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# Urban mesopredator distribution: examining the relative effects of landscape and socioeconomic factors

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## Keywords

coyote; raccoon; opossum; urban wildlife; landscape ecology; mesopredators; socioeconomic factors; Chicago.

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## Abstract

Cities harbor biodiversity, which has complex outcomes, both for humans and other animals. The situation is particularly complicated with carnivorous species such as mesopredators, which elicit strong positive and negative responses from urban residents. As cities are dominated by anthropogenic forces, socioeconomic factors likely play a major ecological role that has gone mostly unexplored for mammalian species. We used a large database of motion-triggered camera imagery to investigate relationships between landscape and socioeconomic features and the distribution of three mammalian mesopredator species in Chicago, IL. Coyotes and raccoons were most likely to colonize less urban sites, and coyotes were least likely to go extinct within sites with a high average per capita income. Opossum showed somewhat different dynamics, with added availability of habitat and increased housing density decreasing odds of new colonization. In general the socioeconomic variables performed at least as well as the habitat factors tested, indicating that there is a significant role of both biotic and abiotic features in driving species distribution in this area. We suggest that new ecological frameworks incorporating both socioeconomic and ecological factors will be needed for the long-term management and conservation of wildlife in urban regions.

## Introduction

Increasingly, we live on an urban planet (Pickett *et al.*, 2008; Dearborn & Kark, 2010; Ramalho & Hobbs, 2012). While it has long been apparent that the wildlife communities present in urban areas differ from their counterparts in natural settings (Sukopp, 2002; Adams, 2005; Aronson *et al.*, 2014), only relatively recently have systematic efforts to predict and manage the distribution of wildlife in urban areas emerged (Dearborn & Kark, 2010; Mayer, 2010). Some general principles have been uncovered such as biotic homogenization (McKinney, 2002, 2006; Chace & Walsh, 2006), but there is doubtless significant variation between regions and taxonomic groups in the response of wildlife to urbanization (Adams, 1994; La Sorte, McKinney & Pyšek, 2007). As many studies focus only on a single species in a small geographic area and for a relatively brief period (Magle *et al.*, 2012), significant gaps remain in our knowledge.

Carnivores and other predatory species have always been a focus of wildlife conservation and management efforts (Hudenko, Siemer & Decker, 2010). Ecologically, predators may function as keystone species that shape the composition of a system in a top-down fashion (Wilmers *et al.*, 2003). These changes can often be positive to humans and nature, simultaneously providing increases in diversity of other taxa (e.g. Crooks & Soulé, 1999), ecosystem services to humans (Gompper, 2002) and enhancing tourism (Rasker &

Hackman, 1996). Yet, predators can also negatively impact economic and sociological factors through property damage and concerns for human health and safety (Conover, 2002). Instructive examples include zoonotic diseases (Gehrt & Riley, 2010), which may pose additional threats in urban areas due to the increased density of humans and, potentially, wildlife (Hamer, Lehrer & Magle, 2012). Similarly, animal-vehicle collisions are the leading cause of death for some carnivores in urban areas (Gehrt & Riley, 2010) and pose a threat to human health. As such, mesocarnivores exemplify the tumultuous relationship between humans and nature. Despite these potential areas of conflict, some studies find increased tolerance over time in communities where predators are present (Kleiven, Bjerke & Kaltenborn, 2004; Bjurlin & Cypher, 2005), which suggests that long-term coexistence is possible.

Existing paradigms of how carnivores persist and assemble in urban systems often derive from island biogeography theory (MacArthur & Wilson, 1967). Although the theory possesses lower explanatory power in urban areas (Mendenhall *et al.*, 2014), and some species violate the model by residing in the urban 'matrix' (e.g. Gehrt, Anchor & White, 2009), many mesopredator species have been found to be more prevalent in larger and more connected habitat patches as predicted (Soulé, 1991; Crooks, 2002; Paquet *et al.*, 2006). However, many local factors, including vegetative composition, canopy cover, habitat complexity,

presence of water, and density of prey and other predator species (Harris, 1981; Pedlar & Fahrig, 1997; Crooks, 2002; Gosselink *et al.*, 2003; Gehrt *et al.*, 2009) also play a varying and complex role in the distribution of urban carnivores. As a result, prediction of carnivore habitat use in cities has proven difficult. Mammalian predators are also nocturnal and secretive, and therefore challenging to study (Sargeant, Johnson & Berg, 1998; Crooks, 2002). Given these difficulties, the complexity of urban systems (Alberti *et al.*, 2003), the wide-ranging nature of predatory species and the numerous factors involved in carnivore distribution, it is not surprising that even for relatively well-studied species, many ecological relationships are still not explored, making conservation and management difficult (Riley, Gehrt & Cypher, 2010).

As cities are dominated by anthropogenic forces, socioeconomic factors likely play a major ecological role (Pickett *et al.*, 2001; Kinzig *et al.*, 2005; Luck, Smallbone & O'Brien, 2009). Commonly measured factors include housing age and density, household income, and average educational level. Housing age and income have been found to correlate with species distributions in a number of studies (e.g. Loss, Ruiz & Brawn, 2009), and popular media sources have speculated that foreclosed (and thus vacant) homes may harbor wildlife species including mesopredators (e.g. Miroff, 2008). Social and economic forces can alter public acceptance of wildlife and thus affect management (Kleiven *et al.*, 2004; Morzillo *et al.*, 2010; Owino, Jillo & Kenana, 2012). Additionally, socioeconomic factors can impact habitat quality (Hope *et al.*, 2006; Gledhill & James, 2012) and thus directly correlate with wildlife distribution (e.g. Loss *et al.*, 2009). Many previous studies using socioeconomic predictors have focused on bird species (Kinzig *et al.*, 2005; Melles, 2005; Dallimer *et al.*, 2009; Loss *et al.*, 2009; Strohbach, Haase & Kabisch, 2009; Davis *et al.*, 2012; van Heezik *et al.*, 2013; Luck, Smallbone & Sheffield, 2013). As one example, Loss *et al.* (2009) found bird diversity peaked in higher income neighborhoods. Some studies have also investigated the impact of socioeconomic variables on mammals including giant pandas (*Ailuropoda melanoleuca*, Liu *et al.*, 1999; An *et al.*, 2006) and domestic cats (*Felis catus*, Finkler, Hatna & Terkel, 2011a,b).

Typically, studies using socioeconomic predictors speculate that unmeasured factors correlated to these variables such as human tolerance for wildlife, habitat complexity or quality, home ownership, presence of water, availability of anthropogenic food sources, and/or presence of humans and commensal pets drive the change in wildlife species distributions. However, to date relatively few papers have investigated the role of socioeconomic factors in driving the distribution of terrestrial predators in urban areas, which is surprising and unfortunate given the increase of these species in urban areas, their ecological importance and their potential for human-wildlife conflict (Gehrt & Riley, 2010). There may be environmental justice issues to consider as well, for example if human-carnivore conflicts are more likely for underprivileged groups (Strohbach *et al.*, 2009; Cohen *et al.*, 2012; Davis *et al.*, 2012).

We used a large database of motion-triggered camera imagery to investigate relationships between landscape and socioeconomic features and the distribution of three mammalian species in Chicago, IL. The Chicago region is highly urbanized but also contains a significant portion of conserved land, with Cook County alone consisting of 11% protected areas (Moskovits *et al.*, 2006). We focused on three relatively abundant species in this region, coyotes (*Canis latrans*), raccoons (*Procyon lotor*) and Virginia opossum (*Didelphis virginiana*). Coyotes are the largest carnivore present in the Chicago area. Within urban areas, they typically focus their activities on available green space, where their diet consists primarily of natural food items (Riley *et al.*, 2003; Gehrt *et al.*, 2009; Gehrt & Riley, 2010). Raccoons are smaller, omnivorous, extremely widespread and tend to focus their activities on areas with abundant human food sources (Prange, Gehrt & Wiggers, 2004; Hadidian *et al.*, 2010). The only marsupial native to North America, the Virginia opossum (hereafter opossum) is a small, nocturnal species with high reproductive capacity that tends to thrive in urban areas. However, they are relatively understudied in cities (Wright, Burt & Jackson, 2012). While a marsupial and thus not a carnivore in a taxonomic sense, opossum may scavenge similar anthropogenic food sources and/or occupy a similar niche, and are thus often included with carnivores in landscape-level assessment (e.g. Crooks, 2002). All three species are urban-adapted generalists (Gehrt & Riley, 2010; Wright *et al.*, 2012), but vary in body size, behavioral patterns and life-history traits, such that our results can illustrate the potential range of relationships between predators and socioeconomic factors.

We used a multi-season occupancy modeling framework (MacKenzie *et al.*, 2003, 2006), and hypothesized that landscape factors such as availability of habitat, patch area and nearby housing density would be the most critical drivers of species distribution, but that socioeconomic factors such as home vacancy rate, neighborhood age and average neighborhood income would also play an important role, particularly for species like raccoons that may depend on human food sources. We predicted that, especially for reclusive species such as coyotes and opossum, nearby habitat would have a strong positive influence on occurrence, while older neighborhoods and those with lower vacancy rates would exhibit lower species prevalence (Loss *et al.*, 2009). Determining the relative impact of habitat and socioeconomic factors will help target management and conservation efforts for mesopredators in the Midwest, and may also better our understanding of how different human communities experience and have access to wildlife in urban landscapes.

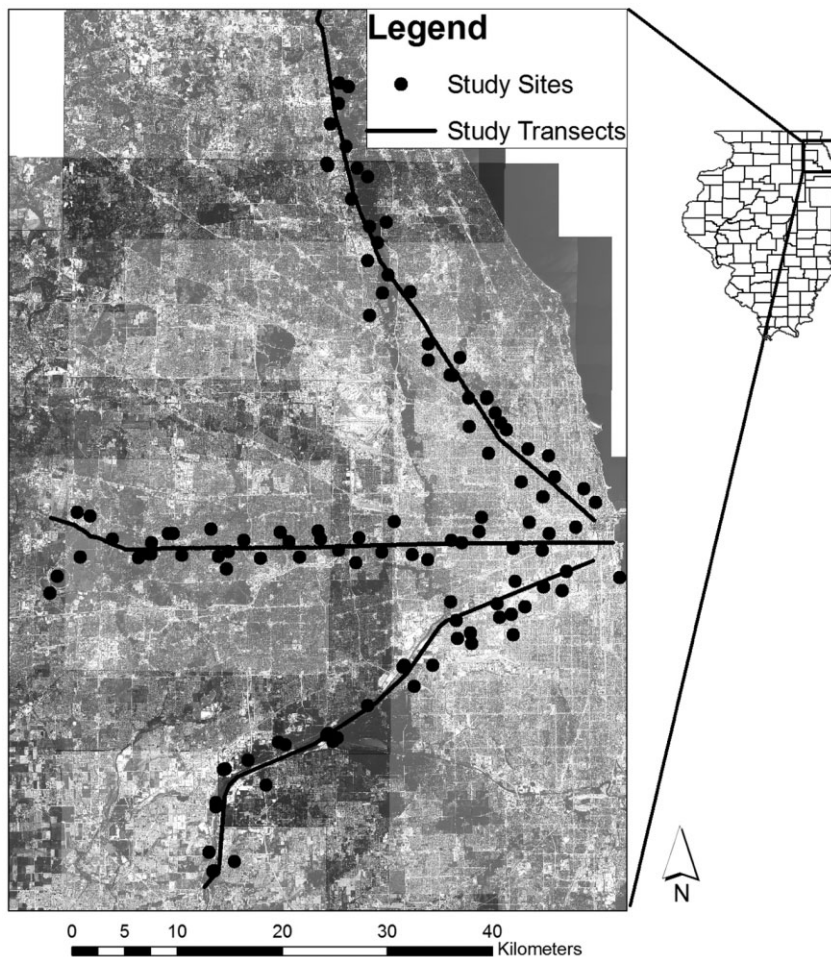
## Materials and methods

### Study sites and sampling

To gather data on species for this study, we deployed camera traps along three transects in the greater Chicago metropolitan area (Fig. 1, Vernon *et al.*, 2014). Transects

were 50 km in length and radiated out from Chicago’s urban center, where wildlife data have rarely been collected previously. Thus, the transects represented gradients of urbanization (McDonnell & Pickett, 1990) that incorporated land use types including urban, suburban, exurban and forest. The northwestern and southwestern transects followed the Des Plaines River and the Sanitary & Ship Canal, respectively. The western transect followed Roosevelt Road, a major roadway. Each transect was divided into 10 5-km-long sections within which we randomly selected sampling stations within 2 km of the transect line, with selection restricted to sites where land-owner permission could be acquired. A maximum of four stations were selected along each section, and stations were separated from one another by at least 1 km. All camera stations were located in sites that represented potential wildlife habitat: city parks, forest preserves, golf courses and cemeteries. Because all transects radiate from a central point, transects were too close together within the first section to support separate stations at > 1-km distances. Hence, we established just four stations within the first section (across all transects).

Four times per year (once per season, beginning in January, April, July and October, respectively) we deployed one Bushnell motion-triggered infrared trail camera (Model #119436C) at each station. Cameras remained in place for approximately 30 days. Sampling began spring of 2010 and continued through summer of 2012, a total of 10 seasons. Cameras were baited with one plaster disk impregnated with synthetic fatty acid scent and two randomly selected carnivore-attracting lures (Willingham, 2008). Within each season, we collected images of coyotes, raccoons and opossums from the camera stations. While other mesopredators such as red fox (*Vulpes vulpes*) and striped skunk (*Mephitis mephitis*) were also captured on cameras, we had insufficient detections for occupancy modeling (models did not converge). During this study, we had 118 active stations, though some stations were not active for the entire study period, and some were replacement stations for others that became unsuitable. Only surveys (defined as sampling at a given site within one season) with ≥ 18 functional nights per season were included in the analysis. Seasons were defined as our primary sampling period, and weeks as secondary sampling occasions (MacKenzie *et al.*, 2003, 2006). Within a season,



**Figure 1** Map showing the distribution of the study sites in the greater Chicago, Illinois area, USA.



at each site, we summarized each week (defined as a 7-day week, beginning with the average day of the week that the cameras were deployed for that season) as either a '1' for a given species (if it was detected), '0' (if not detected), or '-' (indicating censored/missing data if the camera was vandalized, not present or non-functional). Thus, a station provided four possible data points for a given site within each month, and 16 within each year.

### Predictor variables

To identify landscape factors that may influence the distribution of mesopredators in the Chicago area, we quantified the following variables: patch area, housing density and total available habitat, as defined by the land use within the following categories; forest, grassland, wetland, and urban open space. These factors have been shown to impact urban wildlife movement and distribution in past studies (Prange, Gehrt & Wiggers, 2003; Gehrt *et al.*, 2009). We delineated spatial variables using the following existing GIS land cover layers: National Landcover datasets for 2006 (Fry *et al.*, 2011) and a layer describing average housing density (Hammer *et al.*, 2004), with all spatial analysis conducted in ArcGIS ver. 9.3 (ESRI, 2009). As we were also interested in socioeconomic factors, we used census data (at the scale of census blocks) to summarize average household income, average neighborhood age (summarized from the average years houses and other structures were built), and housing vacancy rate (U.S. Census Bureau, 2010).

Each landscape and socioeconomic feature was summarized within a buffer around study sites, except patch area which was simply assigned based on continuous natural habitat nearby the camera station, bounded by paved roads or human development. To ensure that variables were summarized within a region biologically relevant to the study species, we used different buffer sizes based on the approximate average home range of a specific species in urban areas. Thus, we used a 500 m buffer for raccoons (Prange *et al.*, 2004) and opossum (Harmon *et al.*, 2005; Wright *et al.*, 2012), but a 2 km buffer for coyotes (Gehrt *et al.*, 2009; Gehrt & Riley, 2010; Table 1). We were also concerned that canopy cover might impact detection of animals because canopy often correlates with the density of nearby

vegetation, so we assessed canopy cover (National Landcover Database, Fry *et al.*, 2011) within a 100 m buffer of each site. As many mesopredators experience seasonal shifts in range and behavior (Kanda *et al.*, 2009), we also investigated the impact of season on detection probability. Finally, we assessed the impact of lure type used at a site as it may alter the likelihood of detecting each species. To do this, lures were placed into one of four categories based on their contents: fish, gland, meat, and fruit/seed based. Before analysis, all continuous variables were z-transformed to ensure comparability.

### Statistical analysis

Though an all combinations modeling and model-averaging strategy has been suggested for mark-recapture analysis (Doherty, White & Burnham, 2012), the inclusion of four parameters in multi-season occupancy modeling makes this approach computationally intensive and would have resulted in over 1 million models in this analysis. To evaluate this large set of potential models, we used ad hoc hierarchical conditional occupancy modeling to assess variables related to the detection (probability of detecting a species at a field site), occurrence (probability a species is present at a field site), colonization (probability a species not previously present at a field site will begin to inhabit the site between sampling occasions) and local extinction (probability a species previously present at a field site ceases to occur there between sampling occasions) of coyotes, opossum and raccoons (MacKenzie *et al.*, 2003, 2006; Doherty *et al.*, 2012). Each species was modeled separately. All occupancy analyses were conducted in Program R (R Development Core Team, 2014) with version 2.1.8 of the RMark package (Laake, 2013). For all species, we first held occupancy ( $\Psi$ ), colonization ( $\gamma$ ) and local extinction ( $\epsilon$ ) constant, and fit models for detection ( $p$ ) comprised of every possible combination of the variables we expected to impact detection; season, canopy cover, lure type, and patch area (14 total models, including null). Because lure type was known throughout the entire analysis, it was coded as a time-varying individual covariate for detection models. Throughout this process, to maintain a relatively low number of candidate models, we restricted our candidate model sets to

**Table 1** Summary of variables used to predict coyote, opossum, and raccoon occupancy and colonization in the Chicago, IL region

Species	Variable	Mean	Minimum	Maximum	Standard deviation
Coyote (2 km buffer)	Available habitat (30 × 30 m units)	3259.56	0.00	10292.00	2775.88
	Housing density (units)	916.36	3.47	5728.99	969.23
	Average household income (\$1000s)	33.51	12.24	73.95	12.40
	Average neighborhood age (year)	44.69	19.32	70.66	14.97
	Housing vacancy rate (units)	2.63	0.00	9.70	1.71
Raccoon and opossum (500 m buffer)	Available habitat (30 × 30m units)	272.17	0.00	873.00	259.59
	Housing density (units)	776.60	0.00	4950.81	909.85
	Average household income (\$1000s)	32.79	11.25	82.94	13.93
	Average neighborhood age (year)	45.05	16.64	71.00	16.15
	Housing vacancy rate (units)	3.14	0.00	46.96	5.11

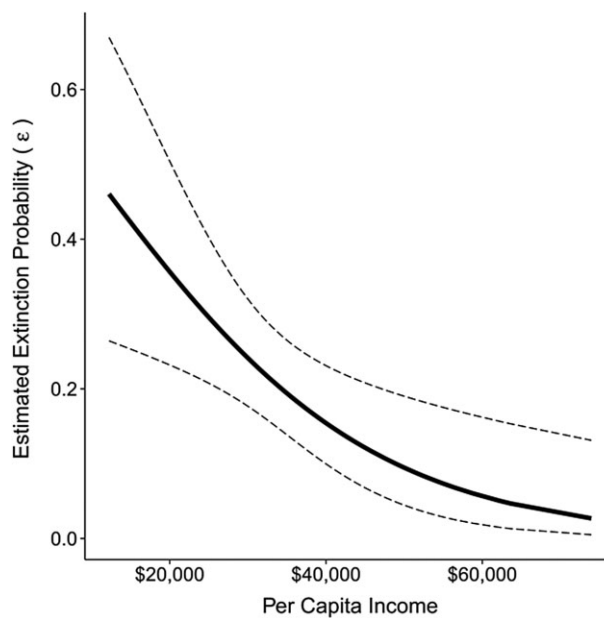
include at maximum three variables (Magle *et al.*, 2010). We modeled each parameter in a step-wise fashion (Fondell *et al.*, 2008). Once the best supported model for detection was identified, we maintained the top performing detection covariates and tested occupancy models comprised of every combination of the variables we expected to influence initial occupancy (patch area, habitat availability, housing density, average household income, housing age, housing vacancy rate, 42 total models before accounting for multicollinearity). Once the top model for occupancy was identified, we maintained the best performing variables for detection and occupancy and tested colonization models comprised of every possible combination of variables we expected to influence colonization, which were the same as those tested for occupancy (42 total models initially). This process continued for modeling extinction.

To address multicollinearity we calculated Pearson correlation coefficients between all species-specific covariates and used a cutoff of  $r \geq 0.60$  as a criterion to exclude correlated variables. For coyotes (2 km buffer), total available habitat was negatively correlated to neighborhood age ( $-0.68$ ) and housing density ( $-0.65$ ). Additionally, neighborhood age and housing density were positively correlated ( $0.62$ ). For the raccoon and opossum analysis, the two species with 500 m buffers, total available habitat was positively related to percent canopy cover ( $0.67$ ). In both cases we used principal components analysis (PCA) to create orthogonal principal components from these covariates, which replaced all correlated variables in analyses. The first principal component for the coyote analysis (WILD) accounted for 77.03% of the variation and was positively correlated to total available habitat (58.55%) but negatively correlated to housing age (57.83%) and housing density (56.80%). Thus, positive values of this component indicate areas with more habitats while negative values imply locations with more houses. For raccoons and opossum, the first principal component (NATURAL) accounted for >99% of the variation and was positively correlated to total available habitat (99.74%) and percent canopy cover (7.14%). Only the first principal component from each PCA was used in occupancy models. No other independent variables present in the same models had correlation coefficients  $\geq 0.60$ .

All models were compared via Akaike's information criteria, adjusted for small sample size ( $AIC_c$ , Burnham & Anderson, 2002). Because we were interested in the relative importance of different variables in predicting the distribution of these three species we calculated variable importance weights (VIW) at each step of the modeling process by summing the weight of each model containing a given variable (Burnham & Anderson, 2002).

## Results

Because of camera malfunction, vandalism, theft and replacement, the average number of camera nights per season per camera was 27.1 days (range = 1–125 days,  $SD = 8.41$ ). A total of 2972, 7292, and 4546 photos of coyotes, raccoons and opossum, respectively, were obtained



**Figure 2** Estimated extinction probability of coyote in the Chicago metropolitan area as a function of per capita income (\$) when all other covariates are held at their median value. Model averaged beta estimates were used in order to address model uncertainty. The solid line represents the predicted extinction probability while the dashed lines represent 95% confidence intervals.

from the camera data. Out of 118 functioning camera stations, 37, 20 and 36 never captured coyotes, raccoons and opossum, respectively. 17 out of the 118 camera stations were never triggered by any study species. With 118 cameras operating for a total of 10 seasons (4 weeks per season), there were 4720 possible total data points for each species, which were summarized as presence or absence of a species within 1 week. However, because additional sites were added during the study, some stations were replacements for others lost during the study, and some experienced malfunctions and vandalism, not all stations were operating during all seasons; thus, 1951 weeks of data were collected in total.

The top model predicting detection of coyotes, based on single-species multi-season occupancy modeling, included the terms for patch area, canopy coverage and season. Detection was highest in winter, followed by spring and summer, with lowest detection in fall. Initial occupancy of coyotes in the top performing model was negatively related to the WILD variable, though other factors also played a role. New colonizations of coyotes were most strongly linked with our WILD term, with areas with more habitat and fewer homes most likely to be colonized. Coyotes were also less likely to experience local extinctions in higher income areas (Fig. 2; Tables 2,5,6).

For raccoons, detection was best predicted by a combination of patch area, season and NATURAL, with detection increased in large patches with high proportions of habitat nearby, and particularly high in the fall. Because of overwhelming initial occupancy of sites (86%), we were

**Table 2** AIC results for multi-season occupancy model selection used to identify covariates to predict first detection (p), followed by occupancy (psi), colonization (gamma) and extinction (epsilon) for coyotes in the Chicago area

Dependent variable	Model	Delta AIC	Model weight	Sum weight	K
Detection	psi(),gamma(),eps(),p(area+canopy+season)	0.00	0.71	0.71	9
	psi(),gamma(),eps(),p(canopy+season)	2.62	0.19	0.90	8
Occupancy	psi(wild),gamma(),eps(),p(area+canopy+season)	0.00	0.25	0.25	10
	psi(wild+vacant),gamma(),eps(),p(area+canopy+season)	1.53	0.12	0.37	11
	psi(wild+income),gamma(),eps(),p(area+canopy+season)	1.54	0.12	0.49	11
	psi(wild+area),gamma(),eps(),p(area+canopy+season)	2.05	0.09	0.58	11
Colonization	psi(wild),gamma(wild),eps(),p(area+canopy+season)	0.00	0.28	0.28	11
	psi(wild),gamma(wild+income),eps(),p(area+canopy+season)	0.80	0.19	0.47	12
	psi(wild),gamma(wild+area),eps(),p(area+canopy+season)	1.20	0.15	0.63	12
	psi(wild),gamma(wild+area+income),eps(),p(area+canopy+season)	1.73	0.12	0.75	13
	psi(wild),gamma(wild+vacant),eps(),p(area+canopy+season)	1.73	0.12	0.87	12
	psi(wild),gamma(income+vacant),eps(),p(area+canopy+season)	2.17	0.09	0.96	13
Extinction	psi(wild),gamma(wild),eps(wild+income+vacant),p(area+canopy+season)	0.00	0.40	0.40	14
	psi(wild),gamma(wild),eps(wild+income),p(area+canopy+season)	0.51	0.19	0.59	13
	psi(wild),gamma(wild),eps(income),p(area+canopy+season)	2.27	0.13	0.72	12

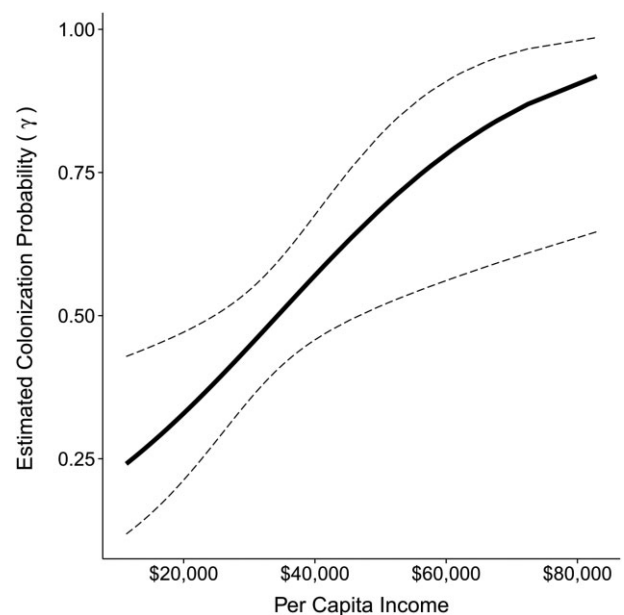
Included are the models at each step (out of 14, 42, 42 and 42, respectively) with AIC values < 2.0, which have the greatest support (Burnham & Anderson, 2002; Magle *et al.*, 2010), plus one additional model beyond. K refers to the number of parameters in each model. 'Wild' refers to the variable derived via PCA from the correlated variables for housing age, housing density and amount of nearby habitat.

unable to identify variables that predicted initial occupancy, and used a null model for this term. Colonization rate for raccoons was most strongly linked to housing density and per capita income based on variable importance weights, with lower colonization in areas with higher housing density and lower income. Local extinction of raccoons was most strongly associated with the NATURAL term and with per capita income, with raccoons least likely to suffer local extinctions in areas with more habitat, higher canopy coverage and higher per capita income. Other variables did not play a major role (Fig. 3; Tables 3,5,6).

Season and patch area played the greatest role in the detection of opossums, with highest detection in large areas and in fall, followed by winter, spring, and finally summer. The top model for occupancy included the term for neighborhood vacancy rate, with initial occupancy being more likely in areas with a large number of vacancies, though there was significant model uncertainty. Colonization for opossums was best predicted by housing density, and NATURAL, with areas of low housing density and low habitat availability most likely to be colonized. Local extinction of opossum was not explained well by any tested variables (Fig. 4, Tables 4–6). Lure type was not among the top models for detection for any species, indicating that our choice of lures had little impact on detection.

## Discussion

As we predicted, both socioeconomic and habitat factors played an important role in the distribution of the three mesopredator species in the Chicago area, but their importance differed among species and had varying influence on species-specific colonization and extinction rates. Occupancy of coyotes and opossum depended most heavily on



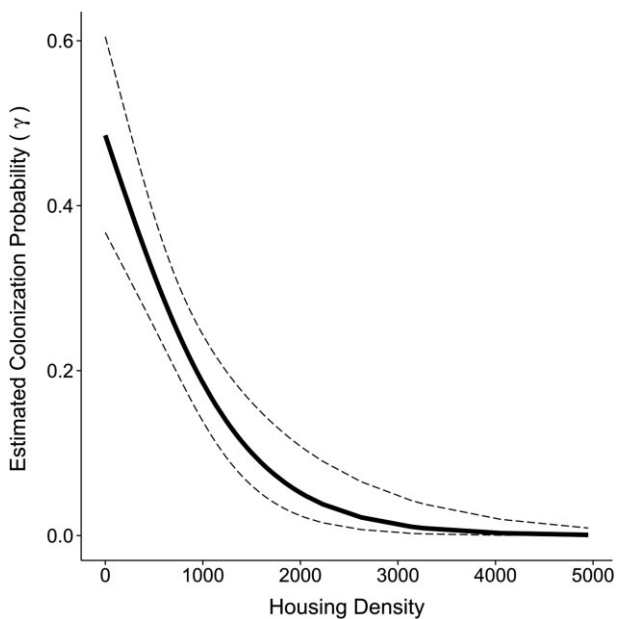
**Figure 3** Estimated colonization probability of raccoon in the Chicago metropolitan area as a function of per capita income (\$) when all other covariates are held at their median value. Model averaged beta estimates were used in order to address model uncertainty. The solid line represents the predicted colonization probability while the dashed lines represent 95% confidence intervals.

housing density and housing vacancy rates, respectively. Colonization events for coyotes and raccoons were most closely linked to housing and also the socioeconomic term for per capita income, while habitat availability also impacted colonization of opossum. Per capita income was

**Table 3** AIC results for multi-season occupancy model selection used to identify covariates to predict first detection (p), followed by occupancy (psi), colonization (gamma) and extinction (epsilon) for raccoons in the Chicago area

Dependent variable	Model	Delta AIC	Model weight	Sum weight	K
Detection	psi(),gamma(),eps(),p(area+natural+season)	0.00	0.73	0.73	9
	psi(),gamma(),eps(),p(habitat+season)	1.96	0.27	0.99	8
	psi(),gamma(),eps(),p(area+season)	16.35	0.00	0.99	8
Occupancy	(Inestimable—see text)				
Colonization	psi(),gamma(area+house+income),eps(),p(area+natural+season)	0.00	0.31	0.31	12
	psi(),gamma(house+income),eps(),p(area+natural+season)	0.07	0.29	0.60	11
	psi(),gamma(habitat+house+income),eps(),p(area+natural+season)	1.12	0.17	0.77	12
	psi(),gamma(house+income+vacant),eps(),p(area+natural+season)	2.03	0.11	0.88	12
Extinction	psi(),gamma(area+house+income),eps(natural+income),p(area+natural+season)	0.00	0.13	0.13	14
	psi(),gamma(area+house+income),eps(natural+house+income),p(area+natural+season)	1.14	0.07	0.20	15
	psi(),gamma(area+house+income),eps(house+income),p(area+natural+season)	1.16	0.07	0.27	14
	psi(),gamma(area+house+income),eps(natural),p(area+natural+season)	1.33	0.07	0.34	13
	psi(),gamma(area+house+income),eps(natural+income+vacant),p(area+natural+season)	2.02	0.05	0.39	15

Included are the models at each step (out of 14, 42, 42 and 42, respectively) with AIC values < 2.0, which have the greatest support (Burnham & Anderson, 2002; Magle *et al.*, 2010), plus one additional model beyond. K refers to the number of parameters in each model. ‘Natural’ refers to the variable derived via PCA from the correlated variables for the amount of nearby habitat and canopy cover.



**Figure 4** Estimated colonization probability of opossum in the Chicago metropolitan area as a function of housing density (units) when all other covariates are held at their median value. Model averaged beta estimates were used in order to address model uncertainty. The solid line represents the predicted colonization probability while the dashed lines represent 95% confidence intervals.

related to local extinction rates for both coyotes and raccoons, while habitat availability had an effect only on raccoon extinctions.

Coyotes are the largest carnivore species present in the Chicago area, and a great deal is known about their habitat preferences (Riley *et al.*, 2003, 2006; Atwood, Weeks & Gehring, 2004; Gehrt, 2007). Even in urban areas, coyotes

tend to prefer patches of natural habitat (Riley *et al.*, 2003; Way, Ortega & Strauss, 2004; Gehrt *et al.*, 2009). The relationship between habitat availability and coyote occupancy in our study was positive, as represented by the variable (WILD) used to combine our correlated explanatory factors. The same variable indicates that less densely populated neighborhoods are most likely to contain coyotes, and are also quite closely associated with colonizations. Coyotes typically attempt to avoid people, even in highly urban areas, and as such this pattern is unsurprising (Gehrt & Riley, 2010). However, a socioeconomic variable, average nearby household income, was also a key predictor of both coyote colonization and extinction in this system. We suspect that, as suggested by previous studies, income correlates with fine-scale environmental variables we did not measure (Loss *et al.*, 2009; Luck *et al.*, 2013), such as habitat complexity or quality, home ownership, presence of water, availability of anthropogenic food sources, and/or presence of humans and commensal pets. It also likely correlates with property size, education level and other demographic factors that may impact how homeowners manage their lawns and gardens and/or engage in direct control or management of wildlife. Studies with birds have found equivocal results with income, some studies relating high-income areas to higher avian richness (Kinzig *et al.*, 2005; Melles, 2005; Strohbach *et al.*, 2009; Luck *et al.*, 2013), and others with lower presence of native species (Loss *et al.*, 2009). The finding that coyotes, and the potential benefits and costs associated with them, are more likely to colonize and less likely to disappear in the more affluent areas may have important management implications such as an improved ability to target control and conservation efforts.

Urban raccoons are known to consume anthropogenic food sources (Rosatte, 2000; Prange *et al.*, 2003; Hadidian *et al.*, 2010), and as such, we expected socioeconomic factors to play a larger role in predicting their distribution. Rac-



**Table 4** AIC results for multi-season occupancy model selection used to identify covariates to predict first detection (p), followed by occupancy (psi), colonization (gamma) and extinction (epsilon) for opossum in the Chicago area

Dependent variable	Model	Delta AIC	Model weight	Sum weight	K
Detection	psi(),gamma(),eps(),p(area+season)	0.00	0.40	0.40	8
	psi(),gamma(),eps(),p(season)	0.96	0.25	0.65	7
	psi(),gamma(),eps(),p(area+natural+season)	1.36	0.20	0.85	9
	psi(),gamma(),eps(),p(natural+season)	2.27	0.13	0.98	8
Occupancy	psi(vacant),gamma(),eps(),p(area+season)	0.00	0.11	0.11	9
	psi(income),gamma(),eps(),p(area+season)	1.26	0.06	0.17	9
	psi(income+vacant),gamma(),eps(),p(area+season)	1.33	0.06	0.23	10
	psi(natural+vacant),gamma(),eps(),p(area+season)	1.62	0.05	0.28	10
	psi(),gamma(),eps(),p(area+season)	1.63	0.05	0.33	8
	psi(area+vacant),gamma(),eps(),p(area+season)	1.73	0.05	0.38	10
	psi(age+vacant),gamma(),eps(),p(area+season)	1.91	0.04	0.42	10
	psi(house+vacant),gamma(),eps(),p(area+season)	2.06	0.04	0.46	10
Colonization	psi(vacant),gamma(area+house+natural),eps(),p(area+season)	0.00	0.27	0.27	12
	psi(vacant),gamma(house+natural),eps(),p(area+season)	0.44	0.21	0.48	11
	psi(vacant),gamma(age+house+natural),eps(),p(area+season)	1.04	0.16	0.64	12
	psi(vacant),gamma(house+natural+vacant),eps(),p(area+season)	2.34	0.08	0.72	12
Extinction	psi(vacant),gamma(area+house+natural),eps(),p(area+season)	0.00	0.12	0.12	12
	psi(vacant),gamma(area+house+natural),eps(area),p(area+season)	0.43	0.10	0.22	13
	psi(vacant),gamma(area+house+natural),eps(house+natural),p(area+season)	1.78	0.05	0.27	14
	psi(vacant),gamma(area+house+natural),eps(natural),p(area+season)	1.99	0.05	0.32	13
	psi(vacant),gamma(area+house+natural),eps(income),p(area+season)	2.05	0.04	0.36	13

Included are the models at each step (out of 14, 42, 42 and 42, respectively) with AIC values < 2.0, which have the greatest support (Burnham & Anderson, 2002; Magle *et al.*, 2010), plus one additional model beyond. K refers to the number of parameters in each model. 'Natural' refers to the variable derived via PCA from the correlated variables for the amount of nearby habitat and canopy cover.

coons are among the most successful carnivores in North America (Hadidian *et al.*, 2010) and unfortunately, raccoons were present at such a high proportion of our sites that we had difficult modeling initial occupancy. We did find, however, that both housing density and per capita income impacted colonization and extinction dynamics of raccoons. As with coyotes, neighborhoods characterized by high incomes and low housing density were most often colonized, and least often associated with disappearance of raccoons. We were somewhat surprised that raccoons, who are known to consume largely anthropogenic food (Hadidian *et al.*, 2010) were less prevalent in the densest urban areas. It is possible that a lack of trees in urban areas impact raccoon distributions, or that our cameras, located in parks and open space, were placed insufficiently close to dumpsters and other sources of anthropogenic food. Disease has also been found to be a significant factor in limiting urban raccoon populations (Prange *et al.*, 2003), and if disease prevalence is increased in more highly urban neighborhoods (as in Hamer *et al.*, 2012), it may provide an alternate explanation for the reduced occurrence of raccoons in these areas. As with coyotes, the relationship with household income likely reflects an unmeasured factor of high-income neighborhoods.

Less is known about the habitat preferences of opossum in urban areas. In contrast to coyotes and raccoons, housing vacancy rate was the best predictor of initial opossum occupancy, which may indicate opossum are finding a way to make use of residential spaces that have been foreclosed on

or are otherwise unused, though the relationship was relatively weak. However, natural habitat and housing density were also very strong predictors of opossum colonization. While areas of lower housing density were more likely to be colonized, as with coyotes and raccoons, the relationship with habitat was somewhat surprising, with areas characterized by a high degree of nearby habitat with high canopy cover actually less likely to be colonized. We suspect this is an artifact of opossum having already occupied all the potential habitat fragments in the area with a large amount of nearby habitat, leaving only the patches lacking nearby habitat for colonization events. This may provide indirect evidence for adaptation, if opossum are now colonizing patches previously unsuitable. It is also possible that opossum are selecting for edge habitat (Dijak & Thompson, 2000; Crooks, 2002) in which case habitat patches surrounded by dissimilar urban habitat may represent an urban edge that attracts this species. We speculate that unmeasured factors that correlate with housing density may be responsible. Water availability, for example, is known to impact opossum distribution (Lay, 1942; Reynolds, 1945; Llewellyn & Dale, 1964; Fidino, Lehrer & Magle, unpubl. data), but we did not include distance to water in our models, both to maintain a reasonable candidate model set, and because distance to water is correlated with other tested variables such as housing density.

In general, our findings for habitat variables were consistent, though in many cases weaker, than in previous research with respect to landscape factors. However, we also found

**Table 5** Parameter estimates from top models used to predict coyote, raccoon, and opossum occupancy, colonization and local extinction in the Chicago area

Species	Dependent variable	Parameter	Beta estimate	Standard error
Coyote	Detection	Intercept	0.19	0.16
		Season (spring)	-0.59	0.17
		Season (summer)	-0.85	0.17
		Season (fall)	-0.45	0.18
		Canopy coverage	0.16	0.17
	Occupancy	Intercept	-0.29	0.46
		Wild (PCA)	0.47	0.33
	Colonization	Intercept	-1.22	0.19
		Wild (PCA)	0.57	0.13
	Extinction	Intercept	-1.44	0.22
		Per capita income	-0.59	0.24
		Wild (PCA)	0.23	0.17
		Vacancy rate	0.20	0.22
Raccoon	Detection	Intercept	0.01	0.13
		Season (spring)	0.01	0.17
		Season (summer)	0.02	0.16
		Season (fall)	0.08	0.18
		Natural (PCA)	0.02	0.06
		Patch area	0.07	0.05
	Occupancy	Intercept	0.87	0.08
	Colonization	Intercept	-0.54	0.19
		Patch area	0.10	0.18
		Housing density	-1.49	0.28
		Per capita income	0.69	0.18
	Extinction	Intercept	-1.19	0.13
		Natural (PCA)	-0.18	0.15
Per capita income		-0.15	0.14	
Opossum	Detection	Intercept	0.28	0.24
		Season (spring)	-0.15	0.26
		Season (summer)	-0.40	0.26
		Season (fall)	0.38	0.27
		Patch area	0.06	0.05
	Occupancy	Intercept	-0.52	0.45
		Vacancy rate	0.77	0.81
	Colonization	Intercept	-1.16	0.15
		Housing density	-1.29	0.29
		Natural (PCA)	-0.29	0.16
		Patch area	0.08	0.11
	Extinction	Intercept	-0.83	0.22

For occupancy, seasonal effects are with respect to the winter season. For colonization and extinction, seasonal effects are calculated between seasons and are with respect to the period between winter and spring.

that in many cases, socioeconomic variables such as household income predicted species occupancy as well or better than habitat variables, based on variable importance weights. While species responded strongly to degrees of urbanization, as represented by housing density, amount of available habitat (defined largely as green space) had a lesser effect, perhaps indicating that in human-dominated environments, human factors may more directly impact distribution of carnivore species. It has been previously suggested that

socioeconomic factors may constitute an unstudied gradient (Kinzig *et al.*, 2005), one perhaps as important to wildlife abundance and distribution as urbanization gradients, elevation gradients or any other spatially predictive factors, and may link to habitat changes. For example, neighborhoods with more per capita income may have larger trees and shrubs (Melles, 2005). It is possible that these vegetative changes may decrease availability of daytime resting sites, denning sites, or may negatively influence the distribution of potential prey species. However, multiple explanations for these observed changes exist, and should be verified by future study. It should be noted that there are countless measurable socioeconomic factors, and our results are constrained onto those variables we chose to test. Human attitudes, for example, were not directly measured in this study, though they may be important for the population biology of carnivore species (Bjurlin & Cypher, 2005).

In addition to providing extra explanatory power for predicting wildlife presence, by considering socioeconomic factors, we can also gain insight into how various human communities may experience or interact with wildlife species (Kinzig *et al.*, 2005; Melles, 2005; Strohbach *et al.*, 2009; but see Loss *et al.*, 2009). There may be environmental justice implications to the uneven distribution of wildlife, with impoverished communities less likely to experience biodiversity in their neighborhoods (Strohbach *et al.*, 2009; Cohen *et al.*, 2012; Davis *et al.*, 2012). Some have suggested that when economic poverty is compounded by biological poverty, it may lead to reduced public support for the conservation of biodiversity in the long term (Melles, 2005). For two of the three species we studied (coyotes and raccoons), relationships between predator distribution and socioeconomic factors identified in our study seem to mirror previous findings for birds, with both species more prevalent in higher income neighborhoods. However, the resultant outcome for human communities may differ. Birds are widely viewed as providing chiefly positive outcomes for humans in urban neighborhoods, including increased property values, bird watching and feeding opportunities (Jones & Reynolds, 2008), and psychological benefits that accrue as a result (Fuller *et al.*, 2007). Public attitudes toward predators are decidedly more mixed (Vaske & Needham, 2007), with some people opposed to any control of predators in urban areas, and others insistent on removal of these species by any means possible. Predatory species may reduce songbird diversity (Crooks & Soulé, 1999), can harbor diseases (e.g. Riley, Hadidian & Manski, 1998; Gehrt & Riley, 2010) and may pose a threat to pets (Morey, Gese & Gehrt, 2007). However, top predators such as coyotes may actually increase songbird diversity because of top-down effects on smaller mesopredators (Crooks & Soulé, 1999), and may also prey on problematic species such as rats (*Rattus norvegicus*), and Canada geese (*Branta canadensis*). As predators have both negative and positive impacts on human communities in urban areas, the overall implications for environmental justice remain unclear, and likely require further exploration.

Our study is among the first to explore the relationship between socioeconomic metrics and carnivore distributions

**Table 6** Summary of variable importance weight values for variables used to predict occupancy, colonization, and extinction of coyotes, raccoons and opossum in the greater Chicago, IL, USA region

Dependent variable	Species	Independent variables						
		Age	Area	Housing	Income	Vacant	Wild <sup>a</sup>	Natural <sup>a</sup>
Occupancy	Coyote		0.25 (+)		0.40 (+)	0.36 (-)	0.74 (+)	
	Raccoon	N/A	N/A	N/A	N/A	N/A		N/A
	Opossum	0.25 (+)	0.28 (-)	0.22 (-)	0.38 (+)	0.53 (+)		0.27 (-)
Colonization	Coyote		0.32 (+)		0.40 (+)	0.27 (-)	0.99 (+)	
	Raccoon	0.11 (-)	0.31 (+)	0.99 (-)	0.99 (+)	0.11 (+)		0.17 (+)
	Opossum	0.20 (-)	0.38 (+)	0.99 (-)	0.13 (-)	0.12 (+)		0.80 (-)
Extinction	Coyote		0.17 (-)		0.95 (-)	0.52 (+)	0.69 (+)	
	Raccoon	0.24 (+)	0.20 (+)	0.43 (+)	0.57 (-)	0.21 (-)		0.61 (-)
	Opossum	0.25 (+)	0.39 (+)	0.27 (-)	0.22 (-)	0.22 (+)		0.31 (-)

Variable importance weights are derived by summing the model weights for each model containing a given variable. Variables positively impacting occupancy, colonization or extinction are marked with a (+), and those negatively impacting occupancy, colonization or extinction are marked with (-). <sup>a</sup>Wild and Natural are variables derived via PCA from other, correlated predictor variables, see Methods.

in a North American city. Because of the high potential of these species to create conflict with humans (Conover, 2002; Gehrt & Riley, 2010), clarifying the relationship between neighborhood characteristics and species presence has implications for conservation and management. Efforts to study or manage urban coyotes and raccoons should thus presently focus on high-income areas with low housing density. The lack of apparent relationship between habitat availability and colonization may indicate that urban species follow specific corridors rather than simply diffusing freely throughout the urban matrix (Crooks & Sanjayan, 2006). These corridors could be identified using radio-telemetry and enhanced or removed as appropriate. The situation is different for opossum, which respond somewhat to housing vacancies as well as habitat availability. Management of this species should perhaps focus on the interface between urban areas and open space.

Urban areas change extremely rapidly in response to human demand (Pickett *et al.*, 2008). As such, it is unsurprising that existing ecological theory from natural systems is often inadequate to describe species distributions in cities (Magle *et al.*, 2012). The addition of socioeconomic factors to existing models partially accounts for the wide range of human activities that doubtless impact urban wildlife (Melles, 2005). In addition, if socioeconomic metrics are updated more rapidly, for example, by entities such as census bureaus, than landscape-level habitat factors are updated (often by acquisition of new satellite imagery), they may do a better job of mirroring the ongoing change in urban communities. As urban areas are expected to continue to increase rapidly, both in spatial extent and in human population (Kinzig *et al.*, 2005), their relative importance for wildlife management and even conservation must increase accordingly. Humans are the drivers of land-use change and the managers of habitat in these areas, and efforts to modify urban wildlife communities that do not incorporate knowledge of varying human demography, culture and attitudes are likely to fail. In the long-term, we must develop new and innovative approaches that combine ecological principles with a deep understanding of urban

planning and human attitudes toward wildlife. Knowing that socioeconomic factors influence wildlife distributions can help us target educational and management actions to the appropriate areas. For coyotes, this may take the form of advocating keeping pets close to the home. For raccoons, it could direct placement of secure garbage containers. In addition, fine-scale analysis of movement behavior could determine the specific elements proxied by these socioeconomic terms, which would enable city and landscape planners to create and modify neighborhoods to attract or repel target species. Both wildlife and human behavior, and the interactions between them, must be better understood if we are to conserve and manage species as an integral part of our urbanizing planet.

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