trigger times, allowing them to record animals passing rapidly in front of the camera without the addition of bait. Volunteers attached the cameras to trees at 40 cm above the ground and returned after 3 weeks to retrieve the images and move the cameras. Cameras were set on maximum trigger sensitivity and recorded multiple photographs per trigger, re-triggering immediately if the animal was still in view.

Volunteers used custom eMammal software to provide initial identification of all wildlife species in camera trap images, enter camera metadata (e.g., location), and uploaded pictures to our database. We then reviewed the quality of all data using the eMammal Expert Review Tool, confirming or correcting all volunteer species identifications, and evaluating camera setup from the view of the camera. After expert review, all data were downloaded to a Smithsonian data repository for storage.

We grouped consecutive photos into sequences if they were < 60 s apart and used these sequences as independent records for subsequent analysis of detection rate and daily activity patterns. Cats photographed from protected areas were identified to individuals based on coat color pattern independently by 2 reviewers, who agreed on 100% of identifications. The Raleigh area cats were not identified to individual because most cameras were too widely scattered to obtain recaptures of the same animals in different cameras.

Environmental variables.—We used ArcMap (ESRI 2012) to obtain 2 environmental variables for each of our camera sampling points: housing density and coyote (*Canis latrans*) relative abundance. We used the Silvis housing density dataset (Hammer et al. 2004) to calculate the average housing density (houses/km^2) at 2 spatial scales for each camera using a 250-m and 5-km radius. We also used a 5-km buffer around each camera and calculated the average coyote detection rate (count/day) from our cameras within each buffer. On average, these 5-km buffers included 73 cameras ($SE = 1$).

Statistical models.—We used spatial statistics (R package GeoR— Ribeiro and Diggle 2015) to evaluate if detection rates spatially autocorrelated using a semivariogram to calculate a minimum distance at which spatial autocorrelation becomes negligible (semivariogram range). We fitted a semivariogram model to each empirical semivariogram using weighted least squares and assessed goodness-of-fit by the minimized sum of squares. We examined detections for cats and coyotes across sites to consider removing outliers that could represent a den or feeding station with very high detection rates. To evaluate the spatial determinants of cat distribution, we fitted a Poisson count model with a log-link to predict the count of cat detections, offset by camera deployment duration ($n = 2{,}117$). We used 6 covariates as fixed effects: habitat type (dummy variable for yard or not yard, small urban forests, protected areas), latitude and longitude of site, average housing density (houses/km^2) in a 250-m and 5-km radius of the site, rate of coyote detection at the site (total count/number of camera days), and average rate of coyote detection from all cameras within a 5-km radius of the site. We tested all covariates for multicollinearity using a correlation matrix in Program JMP and considered any correlation below 30% to be acceptable. We ran our model in a Bayesian framework using OpenBUGS (Thomas et al. 2006) and R (R Development Core Team 2011). Our model included a term for extra-Poisson variation (Breslow 1984) to account for overdispersion and excess zeros in our dataset. We compared a suite of 18 covariate combinations which we felt best tested potential relationships affecting cat distribution. We assessed relative model deviance using deviance information criterion (DIC) and fit of the top model using Pearson's goodness-of-fit statistic drawn from the posterior distribution (Johnson 2004). We calculated posterior means and 95% Bayesian credibility intervals using the most parameterized model within the top 4 DIC points. We separately assessed the significance of differences in the intensity of use of different habitat types by cats and coyotes using a Kruskal–Wallis rank-sum test and Mann–Whitney *U*-test for pairwise comparisons in Program JMP (SAS Institute 2012).

To estimate probabilities of occupancy, we used a single season occupancy model (MacKenzie et al. 2006) and estimated

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detection probability (P), defined as the probability of detecting an occurring species at a site and occupancy (ψ), defined as the expected probability that a given site is occupied. For each species (cat and coyote), we used RMark (Laake 2011) in R (R Development Core Team 2011) to build and fit models for each of our covariates, including no covariates (i.e., assuming probabilities were constant across the sites), each combined with a null model of detection. For each model, we computed Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c, and Akaike weights (w_{ij}, weight of covariate i for species j) (Burnham and Anderson 2002) and used these values to assess model fit. We used the most parsimonious model of occupancy probability for cats (containing the "habitat" variable) to estimate the probability of occupancy in each habitat type.

We created daily animal activity patterns by fitting density functions based on circular statistics to independent animal detections (MacKenzie et al. 2006) using package overlap (Meredith and Ridout 2014) in R (R Development Core Team 2011). We tested for significant differences in activity patterns using Watson's 2-sample test for homogeneity in package CircStats (Lund and Agostinelli 2014) in R (R Development Core Team 2011).

Results

Mammal surveys.—With 42,874 camera nights of survey effort across 1,953 locations in 32 protected areas, we obtained 52,863 detections of native wildlife. This same effort returned only 55 detections of cats (0.0012 detections/day). Our semivariogram showed that autocorrelation for cat rate became negligible after only 3 m, indicating spatial independence. One camera had very high detection rates for coyotes, probably representing a den site or feeding station and so was removed from the analyses. Cats were detected at 31 camera sites scattered through half of the protected areas surveyed (Fig. 1; Supporting Information S1), resulting in an occupancy rate (ψ) of 0.027 ($SE = 0.0060$) across the region. Based on coat coloration, we were able to identify all cats from protected areas to individual; in 14 of the 32 protected areas, we detected only a single cat (some

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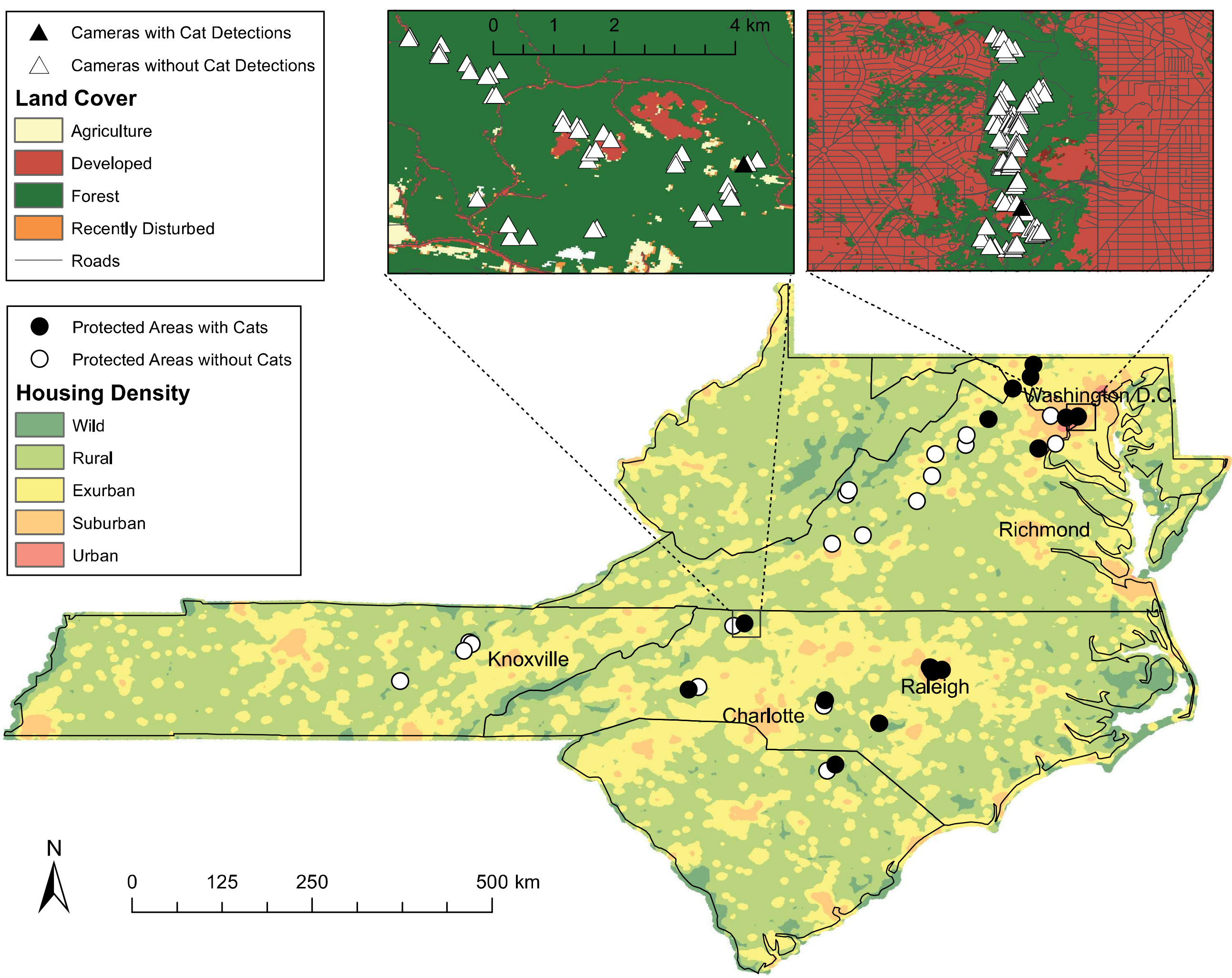

Fig. 1.—Distribution of cats detected across 32 protected areas: 50% had no cats (*Felis catus*) detected, while 44% had just 1 cat, and 2 (6%) had multiple cats. The 2 map insets are at the same scale and show typical camera arrangement and detection patterns for cats in rural (left, Stone Mountain State Park) and urban protected areas (right, Rock Creek Park).

photographed multiple times). In the 2 protected areas with the highest levels of cat activity, we detected 5 or 6 individual cats photographed multiple times (Supporting Information S1). Coyotes (Supporting Information S2) were detected 33 times more often than cats in protected areas (0.044/day), occurred at a higher level of occupancy ($\psi = 0.49 \pm 0.020$), and were found in all but one of the 32 protected areas.

We also used camera traps to survey mammals at 171 locations in Raleigh, North Carolina for a total of 2,760 camera nights: including 60 sites in residential yards, and 111 in small urban forests, 45 of which were along greenway trails. Domestic cats (Supporting Information S3) were detected more often on trail than off-trail, but were found at the highest rates in yards, followed by small urban forests, which were both much higher than in larger protected areas (Fig. 2; Tables 1 and 2). Indeed, residential yards (0.44 detections/day) had 300 times more cat activity than protected areas (0.11 detections/day). Coyotes were detected in all habitats but were rare in residential areas. Similarly, probability of occupancy for cats was highest in yards (0.53 ± 0.067), followed by small urban forests (0.27 ± 0.044), with the lowest rates in protected areas (0.016 ± 0.0029). Coyotes had the lowest probability of occupancy in yards (0.085 ± 0.041), with higher rates in small urban forests (0.57 ± 0.061) and protected areas (0.35 ± 0.013).

Spatial and temporal model results.—None of our covariates were highly correlated, all pairwise correlations fell below 30%. Our top models predicting cat distribution across all sites fit well ($\chi^2 > 0.4$). Parameter estimates from the most parameterized model within the top 4 DIC points showed that coyote activity levels and housing densities had the strongest effects on cat detections (Tables 1 and 2). Housing density was included in only one of the top models (Table 1), showing it was less important than coyote activity. Although habitat was not an important covariate in the top multivariate

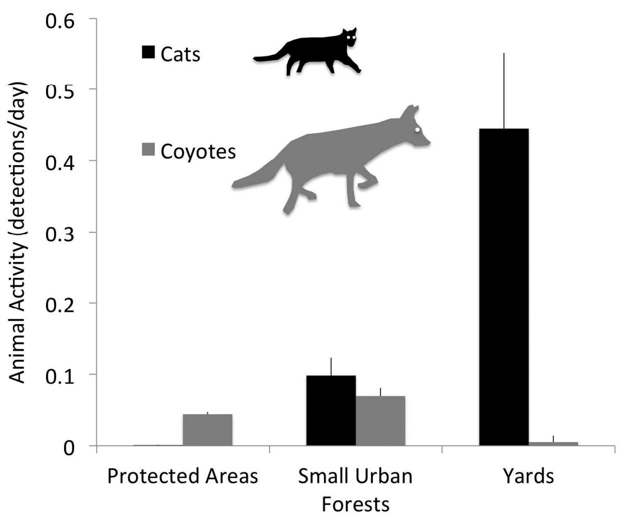

Fig. 2.—Average detection rates of cats and coyotes (*Canis latrans*) recorded by camera traps set in different habitats including 32 protected areas in the eastern United States and 177 urban sites around Raleigh, North Carolina. Error bars show *SE* of the mean. Rates were statistically different across habitats for both coyotes and cats (Kruskal–Wallis test, $P < 0.0001$).

models of cat distribution, we note that cat detection rate differed significantly across these categories (Kruskal–Wallis test, $\chi^2 = 502.35$, $P < 0.0001$). Cat rate was significantly higher in yards than small urban forests (mean difference = 24.82, $SE = 6.76$, $Z = 3.67$, $P = 0.0002$) and protected areas (mean difference = 508.17, $SE = 22.76$, $Z = 22.33$, $P < 0.0001$). Cat rate was also significantly higher in small urban forests than protected areas (mean difference = 254.91, $SE = 16.89$, $Z = 15.09$, $P < 0.0001$; Fig. 2). The intensity of use by coyotes across these 3 habitats was also significantly different (Kruskal–Wallis test, $\chi^2 = 31.1927$, $P < 0.0001$, protected areas versus small urban forests $P < 0.0001$, yards versus small urban forests $P < 0.0001$, yards versus protected areas $P = 0.001$).

Our distribution model found a strong negative relationship between the detection rate of coyotes at the 5-km scale and cats across all sites (Tables 1 and 2; Supporting Information S1). Additional support for the hypothesis that coyotes exclude cats from protected areas comes from the only protected area in which we found no coyotes, Gambrill State Park, which also had the highest level of cat detections; the detection rate there (0.023/day) was 3 times higher than the next most cat-rich protected area.

Table 1.—Model selection for describing variation in cat (*Felis catus*) distribution as ranked by the deviance information criterion (DIC). The yard variable is a categorical classification (yard, not yard), the house variables are measures of housing density, and the coyote (*Canis latrans*) variables are detection rates from camera traps. LatXLong is a spatial term to account for broadscale geographic trends.

Model	DIC	Delta DIC
Coyotes 5 km	638	0
Coyotes 5 km + House 5 km	639	1
Coyotes at site	644	6
Null	645	7
Houses 5 km	645	7
LatXLong	650	12
LatXLong + Houses 5 km	651	13
Houses 250 m	651	13
LatXLong + Coyotes 5 km	652	14
Yard + Coyotes 5 km	653	15
LatXLong + Yard + Houses 250 m + Houses 5 km + Coyotes at site + Coyotes 5 km	654	16
Yard	655	17
Yard + Houses 5 km	655	17
Yard + Coyotes 5 km + Houses 5 km	656	18
LatXLong + Yard + Coyotes 5 km + Houses 5 km	656	18
LatXLong + Yard + Coyotes at site + Houses 250m	657	19
LatXLong + Yard + Coyotes 5 km	659	21
LatXLong + Yard	660	22

Table 2.—Parameter estimates results for Coyote (*Canis latrans*) 5 km + Housing Density 5 km model predicting cat (*Felis catus*) use of protected and urban areas. Both variables were considered significant because the 95% credible intervals did not include 0.

Variable	Posterior mean	95% Credible interval
House 5 km	0.79	0.35, 1.20
Coyote 5 km	−1.46	−2.08, −0.86

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Coyotes and cats in protected areas showed nocturnal activity patterns that were not different from each other (Watson's $U^2 = 0.077$, $P = 0.50$) but were both different than the more diurnal activity of urban cats (coyotes-urban cats: Watson's $U^2_1 = 2.242$, $P < 0.0001$; park cats–urban cats: Watson's $U^2_1 = 0.300$, $P = 0.005$; Fig. 3).

Discussion

Our large-scale survey shows that free-ranging cats are not widespread in large protected areas in the eastern United States. We detected no domestic cats in half of the 32 protected areas we surveyed, and more than 1 individual cat in only 2 of them. This is the first study to address cats in North American protected areas and suggests that they are not a widespread conservation concern for the larger protected areas in this region.

We found evidence that predators may be preventing cats from colonizing protected areas, as most cat-free areas had high activity rates of coyotes. Additionally, our measures of coyote activity were negatively associated with cat activity in our spatial model. Finally, the only protected area in which we detected no coyotes had, by far, the highest levels of cat activity. Coyotes have been shown to prey on cats (Quinn 1997) and prevent cats from using some urban natural areas (Crooks and Soule 1999; Gehrt et al. 2013), but this is the first study to document the partitioning of space between coyotes and cats across large scales. The virtual absence (one or fewer) of cats in 94% of the protected areas we surveyed suggests that there is a low threshold level of coyote activity that effectively prevents cats from using an area, and that most of the relatively large, protected areas we surveyed were above that level.

Compared to these protected areas, we detected many more cats in our surveys of residential yards and small urban forests, showing the extent to which cat activity is focused in urban areas. Not surprisingly, cats were most common in yards, which had 300 times more cat activity than protected areas. This shows the limited degree to which most urban cats venture past their neighborhoods, which is similar to what was found for radio-tracked pet cats (Kays and DeWan 2004). Habitat type was not featured in our top multivariate distribution models, presumably because coyote distribution was a better predictor, and was also correlated with habitat types (Fig. 2).

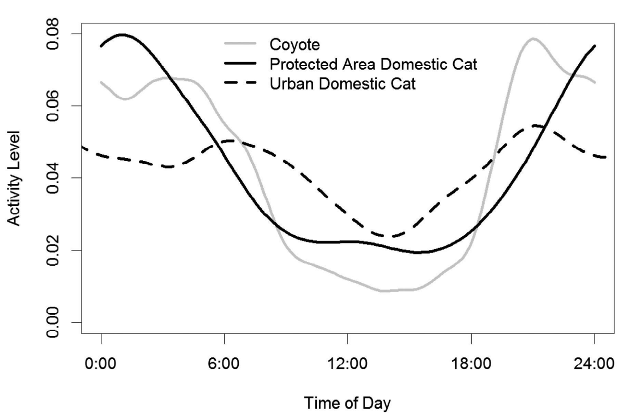

Fig. 3.—Daily activity patterns showing high overlap for coyotes (*Canis latrans*) and cats (*Felis catus*) in protected areas and less in urban areas, where cats are more diurnal. The activity patterns of coyotes from protected and urban areas were not different, and thus are combined into one line.

Why populations of cats and coyotes have virtually no overlap in protected areas but substantial spatial overlap in small urban forests remains an important question. A tracking study in Chicago also found spatial overlap between coyotes and cats in small urban forests, although their core areas were separate (Gehrt et al. 2013). We suspect that the fragmented arrangements of natural and developed areas typical of American cities may provide cats with sufficient nearby refuges they can access if they encounter a predator. Our data confirm that residential yards in Raleigh are safe havens for cats, with coyotes detected in only 5 of the 64 yards we surveyed. This may be different from some cities where coyotes are more urbanized (Gehrt et al. 2009). The increased diurnal activity we found in urban cats could also be a strategy, by cats or their owners, to avoid nocturnal coyotes.

We used our camera trap photos as measures of local cat relative abundance in 3 different ways, all showing the same results, with cats rare in larger protected areas, present in small urban forests at varying levels, and common in residential yards. Because our camera traps were unbaited and simply recorded the frequency that cats and coyotes walked by, we could use this as a measure of relative abundance, as well as a measure of the ecological impact of these 2 predators (Rowcliffe et al. 2008). Our occupancy models mirrored our results based on raw detection rate. Finally, for the protected areas, we were able to identify individual cats based on coat coloration, confirming that few individuals (typically one) were present.

We were not able to evaluate the origin of the cats we photographed, i.e., whether they were pets, wide-ranging feral cats, or from a cat colony. Free-ranging cats are thought to prey on substantially more native prey than pet cats (Loss et al. 2013), and the establishment of localized cat colonies is of special conservation concern due to the incredibly high predator densities that can result, in addition to disease concerns (Clarke and Pacin 2002). We did not specifically target sampling of cat colonies and, given the relatively low cat detection rates, apparently did not detect any within the protected areas or small urban forests we surveyed. We were surprised to detect single cats in the middle of large protected areas, far from houses or neighborhoods. We think this detection rate is too low to represent truly feral populations, and suspect that some of these could be cats that were abandoned at the parks by their owners. Another alternative is that these were unusual pet cats that moved much further from their house than is typical, which has also been observed in one radio-tracked cat (Kays and DeWan 2004). Such wandering cats in protected areas might not have knowledge of the local coyote populations, which could also explain why they are temporally overlapping with them in being primarily nocturnal.

The large scale of our survey, with more than 2,000 sample points across 6 states, shows that our main result of few to no cats in protected areas is a consistent pattern across the region. This also shows the benefit of working with volunteer citizen

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scientists to scale-up this mammal survey (Cooper et al. 2007), allowing us to not only sample more parks, but also efficiently survey urban areas. By reviewing all photographic data collected by citizens, we were able to ensure the high quality of the data, unlike other citizen science work, which may not collect vouchers (Cooper et al. 2007).

Because our urban results were from only one city, additional research will be needed to evaluate how predators and cats interact in the varied urban landscapes around the country, including those with more urbanized coyotes (Gehrt et al. 2013), or even larger predators. Additional surveys of cats in protected areas around the world with varied predator communities could also shed more light on which situations require active management to reduce cats (Loyd and Devore 2010) and which can allow their native predators to keep the cats out.

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Supporting Information

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Summary of the cats and coyotes detected by citizen science camera trap surveys of 32 protected areas across six states and Washington, DC. Rates are detections/day.

Supporting Information S2.—Camera trap picture of a pack of coyotes hunting Sand Hills State Forest, South Carolina.

Supporting Information S3.—Camera trap picture of a domestic cat walking on the Raleigh greenway through a small urban forest in North Carolina.

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