

Habitat Dynamics of the Virginia Opossum in a Highly Urban Landscape

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ABSTRACT.—As urban habitats vary in composition and structure along the urban to rural gradient, different degrees of urbanization likely result in a diversity of landscape responses from wildlife. We investigated this relationship with the Virginia opossum (*Didelphis virginiana*), an urban adapted species that is both common and understudied in highly metropolitan landscapes. We investigated which landscape factors affect opossum occupancy, colonization, extinction, and detection by using a large system of motion-triggered camera traps in the Chicago metropolitan area over 10 seasons from spring 2010 to summer 2012. Opossum patch occupancy rates were highest near natural water sources regardless of urbanization, whereas occupancy rates in patches ≥ 1000 m from natural water sources decreased with increasing urbanization. Our results suggest opossums have relaxed habitat needs at intermediate levels of disturbance, as the ability to locate anthropogenic water sources may allow them to occupy previously uninhabitable patches.

INTRODUCTION

Though one of the ecological trademarks of cities is decreased species diversity (Aronson *et al.*, 2014), wildlife still exist within these highly urban landscapes and little is known about the habitat dynamics that drive their distribution. As the world steadily becomes more urban, and more people occupy cities (McDonnell and Hahs, 2008), it is necessary to better understand the habitat needs of species within highly urban landscapes to conserve biodiversity, increase the quality of wildlife management practices, and improve how cities are built. While urban habitats can negatively impact wildlife in many ways (*e.g.*, human-induced disturbance regimes, spatial heterogeneity, novel competitors, *etc.*), species that adapt to the challenges associated with urban systems often benefit indirectly from these habitats. Of the benefits associated with urban environments, subsidized food and water sources arguably provide the largest influence in that they can increase a species' density (Luniak, 2004; Prange and Gehrt, 2004), individual survival rates (Kanda *et al.*, 2009), and relax selective pressures on natural habitats (Bozek *et al.*, 2007). Yet, as urbanization increases and the landscape is dominated by impervious surfaces, humans, and traffic, energy gained from these subsidized resources may not overcome the energetic cost of survival. For example our largest cities likely contain a wealth of anthropogenic food for wildlife; however, the ability to successfully acquire these resources may be more difficult as available habitat becomes more fragmented and the human population increases (Magle *et al.*, 2014). Additionally, the lower proportion of green space within cities may decrease the availability of water sources, anthropogenic or otherwise, thereby limiting species to areas where they can locate water. In response species may make different habitat choices to lessen the impact of increased human presence and habitat fragmentation within highly urban landscapes.

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The Virginia opossum (*Didelphis virginiana*, hereafter opossum) is an excellent candidate to study this potential trend. North America's only marsupial, the opossum is predominately nocturnal, roughly the size of a domestic house cat, and largely opportunistic in diet (Gardner and Sunquist, 2003). An urban adapted species (*sensu*, McKinney, 2002), the opossums' ability to access water sources may be a crucial habitat requirement throughout its distributional range, and many rural studies observe surface water to be a key habitat requirement (Lay, 1942; Reynolds, 1945; Llewellyn and Dale, 1964; Gardner and Sunquist, 2003; Babb *et al.*, 2004). Urban studies of the opossum, however, have not found proximity to surface water to be necessary (Kanda *et al.*, 2006; Markovchick-Nicholls *et al.*, 2008), which may be due to the prevalence of anthropogenic water sources such as irrigation canals, drainage ditches, and bird baths. Therefore, the opossum may have different habitat requirements in urban and rural areas.

Despite their prevalence along the entirety of the urban to rural gradient, opossums have never been studied within highly urban landscapes. To date, urban opossums have only been studied in small towns and suburbs (Meier, 1983; Kanda *et al.*, 2005; Bozek *et al.*, 2007), forest preserves near cities (Prange and Gehrt, 2004; Markovchick-Nicholls *et al.*, 2008), inside of zoos (Harmon *et al.*, 2005), and in fragments of remnant habitat within the steep-sloped canyons of the San Diego Metropolitan region (Crooks, 2002). Due to the opossum's large distributional range and ubiquity in urban habitats there is a significant knowledge gap regarding the habitat needs of this urban adapted species at high degrees of urbanization. As such opossums represent a significant opportunity to better understand the ecology of our cities. Additionally, the opossum is an excellent candidate to explore shifting habitat needs in highly urban areas because opossum patch colonization and extinction events can be observed over a short time frame. At the northern portion of their range, opossums may breed up to twice a year but rarely survive more than one winter (Prange and Gehrt, 2004; Kanda *et al.*, 2009). Moreover, opossums are able to rapidly expand their range and occupy new areas because pregnant females and juvenile opossum often disperse great distances (>1.5 km) to new habitats in a single night (Gillette, 1980), though dispersal distances may be less within cities due to their highly fragmented nature.

To determine if varying amounts of urbanization affect the habitat dynamics of opossums we set motion-triggered camera traps in city parks, cemeteries, forest preserves, and golf courses along three 50 km transects that originated in downtown Chicago, Illinois, U.S.A. and radiated outward along an urbanization gradient. We used a single species, multiple season occupancy modeling framework (MacKenzie *et al.*, 2006) to predict the distribution of opossum and determine the key landscape, local, and temporal factors that influence their habitat dynamics in a highly urban landscape. Two nonmutually exclusive hypotheses were considered for this study: (i) as opossums have been shown to have a need for green space in less urban environments (Meier, 1983), opossum patch dynamics should be positively related to factors associated to green space and negatively related to factors associated to the built environment and (ii) if anthropogenic water sources are either more difficult to access or less abundant with increasing urbanization, then opossum patch occupancy rates should decrease far from water as urbanization increases, whereas opossum patch occupancy rates close to natural water sources should stay high regardless of the degree of urbanization.

MATERIALS AND METHODS

STUDY AREA

This study was part of an ongoing camera trap survey to determine the distribution of medium to large mammals throughout the Chicago Metropolitan area (41°50'15''N,

87°40'55'W). Located on the southwestern shore of Lake Michigan, Chicago experiences four distinct seasons that consists of warm summers (average low = 16.8 C), cold winters (average low = 3.6 C), intermediate springs (average low = 8.1 C), and autumns (average low = 4.7 C; WolframAlpha, 2014). Chicago is the most populous midwestern city in the United States with ≥ 2.7 million residents and an average population density of 7355 people km^{-2} , whereas the greater metropolitan area surrounding the city contains an estimated 9.5 million people (U.S. Census, 2013a).

Four different site types were included in this study, which together represent the majority of potential habitats throughout the Chicago metropolitan area: forest preserves, city parks, cemeteries, and golf courses. We solely focused on these types of habitat as they make up the largest proportion of green space in the metropolitan area. Forest preserves had varying degrees of native and/or natural plant vegetation with some sites being heavily landscaped, highly invaded by invasive plant species [e.g., common buckthorn (*Rhamnus cathartica*)], or both (Vernon *et al.*, 2014). Small city parks (<2 ha) consisted of mature trees within a landscape of turf grass, whereas large city parks (>2 ha) had areas of natural vegetation interspersed throughout the park or around the shoreline of man-made ponds. Cemeteries differed greatly in habitat characteristics with some being large (>2 ha) but functionally similar to small (<2 ha) city parks and others small but directly abutting or containing wooded areas. Golf courses were large (mean 82.7 ± 34.5 ha), heavily landscaped, and contained man-made water features. However, most golf courses retained some natural areas within and around their expansive property.

STUDY DESIGN

A gradient based design was used to determine how varying amounts of urbanization affected the habitat dynamics of opossums. This method has become an increasingly common and useful approach to assess how urbanization alters ecological processes (McDonnell and Hahs, 2008). We delineated three 50 km transects that originated from Union Station in downtown Chicago and radiated outward in three different directions: north following the Des Plaines River, west along Roosevelt Road, and south following the Ship and Sanitary Canal (Fig. 1). Transects included a variety of landscape types such as urban, suburban, exurban, open space, grassland, and forest. Each transect was equally split into ten 5 km sections and a maximum of four sites were sampled within each section. Sites were selected within 2 km of each transect (dependent upon access) with a minimum distance between sites of 1 km. Because the three transects originated from a central location, only four sites were sampled within the first section of all transects combined, but otherwise attempts were made to create an equal distribution of sites across all portions of the gradient, with available sites otherwise randomly chosen (Fig. 1). A total of 118 sites were sampled, and sites represented both public and private ownership.

DATA COLLECTION

One Bushnell motion-triggered infrared Trail Camera (Model #119436C) was placed at each site for approximately 4 w per season (*i.e.*, spring, summer, autumn, and winter) from spring 2010 to summer 2012 (10 seasons total, details in Vernon *et al.*, 2014). Each season, in addition to the camera trap, one plaster disk impregnated with synthetic fatty acid scent and two randomly selected carnivore-attracting lures were placed at each site within view of the camera trap in order to increase the probability of detecting species (Magle *et al.*, 2015). While lures may draw individuals in from a somewhat larger area, which could alter small scale habitat choices made by species within a patch, this study is solely focused on habitat dynamics at the home range scale and differences in occupancy, colonization, and extinction

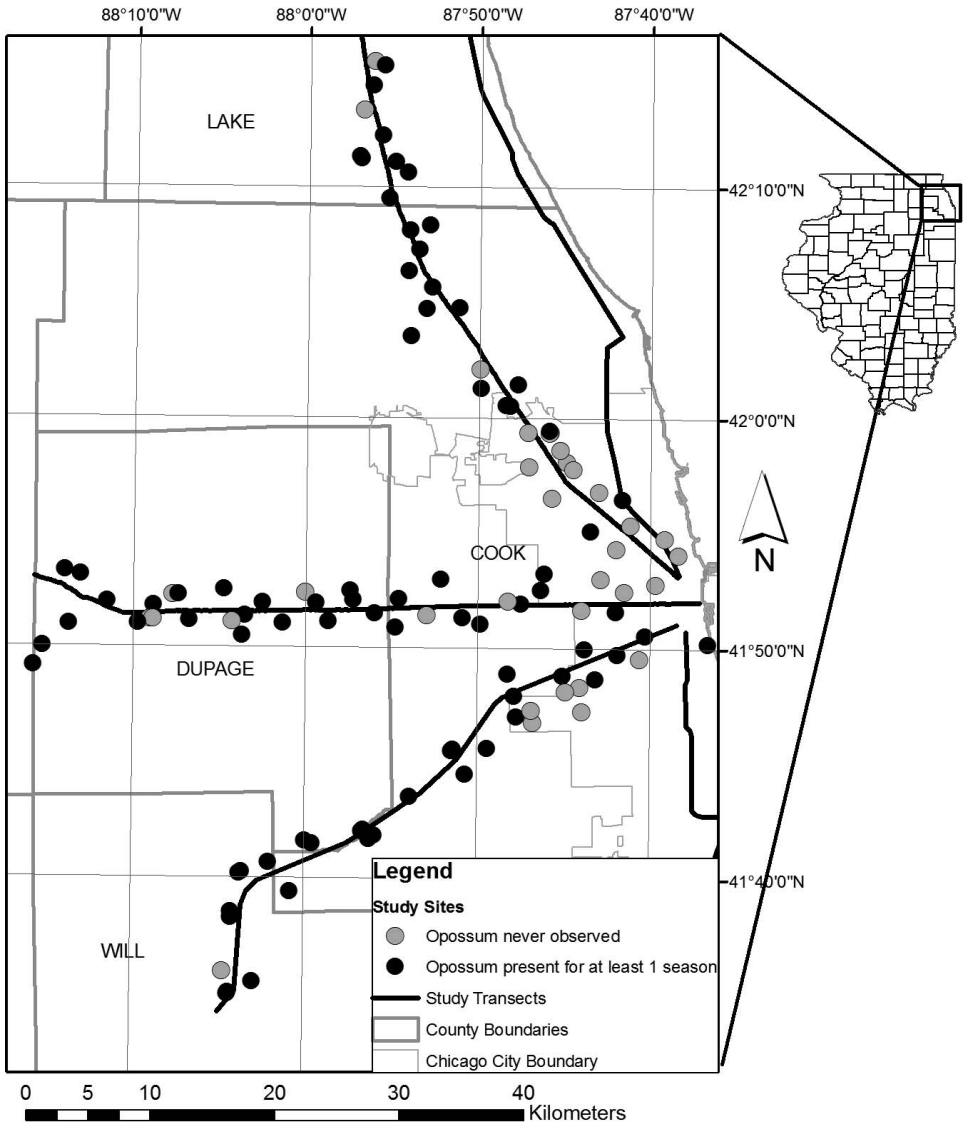


FIG. 1.—Map of study sites and transects in the Chicago Metropolitan area, Illinois, U.S.A. The dark black lines delineate our three study transects, which follow the Des Plaines River to the northwest, Roosevelt Road to the west, and the Ship and Sanitary Canal to the southwest

between patches. Therefore, lure placement should not bias our analysis. Sampling season was considered the primary sampling period, whereas weeks within a season constituted secondary sampling occasions. Because all cameras were not placed on the same date, the start of the first sampling week was defined as the average starting camera date per season and each successive sampling week began 7 d after the previous one. Therefore, each site

produced four data points per season and 16 data points per year. Each sampling week was either coded as “1” if an opossum was detected at least once within that time frame, “0” if they were not, or “.” (censored) if the camera was not present or not operable. A site was seasonally censored from the analysis if the camera was not functional for at least 18 d. A subset of sites ($n = 25$, 22%) were retired during the study due to repeated vandalism, theft of a camera trap, or change in site accessibility. Data from functional seasons at a site prior to being retired were included in the analysis, whereas seasons following this designation were censored.

PREDICTOR VARIABLES

To identify landscape factors influence opossum patch dynamics, ArcGIS ver.9.3 (ESRI, 2008) was used to create layers of landscape factors within a 500 m buffer centered on the location of the camera trap (Table 1). A 500 m buffer (78.5 ha) was chosen based on previous research that found opossum home range sizes varied from 51 ha to 108 ha (Gillette, 1980). All layers used were in raster format and had 30 m resolution. Two landscape factors were selected to represent both the human and habitat impacts of urbanization: average housing density (derived from U.S. Census, 2010) and average amount of impervious surface (Illinois Geospatial Clearinghouse, 2003). We predicted both factors would be negatively associated to opossum occupancy and colonization but positively associated to extinction because areas with high housing densities have been shown to deter wildlife (Magle *et al.*, 2014) and areas with large tracts of impervious surface may have fewer anthropogenic water sources due to stormwater management practices (*i.e.*, grey infrastructure) as well as higher chances of road mortality.

Additionally, three factors were selected to represent the natural environment: percent canopy cover of trees (Fry *et al.*, 2011); distance to nearest natural water source (Illinois GAP data); and total available landscaped habitat, which represented the summation of the following land use categories within 500 m of a camera trap: city parks, cemeteries, and golf courses. As opossums have broad habitat tolerances but a preference for deciduous forest close to water (Gardner and Sunquist, 2003), we predicted these factors would increase patch quality and occupancy. Furthermore, interactions between distance to natural water sources and our two covariates related to urbanization (*i.e.*, housing density and impervious surface) were considered to test if opossums have a stronger need for sites closer to water as urbanization increases. Seasonal variation in detection probability also was investigated because opossums alter their movement patterns seasonally (Gillette, 1980; Kanda *et al.*, 2009), which may increase or decrease the likelihood of encountering a camera trap. Finally, the impact of canopy cover on detection probability was assessed as it is correlated to the density of nearby vegetation (Fry *et al.*, 2011).

TABLE 1.—Summary of variables used to predict opossum occupancy, colonization, and extinction in the Chicago, Illinois region, U.S.A.

Variable	Mean	Minimum	Maximum	Standard deviation
Housing Density (Units)	776.61	0	4950.81	909.85
Impervious Surface (%)	38.33	0	85.59	22.52
Canopy Cover (%)	17.85	0	75.88	19.63
Distance to Water (m)	1008.95	0	5490.25	1179.44
Total Available Landscaped Habitat (30 x 30 m units)	168.75	0	862	192.16

STATISTICAL ANALYSIS

We used single-species, multiple-season occupancy models with the RMark package ver 2.1.8 (Laake, 2013) in Program R ver 3.1.1 (R Core Team, 2014) to determine which landscape and local variables best explained our data with respect to initial occupancy (Ψ), colonization (γ), extinction (ε), and detection (ρ), and then estimated future occupancy rates to determine habitat suitability using the recursive equation $\Psi_{t+1} = \Psi_t(1 - \varepsilon_t) + (1 - \Psi_t)\gamma_t$ (MacKenzie *et al.*, 2003, 2006).

For this analysis we constructed alternate parameterizations of Ψ , γ , ε , and ρ using our predictor variables, then tested all combinations of each parameterization (including the null model, $n = 336$). To test for multicollinearity, we calculated Pearson's correlation coefficients between all covariates used in this analysis and did not use any covariates in the same model if $r \geq 60$. Two sets of covariates were highly correlated: Housing density and impervious surface ($r = 0.65$) and canopy cover and impervious surface ($r = -0.81$), therefore we omitted models that included combinations of these covariates.

As the initial distribution of opossum represents a snapshot of patch dynamics rather than the processes that occurred throughout this survey (MacKenzie *et al.*, 2006), we only considered four parameterizations for Ψ , which included factors associated with natural habitat as singular covariates (*i.e.*, distance to water, total available landscaped habitat, and canopy cover) as well as the null model. We input identical parameterizations for γ and ε within a model, which resulted in 21 different combinations. To test our first hypothesis, we created additive combinations of our five landscape variables, constrained to a maximum of three covariates in order to decrease over-parameterization (Magle *et al.*, 2010). To test our second hypothesis, we included models with an urbanization covariate (*i.e.*, housing density or impervious surface), distance to water, and an interaction term between the two. Finally, we considered four parameterizations for ρ , which included additive combinations of season and canopy cover as well as the null model.

We used Akaike's information criterion, adjusted for small sample size (AIC_c) to rank models, and models within 2 ΔAIC_c units of the top-ranked model were considered to have substantial support (Burnham and Anderson, 2002). We did not test for overdispersion as currently, there is no adequate method for testing this in multiple-season modelling with covariates (MacKenzie *et al.*, 2006). Before analysis, all variables were z-transformed to ensure comparability.

RESULTS

From spring 2010 to summer 2012, a total of 4546 photos of opossum were taken at the 118 sites. Autumn (48.50%) had the greatest number of opossum photos, followed by spring (21.20%), summer (18.30%), and winter (12.00%). Furthermore, opossum exhibited a strong nocturnal trend throughout every season, and almost all (97.30%) photos were taken between sundown and sunrise in all seasons. Opossums were photographed at 75 of the 118 sites and average naïve occupancy per season was $23.87 \pm 14.04\%$, which increased to $41.41 \pm 11.94\%$ after accounting for imperfect detection. A total of 4720 camera trapping data points were possible (118 sites * 10 seasons * 4 w per season), but not all sites were sampled throughout the study, and some cameras were stolen or vandalized. Ultimately, 1951 site-weeks of data were collected for this study. On average camera traps were functional for 27.10 ± 8.41 nights per site per season (range = 1 – 125).

Only one model within the model set was considered to have substantial support ($\Delta AIC_c < 2$; Table 2). Hence, we did not conduct model averaging to address model uncertainty and made all of our inferences from this top model (Burnham and Anderson, 2002).

TABLE 2.—Rankings of occupancy models for opossum in Chicago, U.S.A., based on Akaike's Information Criterion corrected for small sample size (AIC_c). This table includes models whose cumulative summation of model weights are ≤ 0.95 . $\Delta AIC_c = AIC_c - \text{min } AIC_c$ for the top performing model. K= the number of estimable parameters

Model	K	ΔAIC_c	Weight	Deviance
$\Psi(\sim\text{water})\varepsilon(\sim\text{water} + \text{house} + \text{water} * \text{house})\gamma(\sim\text{water} + \text{house} + \text{water} * \text{house})\rho(\sim\text{season})$	14	0.00	0.42	1395.55
$\Psi(\sim\text{water})\varepsilon(\sim\text{water} + \text{house} + \text{water} * \text{house})\gamma(\sim\text{water} + \text{house} + \text{water} * \text{house})\rho(\sim\text{canopy} + \text{season})$	15	2.06	0.15	1395.52
$\Psi(\sim\text{water})\varepsilon(\sim\text{water} + \text{house} + \text{water} * \text{house})\gamma(\sim\text{water} + \text{house} + \text{water} * \text{house})\rho(\sim\text{season})$	12	2.66	0.11	1402.36
$\Psi(\sim\text{water})\varepsilon(\sim\text{water} + \text{house} + \text{water} * \text{house})\gamma(\sim\text{water} + \text{house} + \text{water} * \text{house})\rho(\sim\text{canopy} + \text{season})$	10	3.20	0.09	1407.05
$\Psi(\sim 1)\varepsilon(\sim\text{water} + \text{house} + \text{water} * \text{house})\gamma(\sim\text{water} + \text{house} + \text{water} * \text{house})\rho(\sim\text{season})$	13	3.74	0.07	1401.37
$\Psi(\sim\text{water})\varepsilon(\sim\text{water} + \text{house} + \text{water} * \text{house})\gamma(\sim\text{water} + \text{house} + \text{water} * \text{house})\rho(\sim\text{canopy} + \text{season})$	11	4.71	0.04	1402.33
$\Psi(\sim\text{water})\varepsilon(\sim\text{water} + \text{house} + \text{water} * \text{house})\gamma(\sim\text{water} + \text{house} + \text{water} * \text{house})\rho(\sim\text{canopy} + \text{season})$	11	5.23	0.03	1407.00
$\Psi(\sim 1)\varepsilon(\sim\text{water} + \text{house} + \text{water} * \text{house})\gamma(\sim\text{water} + \text{house} + \text{water} * \text{house})\rho(\sim\text{season})$	11	5.63	0.03	1407.40
$\Psi(\sim 1)\varepsilon(\sim\text{water} + \text{house} + \text{water} * \text{house})\gamma(\sim\text{water} + \text{house} + \text{water} * \text{house})\rho(\sim\text{canopy} + \text{season})$	14	5.79	0.02	1401.33

In this model, distance to natural water sources was negatively related to initial occupancy ($\beta_{\text{water}} = -2.14$, $SE = 1.09$), while housing density, distance to water, and the interaction term between the two influenced colonization and extinction. Housing density was negatively related to colonization ($\beta_{\text{house}} = -1.36$, $SE = 0.29$) and extinction ($\beta_{\text{house}} = -1.67$, $SE = 0.49$), whereas distance to water was negatively related to colonization ($\beta_{\text{dist2water}} = -0.05$, $SE = 0.23$) but positively related to extinction ($\beta_{\text{dist2water}} = 0.51$, $SE = 0.26$). The interaction term between housing density and distance to water was positively related to colonization ($\beta_{\text{dist2water*house}} = 0.34$, $SE = 0.16$) and extinction ($\beta_{\text{dist2water*house}} = 0.40$, $SE = 0.19$). Season was the only term related to detection probability. Relative to winter, autumn had the highest detection probability ($\beta_{\text{autumn}} = 0.54$, $SE = 0.27$), followed by spring ($\beta_{\text{spring}} = 0.01$, $SE = 0.26$), and summer ($\beta_{\text{summer}} = -0.25$, $SE = 0.25$).

With this top model, we quantitatively estimated occupancy rates in the remaining sampling sessions (seasons 2 – 10) using the recursive equation at varying intensities of housing density (0 – 4000 units in intervals of 1000) and distances to natural water sources (0 – 4000 m in intervals of 1000). Then we averaged these occupancy rates across all estimated seasons to determine how opossum habitat dynamics vary along a gradient of urbanization (Fig. 2). Across all seasons probability of occupancy near natural water sources averaged ~50% and stayed relatively constant regardless of housing density, although there was a slight increase to 60% when housing density was set to 1000 units (Fig. 2b). Additionally, when housing density increased from 0 units to 4000 units occupancy probability in patches further from natural water sources (≥ 1000 m) decreased an average of $28.15 \pm 8.59\%$. At low housing densities (1000 units), occupancy rates far from natural water sources (≥ 1000 m) remained relatively high (mean = $33.24 \pm 7.28\%$), while occupancy rates at high housing densities (4000 units) were much lower (mean = $9.90 \pm 5.31\%$).

DISCUSSION

Opossum patch occupancy rates stayed relatively constant and high near natural water sources regardless of urbanization but greatly decreased in patches ≥ 1000 m from natural water sources. Therefore, we conclude opossum have a strong need for natural water sources in highly urban landscapes. This trend was not found at lower levels of urbanization and likely indicates that characteristics associated with these less urban environments such as drainage ditches and larger yards uncouple this habitat requirement. Additionally, opossum choice of patches close to natural water sources only appears to be relaxed at intermediate levels of disturbance as opossum also require habitat patches close to natural water sources in rural environments (Lay, 1942; Reynolds, 1945; Llewellyn and Dale, 1964; Gardner and Sunquist, 2003). We suggest the most likely explanation for this apparent trend is the abundance of and ease of access to anthropogenic water sources at intermediate levels of urbanization, as evidenced by opossum exhibiting higher occupancy rates further from natural water sources at low housing densities (Fig. 2). Furthermore, this observed relationship accounts for the results of Kanda *et al.* (2006), who did not find proximity to water to be a key habitat feature of road-killed opossum around Amherst, Massachusetts, a city whose average housing density is an order of magnitude less than Chicago (Amherst = 134.90 houses km^{-2} , Chicago = 1970.50 houses km^{-2} ; U.S. Census, 2013b).

Though we could not quantify the abundance of anthropogenic water sources at our study sites, we believe housing density was a sufficient proxy. Irrigation, for example, accounts for a large proportion of external water usage in cities (Syme *et al.*, 2004) that would not be as available in areas with increased housing density because the proportion of green space and gardens decreases as housing density increases (Tratalos *et al.*, 2007; Fuller

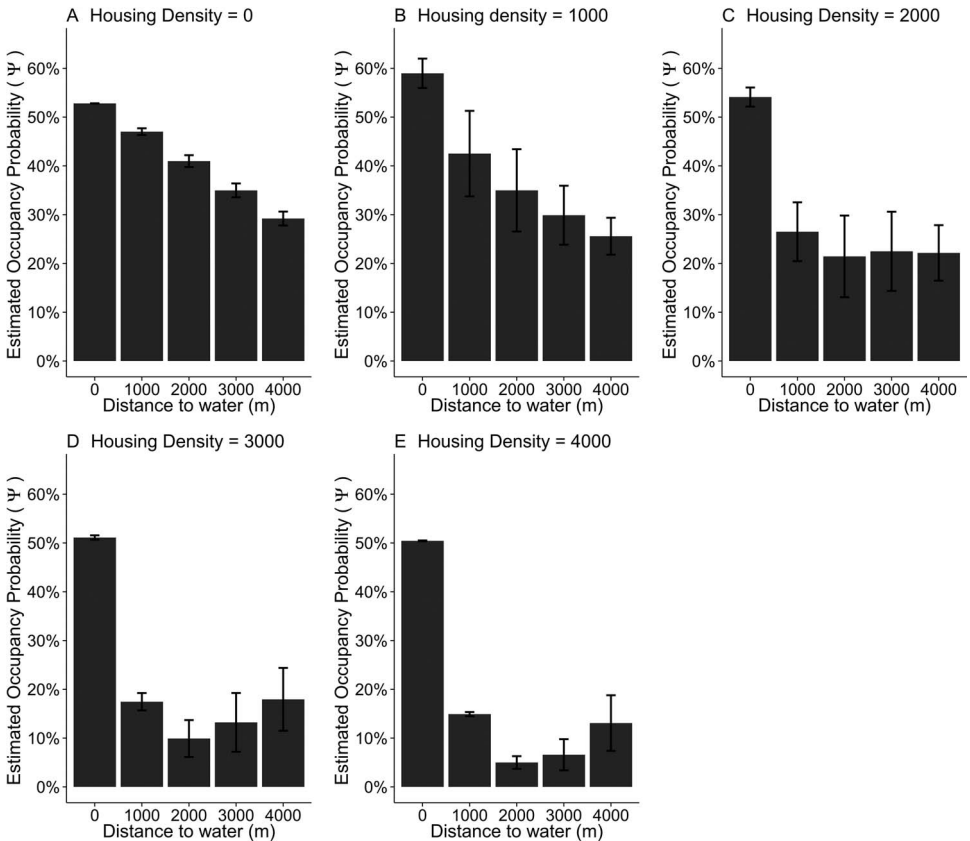


FIG. 2.—Estimated occupancy probability (Ψ) of opossums in the Chicago Metropolitan area, Illinois, U.S.A., across all seasons ($n = 10$) from spring 2010 to summer 2012 at varying rates of housing density and distances to natural water sources

and Gaston, 2009). Additionally, the greater density of impervious surfaces in cities shifts stormwater infrastructure from green infrastructure (*e.g.*, drainage ditches) to elaborate sewer systems (*i.e.*, grey infrastructure). As a result, available habitat for the opossum in highly urban landscapes may be constrained to where they can locate water, which appears to be near natural water sources.

While proximity to water strongly predicts the distribution of opossum throughout Chicago, other elements associated with water sources may be responsible for this pattern. Because opossums tend to forage near den sites (Gilette, 1980), having reliable food sources nearby is likely crucial to their survival. As riparian corridors are high in biodiversity and have greater food availability (Naiman *et al.*, 1993), opossum may need such locations to access reliable food sources. Furthermore, opossums may select sites close to natural water sources because these patches are more connected within the city. Just as road networks move humans from place to place, Chicago's river system, which travels almost to the center of downtown, may function as a crucial corridor for dispersal. As the majority of the world's largest cities are built on fertile habitats near rivers or oceans, we hypothesize that natural water sources within urban landscapes may function as important habitat for wildlife and

allow some species to persist within highly urban environments. In fragmented landscapes riparian corridors have a greater diversity of mammalian predators (Hilty and Merenlender, 2004) and generally are high in biodiversity (Naiman *et al.*, 1993). Though highly urban landscapes are generally low in species diversity (Marzluff, 2005), increasing suitable habitat near rivers and other water sources may be a useful method for cities to increase biodiversity, facilitate travel through urban cores, and increase city residents' urban experience.

In addition to the impact of water, opossums were also more likely to occupy patches with lower housing densities, even at distances to water ≥ 1000 m (Fig. 2). This result contradicts previous research on this species (Kanda *et al.*, 2009) but likely is due to the highly metropolitan nature of Chicago. Highly urban landscapes represent a heterogeneous mosaic of habitable (lower housing density) and uninhabitable (higher housing density) patches, regardless of proximity to the urban core. Indeed, opossums were observed throughout the entirety of the gradient (Fig. 1) and housing density at sites within the city of Chicago that had opossums at least once ($n = 14$) averaged 1097 ± 953 units, whereas sites that never had opossums present ($n = 22$) averaged 1863 ± 1026 units. A post-hoc analysis of this difference produced significant results [$t(35) = -2.48$, $P = 0.02$]; which does provide some additional evidence that opossums do indeed select for sites with lower housing densities within the city, but our model suggests the negative aspects associated to areas with higher housing densities may be offset by proximity to natural water sources.

Despite being highly correlated with housing density, degree of impervious surface performed poorly in this analysis as a predictor of opossum colonization and extinction. One possible explanation is that urban mesocarnivores respond more to the presence of humans within cities than the patchy distribution of the natural habitat within the landscape. Many urban adapted mesocarnivores, for instance, alter their temporal activity to avoid people (Ditchkoff *et al.*, 2006). As cities are highly complex and controlled by natural and social factors, wildlife may consider more than just the bricks and mortar of an urban landscape and select locations where they can maximize the benefits associated with urban life (*i.e.* subsidized resources) while minimizing the costs. Hence, although impervious surfaces significantly alter ecological processes (Shochat *et al.*, 2006), factors that account for both the landscape and human aspects of the environment, like housing density, may play a more important part in determining the distribution of opossums and potentially other urban adapted mammals, but more research is needed to confirm this generalization.

Furthermore, total available landscaped habitat and canopy cover had less support than distance to water in our analysis. Opossums have been shown to prefer green space in urban areas (Meier, 1983) and were present in all landscaped habitats (*i.e.*, golf courses, city parks, and cemeteries) throughout the study. Yet, total available landscaped habitat may be too imprecise a habitat descriptor because it assumes that all landscaped habitat is equal and that opossum do not select for any local characteristics within a patch. Within cities, the built environment increases habitat heterogeneity between patches but decreases habitat heterogeneity within the patch itself (Band *et al.*, 2005). As such habitat quality within a patch may have a greater impact on opossum habitat dynamics than the proportion of green space nearby a patch. Additionally, percent canopy cover may represent different habitat types as urbanization increases. Within the city the majority of landscape below trees is often turf grass that is kept in a constant state of disturbance via landscaping and is less likely to offer opportunities for den sites. Conversely, the landscape below trees in less urban parts of the study area (*e.g.*, forest preserves) is densely vegetated, less likely to be managed,

therefore has a higher probability of containing denning locations. As proportion of canopy cover does not adequately capture this variation, collecting site specific vegetation data around sites in urban studies may be necessary.

Though many studies have shown that habitat associations of mammals in urban habitats differ from their rural counterparts (Bozek *et al.*, 2007; Kanda *et al.*, 2009), very few explore this relationship at high levels of urbanization. We began addressing this gap with an understudied, urban adapted mesocarnivore, the opossum, using a large database of motion-triggered camera images from across the Chicago, Illinois region. Our results suggest opossum habitat dynamics within highly urban landscapes contradict existing knowledge about how this species responds to lower levels of urbanization in two significant ways: opossum in highly urban environments exhibited a strong need for patches near natural water sources, and opossum are negatively impacted by housing density within cities. As cities continue to grow in size and density it is necessary to not only study wildlife at the urban-wild interface but also within urban cores in order to conserve biodiversity in an urbanizing world. Though urban centers today exhibit decreased species diversity (Aronson *et al.*, 2014), this need not be the case for cities in the future with proper research and city planning.

To manage the opossum in urban environments, proximity to natural water sources should be considered. If human-wildlife conflict occurs far from natural water sources it would be necessary to identify and limit potential anthropogenic water sources. As opossums have higher occupancy rates near natural water sources within the city it may be more cost effective to focus educational programs on cohabitating with urban adapted species in these locations, especially in areas with high housing densities. As the world continues to urbanize and metropolitan areas sprawl, discerning the habitat dynamics of urban species can help us to better understand the ecology of our cities and facilitate cohabitation with wildlife, but in order to manage or conserve wildlife in these areas we must first understand how species select habitat within the landscape itself.

Acknowledgments.—We thank M. Ambrocio, L. Bainbridge, J. Bender, C. Chung, F. Cortes, J. Frumkin, H. Grant, D. Hughes, M. Kestufskie, J. Kilgour, K. Limbrick, A. Ravera, J. Rios, M. Vernon, and others for assistance with fieldwork. Detailed suggestions provided by reviewers greatly increased the quality of this manuscript. We are grateful to the many landowners who allowed us access to their property, including the forest preserve districts of Cook, DuPage, Lake, and Will counties, the Illinois Department of Natural Resources' Nature Preserve Commission, the Chicago Park District, and the Archdiocese of Chicago. Funding was provided by the University of Illinois at Chicago, the Lincoln Park Zoo, and the Davee Foundation.

LITERATURE CITED

- ARONSON, M. F., F. A. LA SORTE, C. H. NILON, M. KATTI, M. A. GODDARD, C. A. LEPCZYK, P. S. WARREN, N. S. WILLIAMS, S. CILLIERS, AND B. CLARKSON. 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc. Roy. Soc. Lond. B. Biol.*, **281**:1471–2954.
- BABB, R. D., D. E. BROWN, AND J. L. CHILDS. 2004. On the status of the opossum (*Didelphis virginiana*) in Arizona. *J. Arizona Nevada Acad. Sci.*, **36**:120–126.
- BAND, L. E., M. L. CADENASSO, C. S. GRIMMOND, J. M. GROVE, AND S. T. PICKETT. 2005. Heterogeneity in urban ecosystems: patterns and process, p. 257–278. *In*: G. M. Lovett, C. Jones, M. G. Turner and K. C. Weathers (eds.). *Ecosystem function in heterogeneous landscapes*. Springer-Verlag, New York.
- BOZEK, C., S. PRANGE, AND S. GEHRT. 2007. The influence of anthropogenic resources on multi-scale habitat selection by raccoons. *Urban Ecosyst.*, **10**:413–425.

- BURNHAM, K. P. AND D. R. ANDERSON. 2002. Model selection and multi-model inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- CROOKS, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conserv. Biol.*, **16**:488–502.
- DITCHKOFF, S., S. SAALFELD, AND C. GIBSON. 2006. Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosyst.*, **9**:5–12.
- ESRI. 2008. ArcGIS 9.3. ESRI, Redlands, C.A.
- FRY, J. A., G. XIAN, S. JIN, J. DEWITZ, C. G. HOMER, L. YANG, C. A. BARNES, N. D. HEROLD, AND J. D. WICKHAM. 2011. Completion of the 2006 national land cover database for the conterminous United States. *Photogramm. Eng. Remote. Sensing*, **77**(9):858–864.
- FULLER, R. A. AND K. J. GASTON. 2009. The scaling of green space coverage in European cities. *Biol. Lett.*, **5**:352–355.
- GARDNER, A. AND M. SUNQUIST. 2003. Opossum, p. 3–29. *In*: G. A. Feldhamer, B. C. Thompson and J. A. Chapman (eds.). *Wild mammals of North America: biology, management, and conservation*. 2nd ed. John Hopkins University Press, Baltimore, M.D.
- GILLETTE, L. N. 1980. Movement patterns of radio-tagged opossums in Wisconsin. *Am. Midl. Nat.*, **104**:1–12.
- HARMON, L. J., K. BAUMAN, M. MCCLOUD, J. PARKS, S. HOWELL, AND J. B. LOSOS. 2005. What free-ranging animals do at the zoo: a study of the behavior and habitat use of opossums (*Didelphis virginiana*) on the grounds of the St. Louis Zoo. *Zoo Biol.*, **24**:197–213.
- HILTY, J. A. AND A. M. MERENLENDER. 2004. Use of riparian corridors and vineyards by mammalian predators in northern California. *Conserv. Biol.*, **18**:126–135.
- ILLINOIS GEOSPATIAL DATA CLEARINGHOUSE. 2003. Illinois Geospatial Data Clearinghouse. Retrieved November 20, 2014 from <http://crystal.isgs.uiuc.edu/nsdihome/webdocs/>
- KANDA, L. L. AND K. FRIEDLAND. 2005. Variation in winter microclimate and its potential influence on Virginia opossum (*Didelphis virginiana*) survival in Amherst, Massachusetts. *Urban Ecosyst.*, **8**:215–225.
- , T. K. FULLER, AND P. R. SIEVERT. 2006. Landscape associations of road-killed Virginia Opossums (*Didelphis virginiana*) in Central Massachusetts. *Am. Midl. Nat.*, **156**(1):128–134.
- AND R. L. KELLOGG. 2009. Seasonal source-sink dynamics at the edge of a species' range. *Ecology*, **90**:1574–1585.
- LAAKE, J. L. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep 2013-01, 25 p. Alaska, Fisheries Science Center, NOAA, National Marine Fisheries Service, Seattle, W.A.
- LAY, D. W. 1942. Ecology of the opossum in Eastern Texas. *J. Mammal.*, **23**:147–159.
- LLEWELLYN, L. M. AND F. H. DALE. 1964. Notes on the ecology of the opossum in Maryland. *J. Mammal.*, 113–122.
- LUNIAK, M. 2004. Synurbization—adaptation of animal wildlife to urban development, p. 50–55. *In*: W. W. Shaw, L. K. Harris and L. Vandruuff (eds.). *Proceedings of the 4th International Symposium on Urban Wildlife Conservation*. Tucson, A.Z.
- MACKENZIE, D. I., J. D. NICHOLS, J. E. HINES, M. G. KNUTSON, AND A. B. FRANKLIN. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, **84**:2200–2207.
- , J. A. ROYLE, K. H. POLLOCK, L. L. BAILEY AND J. E. HINES. 2006. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Academic Press, Burlington, MA.
- MAGLE, S. B., E. W. LEHRER, AND M. A. FIDINO. 2015. Urban mesopredator distribution: examining the relative effects of landscape and socioeconomic factors. *Anim. Conserv.* Advance online publication. DOI: 10.1111/acv.12231.
- , P. REYES, J. ZHU, AND K. R. CROOKS. 2010. Extirpation, colonization, and habitat dynamics of a keystone species along an urban gradient. *Biol. Conserv.*, **143**:2146–2155.
- , L. S. SIMONI, E. W. LEHRER, AND J. S. BROWN. 2014. Urban predator–prey association: coyote and deer distributions in the Chicago metropolitan area. *Urban Ecosyst.* 1–17.

- MARKOVCHICK-NICHOLLS, L., H. M. REGAN, D. H. DEUTSCHMAN, A. WIDYANATA, B. MARTIN, L. NOREKE, AND T. A. HUNT. 2008. Relationships between human disturbance and wildlife land use in urban habitat fragments. *Conserv. Biol.*, **22**:99–109.
- MARZLUFF, J. M. 2005. Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. *Urban Ecosyst.*, **8**:157–177.
- MCDONNELL, M. AND A. HAHS. 2008. The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. *Landscape Ecol.*, **23**:1143–1155.
- MCKINNEY, M. L. 2002. Urbanization, biodiversity, and conservation: the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *Biol. Sci.*, **52**:883–890.
- MEIER, K. E. 1983. Habitat use by opossums in an urban environment. Ph.D. Dissertation, Oregon State Univ., Corvallis, OR.
- NAIMAN, R. J., H. DECAMPS, AND M. POLLOCK. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecol. Appl.*, **3**:209–212.
- PRANGE, S. AND S. D. GEHRT. 2004. Changes in mesopredator-community structure in response to urbanization. *Can. J. Zool.*, **82**:1804–1817.
- R CORE DEVELOPMENT TEAM. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- REYNOLDS, H. C. 1945. Some aspects of the life history and ecology of the opossum in central Missouri. *J. Mammal.*, **26**:361–379.
- SHOCHAT, E., P. S. WARREN, S. H. FAETH, N. E. MCINTYRE, AND D. HOPE. 2006. From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol. Evol.*, **21**:186–191.
- SYME, G. J., Q. SHAO, M. PO, AND E. CAMPBELL. 2004. Predicting and understanding home garden water use. *Landscape Urban Plan.*, **68**:121–128.
- TRATALOS, J., R. A. FULLER, P. H. WARREN, R. G. DAVIES, AND K. J. GASTON. 2007. Urban form, biodiversity potential and ecosystem services. *Landscape Urban Plan.*, **83**:308–317.
- U.S. CENSUS BUREAU. 2010. Tiger mapping service: Allegany County, N.Y. Retrieved August 15, 2013 from <http://tiger.census.gov/cgi-bin/mapbrowse-tbl>.
- . 2013a. Annual estimates of the resident population for incorporated places over 50,000, ranked by July 1, 2012 population: April 1, 2010 to July 1, 2012. Retrieved November 20, 2014 from <http://factfinder2.census.gov/faces/tableservices/jsf/pages/productview.xhtml?src=bkmk>.
- . 2013b. 2011–2013 American community survey 3-year estimates. Retrieved November 20, 2014 from http://factfinder2.census.gov/faces/tableservices/jsf/pages/productview.xhtml?pid=ACS_13_3YR_DP04andprodType=table.
- VERNON, M. E., S. B. MAGLE, E. W. LEHRER, AND J. E. BRAMBLE. 2014. Invasive European buckthorn (*Rhamnus cathartica L.*) association with mammalian species distribution in natural areas of the Chicagoland region. *Nat. Areas J.*, **34**:134–143.
- WOLFRAM ALPHA LLC. 2014. WolframAlpha. Retrieved November 20, 2014 from <http://www.wolframalpha.com/input/?i=chicago%20monthly%20temperature>.

SUBMITTED 3 JUNE 2015

ACCEPTED 20 DECEMBER 2015