# Tree cavity availability across forest, park, and residential habitats in a highly urban area

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Published online: 26 June 2014 © Springer Science+Business Media New York 2014

Abstract Tree cavities are used by a wide variety of species for nesting, food storage, and cover. Most studies on cavity availability have been conducted in forests, and little is known about urban areas. With urbanization, species that excavate cavities may be less abundant, natural tree-decay processes are managed, and tree densities are reduced, all of which may influence tree-cavity availability. We investigated three questions: 1) What is the prevalence of tree cavities in different habitats in the Chicago area? 2) How do the characteristics of natural and woodpecker-excavated cavities and cavity-trees differ across habitats? 3) How does the urban landscape influence the prevalence of tree cavities? We tested the capacity for large urban parks and residential areas to provide tree cavities at levels similar to forested areas. We surveyed 1,545 trees in these three habitats for excavated and natural (caused by decay) cavities. Cavities were most available in forests, where the density of trees was highest. We found that a similar proportion of trees in forests and parks had excavated cavities, but excavated cavities were rare in residential areas. Trees containing cavities were larger than control trees and had more decay, and excavated cavities were in larger trees with more decay than natural cavity trees. Canopy cover was the main landscape variable influencing excavated cavity availability. Our results suggest that the prevalence of tree cavities may not be a limiting factor for urban wildlife, however that is contingent on the levels of use of natural cavities, which is currently unknown.

Keywords Urban forests · Natural cavity · Excavated cavity · Woodpeckers

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**Electronic supplementary material** The online version of this article (doi:10.1007/s11252-014-0383-y) contains supplementary material, which is available to authorized users.

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# Introduction

Urban wildlife are faced with a litany of anthropogenic challenges that range from landscape fragmentation and habitat loss (Meffert and Dziock 2013), to competition with invasive synanthropic species for limited resources (Batalha et al. 2013). These forces present unique stresses to urban wildlife populations and species show considerable variability in their adaptation to the urban landscape. For example, native species such as American robins (*Turdus migratorius*), red-winged blackbirds (*Agelaius phoeniceus*), and coyotes (*Canis latrans*) may thrive in close association with human populations (Yasukawa and Searcy 1995; Sallabanks and James 1999; Hennessey et al. 2012). However, other species, such as pileated woodpeckers (*Dryocopus pileatus*) and little brown bats (*Myotis lucifugus*) are rarely observed in highly developed urban areas. These latter species both occupy particular niches that are absent in densely urban zones (Bull and Jackson 2011; Coleman and Barclay 2011), a situation that is common among many species excluded from their native range as human development expands (Adams 2005).

Urbanization has led to declines in avian diversity and species abundance (Clergeau et al. 1998; Blair 2004; Chace and Walsh 2004) and an increased impact of habitat fragmentation in and around urban zones (Crooks et al. 2004). As such, examination of habitat availability and species diversity in smaller-scale habitats in urban centers is needed. Studies of green spaces, such as city parks and golf courses, suggest that they could provide appropriate habitat for specialized native species of birds (Evans et al. 2009; Ikin et al. 2013; Strohbach et al. 2013). While small green spaces, such as converted vacant lots or pocket parks (approximately 0.09 ha) may provide patches of suitable habitat which may be appropriate for some avian species, large city parks (110–210 ha) may support even higher avian richness, including specialist guilds such as woodpeckers and other piciformes (Morrison and Chapman 2005; Strohbach et al. 2013). This guild requires the appropriate structural habitat resources in which to create or modify tree cavities as nest sites (Jackson 1977).

Tree cavities are considered "keystone vegetative structures" because they provide resources crucial for the survival of other species (Tews et al. 2004). In North America alone, over 89 different species, including birds, mammals, and reptiles use cavities, making them a vital structure for the maintenance of native biodiversity (Titus 1983). The availability of excavated cavities depends on populations of excavator species in a given habitat (Cockle et al. 2011). However, urban and suburban ecosystems are unique from natural areas in that they are actively managed to accommodate people, often without consideration of the implications to wildlife that also inhabit these sites (Carpaneto et al. 2010). For instance, in urban areas, it is commonplace to remove dead and decaying branches as well as any branches that may pose a threat to people or buildings if brought down by severe weather. As many woodpecker species require dead or decaying branches in which to build cavities (Smith et al. 2000; Blewett and Marzluff 2005), these management practices may discourage nesting by these species in highly managed areas, thus reducing the availability of excavated cavities in this habitat (Du Plessis 1995). Snags (standing dead trees) are rare in urban landscapes, and this has a negative impact on woodpeckers that would normally use these snags as cavity substrates (Blewett and Marzluff 2005). Furthermore, the removal of dead and decaying trees or individual tree limbs may limit the presence of cavity-excavating species to only those species that can use living trees (Kilham 1971). Therefore, excavated cavities may be limited in urban areas where woodpeckers are less common in comparison with forested areas or large city parks that can accommodate populations of breeding woodpeckers (Morrison and Chapman 2005).

Apart from excavated cavities (those created by primary cavity users like woodpeckers) cavities can also be created through natural decay processes. These natural cavities occur most frequently when the bark of a tree has been compromised and bacterial or fungal colonies have inoculated the heartwood. This is largely dependent on climate as moist areas facilitate fungal and bacterial growth which expedites the decay process (Hielmann-Clausen and Boddy 2008). Natural cavities are frequently found at locations where a branch has broken off a tree. When exposed to the elements, the interior wood decays faster than the wood where the bark is intact, creating a usable cavity (Jensen et al. 2002), which may be located at any height or position on the tree (Shigo 1979). Larger (and therefore older) trees are more likely to have cavities than smaller trees (Cockle et al. 2011).

In urban areas, the decline of primary excavators and increased tree maintenance may lead to an overall reduction in tree cavity availability and increased competition for cavities among secondary cavity users (Davis et al. 2013; Orchan et al. 2013). Previous research on the prevalence of tree cavities have focused primarily on forests and many studies have looked at the effect of timber harvest on cavity availability (Mahon et al. 2008, reviewed in Remm and Lõhmus 2011). Few studies have focused on urban areas (but see Blewett and Marzluff 2005; Davis et al. 2013), and those have not quantitatively compared cavity abundance across different habitat types in urban areas. The goal of this study was to understand the availability and types of tree cavities in a highly urban area. We compared excavated and natural cavities across three habitat types found within the greater-Chicago area: forests, large city parks, and residential city blocks. Conducting our research in the Chicago area is highly relevant to the study of urban tree cavity availability because Chicago is the third-largest city by population size in the United States (U.S. Census Bureau 2013). We investigated three main questions: 1) What is the prevalence of tree cavities in different habitats in the Chicago area? 2) How do the characteristics of natural and woodpecker-excavated cavities and cavity-trees differ across habitats? 3) How does the urban landscape influence the prevalence of tree cavities? We hypothesized that tree cavity prevalence would vary across different habitat types within the urban landscape. We predicted that there would be a higher prevalence of excavated cavities in forest areas than in large city parks and residential city blocks due to woodpecker needs for forested areas that support ample insect and plant food sources. We also predicted that natural cavities, arising from decay processes, may be equally abundant in all three habitats as pruning of healthy branches in urban areas may permit heart-rot fungi to enter the tree and speed decay at the wound site. We expected that trees containing cavities will have a larger diameter at breast height than control trees because woodpeckers select large, stable trees for excavating. In addition, larger, older trees are more likely to have exposure to fungi and bacteria necessary that aid in formation of decayed cavities.

# Methods

# Study area

The city of Chicago, Cook County, Illinois ( $41^{\circ} 53'$  N,  $87^{\circ} 38'$  W) includes 606 km<sup>2</sup> of land and is located in an area historically dominated by oak savannahs that were categorized by open grassland expanses and stands of trees, providing habitat for a wide variety of cavity nesting species (Lanham et al. 2002). There are an estimated 3,585,000 trees in the city of Chicago, with a canopy cover of 17.2 % (Nowak et al. 2010). Cook County contains 27,518 ha (~11 %) of Forest Preserves. Parks in Chicago comprise 3,237 ha, and contain 7.6 % of the city's tree population (Nowak et al. 2010). Within Chicago, the highest density of trees occurs in the open spaces (38.2 trees/ha), followed by residential areas of single family (9.6 trees/ha) and multi-family units (6.7 trees/ha; Nowak et al. 2010). Since residential areas are dominant in the Chicago landscape, approximately 45 % of all trees in Chicago are in residential areas. The primary species in forest habitats were Slippery Elm (*Ulmus rubra*), American Basswood (*Tilia americana*), Bur Oak (*Quercus macrocarpa*), Black Cherry (*Prunus serotina*), and White Oak (*Q. alba*), while Silver Maple (*Acer saccharinum*), Box Elder (*A. negundo*), and Slippery Elm were the primary species in parks (E. Anderson, pers. obs.). Norway Maple (*A. platanoides*), Silver Maple, Honeylocust (*Gleditsia triacanthos*), and Green Ash (*Fraxinus pennsylvanica*) were most abundant in residential areas (City of Chicago 2007).

# Habitat types for tree cavity surveys

We assessed tree cavity prevalence in three habitat types within the greater Chicago area that included a 2 km buffer outside the city limits and the suburbs of Oak Park, Cicero and Berwyn (Fig. 1). Forest areas (n=10) are defined as locations with minimal management, such as forest preserves. These areas allow for decomposition of standing trees, as well as the accumulation of coarse woody debris on the forest floor. Forests included in this study were selected as to provide representation in equal North and South cardinal directions radiating from the city center. Large city parks (n=10) with treed and grassy areas are managed by the city, and were a minimum of 28 ha in size to be included in our study; this size classification allowed us to separate out smaller neighbourhood parks, or "pocket parks", which may support fewer avian species (Morrison and Chapman 2005). Large parks were selected based on their limited availability throughout the city, with only 12 found throughout the study area. Parks that we included in the study represent an even distribution across neighbourhoods in Chicago. Residential areas (n=19) were selected based on a randomly generated set of locations within our study area. A residential location was considered for this study if it contained predominantly residences and had sidewalks on all sides of the block and space between the sidewalk and road. We examined trees planted in a one city block area and only on city property (i.e., trees located between the sidewalk and the road). In cities, trees are managed to minimize harm or danger to citizens, through the removal of cracked or broken limbs, and of decaying trees at risk of falling (Terho and Hallaksela 2008). In residential areas, trees that may be ideal for the creation of cavities (i.e., snags) are removed for safety and cosmetic reasons (Blewett and Marzluff 2005).

Sites of a common habitat type were no less than 2 km apart. We did not restrict our site selection to areas based on age or number of trees, as our study question concerns the availability of potential habitat for cavity nesting animals. Because some habitats have more trees than others, and therefore offer more or less potential habitat to cavity-nesting animals, we have included this variability in the analysis.

# Tree cavity sampling methods

Tree cavity availability was assessed between December 2012 and April 2013. To enable the highest level of tree cavity detection possible, we conducted all sampling during this leaf-free period because the presence of leaves would compromise our ability to visually locate tree cavities. To assess tree cavities in each habitat, we used two different methodologies based on the density and distribution of trees in each habitat. We used the first method in residential areas and large parks, and the second in forest areas. In all study sites, only trees with dbh (diameter at breast height) greater than 12 cm were assessed because this is the minimum dbh used by black-capped chickadees (*Poecile atricapillus*), one of the smallest cavity nesting birds found in our study area (Brewer 1963). Our first method involved identifying an area in the site that contains ~50 trees. Based on preliminary fieldwork, one city block in Chicago



Fig. 1 Map of the study area including the greater Chicago, Illinois, USA area. The thick *line* represents the outline of the study area, a buffer 2 km outside of the Chicago city limits

contains approximately 50 trees. Therefore, in residential areas, we assessed all trees present between the sidewalk and the road on one city block, regardless of the number of trees present. In large parks, where trees are in higher abundance, we sampled an area containing minimally 50 trees that was separated from open fields or areas designated for athletic usage (eg. baseball diamonds) and at least 4 m from the edge of roads. The sampling locations in large parks were determined a priori using Google Earth images. In both residential and large park habitat types, all trees >12 cm dbh in the designated area were surveyed by observers on the ground and closely examined for the presence of cavities aided by binoculars. The first, last, and every tenth tree without tree cavities in the residential and large park sites were used as control trees.

Our second methodology was based on a modified point-quarter method (Cottam and Curtis 1956), and was used in forest areas. Here, we randomly selected one central point in a

wooded area and then three sequential central points, each 50 m apart, along a transect. From all four central points, we assessed the nearest 3 or 4 trees in the four quadrants based on cardinal directions (4 trees in the NE quadrant, and 3 in the other quadrants), providing us with 52 trees from each forest habitat. Because tree densities are much higher in forests, this sampling method allowed us to assess ~50 trees over a broader area which should constitute a more random sample of a forested area compared to selecting one small area and including the 50 closest trees to that one point. At each central point, the closest tree without cavities in the NE and SW quadrants were control trees, for n=8 control trees at each forest site. Although we used two sampling methods, both methods yielded similar numbers of treatment and control trees, and we have estimates of tree densities in all habitats, allowing us to compare across sites.

In all three study habitats, the total number of trees surveyed was recorded as well as the number of trees with cavities. For both control trees and cavity trees we measured tree size (dbh), level of decay based on a modified Maser et al. (1979) scale ranging from 1 to 5 (1, healthy and the crown area is 100 % alive; 2, the crown is 1 - 49 % dead; 3, crown is 50-99 % dead; 4, the crown is dead but the branches are still intact; 5, snag with a broken top), and the presence or absence of visible fungal growths. For all trees containing one or more cavities, we recorded the type of cavity (natural or excavated), cavity height, cavity opening size (small (3 cm), medium (3–8 cm), large (8–40 cm), and extra-large (>40 cm)), and orientation (in eight categories based on cardinal directions) for each cavity.

#### Landscape attributes

We used data collected from ArcGIS 9.1 to examine the relationship between tree cavity availability and landscape variables using a 1-km radius area centered on each study site following Blewett and Marzluff (2005), and all raster layers had 10 m resolution. Landscape variables included the % of impervious surface and % canopy cover (National Landcover Database, Fry et al. 2011), total road length and distance to water source (Illinois Geospatial Data Clearinghouse, accessed via http://crystal.isgs.uiuc.edu/nsdihome/), and average household income (U.S. Census Bureau 2010). These variables have been previously found to influence the distribution of other wildlife species (e.g. Loss et al. 2006; Gehrt et al. 2009; Magle et al. 2010) due to impacts on habitat suitability, connectivity, mortality and dispersal.

# Statistical analyses

# Cavity availability

Spearman-rank correlations were run to test whether the prevalence of excavated cavities and natural cavities, or excavated cavity trees and natural cavity trees were correlated with each other within habitats. To assess how residential areas compared to large parks and forest preserves as potential habitat for cavity nesting animals we first examined the density of trees across habitats using ANOVA. We then compared the density of total tree cavities, excavated cavities, and natural cavities using analysis of covariance (ANCOVA), with habitat-type as the main effect and tree density as a continuous covariate because forest habitats had much higher densities of trees than park and residential habitats (see results). Tree densities and cavity densities were log-transformed prior to analysis to better meet the assumptions of ANOVA. Due to the differences in tree densities across habitats, the proportion of trees with cavities (all,

excavated, natural) were compared across habitats after being arcsine square-root transformed (Zar 1999).

Cavity and cavity-tree attributes

To compare differences between excavated and natural cavities, we analyzed the categorical dependent variables of cavity opening size and cavity orientation between the two types of cavities with separate  $\chi^2$ -tests (Zar 1999). Due to differences in the understory vegetation across sites, cavity heights were compared between cavity types and habitats using a two-way ANOVA.

To assess differences in the trees that contain cavities, a two-way ANOVA was used to compare the diameter of trees between cavity types (no-cavity (controls), excavated cavity, and natural cavity) and habitats. Trees that had at least one excavated cavity were classified as 'excavated cavity' trees. Diameter at breast height was log-transformed prior to analysis. We analyzed how the categorical cavity-tree decay class varied between habitats with a  $\chi^2$ -test.

Cavity availability and landscape conditions

While we used frequentist statistics to compare measures of mean characteristics and categorical descriptors of cavities and cavity trees as described above, to simultaneously compare multiple competing hypotheses regarding cavity availability and landscape conditions we used an information theoretic approach. To assess tree-cavity availability in the context of landscape variables in the urban environment, we first ran a multiple regression to examine the influence of the % of impervious surface, % canopy cover, total road length, distance to water source, and average household income on the log-transformed excavated cavity density. Data in percentages were converted to proportions and arcsine square-root transformed while the other terms were log-transformed prior to analysis (Zar 1999). A test of the correlation between pairs of predictor variables returned Pearson correlation coefficients all <0.7, therefore all predictor variables were used in models.

We started our analysis with a full model that included a linear combination of all five landscape variables, and we used all-subsets regressions (n=32 models) to compare simpler landscape models. We used AIC model selection for the landscape attributes to find the most simple landscape model that best fit the pattern of log-transformed excavated-cavity density (Burnham and Anderson 1998). To compare the performance of the multiple regression models, we used Akaike weights based on Akaike information criterion corrected for small sample size (AIC<sub>c</sub>) values (Hurvich and Tsai 1989). Also, differences in AIC<sub>c</sub> values between the best model and another model that are <2 indicate that there is substantial support for both models, if the difference is between 4 and 7, there is considerably less support for the other model, and differences >10 indicate essentially no support for the other model (Burnham and Anderson 1998). Estimates of the relative importance of predictor variables (variable importance weights) were calculated by summing the Akaike weights across the models in the confidence set (Burnham and Anderson 1998). Variables tending to be in all of the top models will have a summed Akaike weight/total confidence set weight closer to 1 (Symonds and Moussalli 2011). We repeated this analysis separately for natural cavities, and then for overall tree densities in the Chicago area. We compared the variables in the best model for excavated cavities with the model for natural cavities to gain insight into the landscape factors that may drive the availability of these two cavity types, and also compared this to tree density. All statistical analyses were conducted in R version 2.15.2.

We surveyed 1,545 trees  $\geq$ 12 cm dbh for cavities across the three habitats (520 in forests, 506) in parks, and 519 in residential areas). We found that, generally, there were more cavities in forest areas, but there were similar proportions of trees with cavities across each habitat type. Forests had a significantly higher log-transformed density of trees than both park and residential habitats (Table 1). With tree density as a covariate, there were significant differences in the log-transformed excavated cavity densities and log-transformed excavated cavity tree densities between habitats, with forest habitats having significantly more cavities and cavity trees than both parks and residential habitats (Table 1). There were not significant differences between habitats for the log-densities of all cavities, all cavity trees, natural cavities, and natural cavity trees. However, for all cavities and natural cavities there were significant interactions between habitat type and tree densities, meaning that residential areas had a steeper increase in cavities with an increase in tree density than the other habitats. There were not significant correlations in the density of excavated cavities with the density of natural cavities across study sites for any of the habitats (forest:  $r_s = -0.12$ , P = 0.751; park:  $r_s = 0.45$ , P=0.192; residential:  $r_s=0.39$ , P=0.102). In other words, within a habitat type, sites that had more excavated cavities did not also have more natural cavities. The proportion of trees with cavities was slightly higher in the park areas, but it was not significantly different across habitats (Table 2). The proportion of trees that had at least one excavated cavity was significantly higher in the forest habitat compared to the park and residential habitat, while the density of natural-cavity trees was higher, though not significantly, in parks.

# Cavity and cavity-tree attributes

There was a significant difference in the distribution of cavity sizes between cavity types across habitats ( $\chi^2$ =13.44, df=3, P<0.001) with 90 % of excavated cavities and 63 % of

Table 1Summary of overall tree density, and the densities of cavity trees, total cavities, excavated cavities, and<br/>natural cavities in each of the habitats surveyed for tree cavities in trees >12 cm diameter breast height in the<br/>Chicago area. Means $\pm$ standard errors are shown, and symbols show significant differences between the habitats<br/>from ANCOVA tests with Habitat type as the main effect, Tree density as a continuous covariate, and the<br/>interaction between tree density and habitat type. The significance of ANCOVA/Tukey tests are based on log-<br/>transformed data

		Habitat type		P-values		
Tree or Cavity properties	Forest	Large park	Residential	Main effect	Covariate	Interaction
Tree density (>12 cm $ha^{-1}$ )	503.7±104.4 <sup>a</sup>	$76.8{\pm}10.1^{b}$	96.4±9.1 <sup>b</sup>	< 0.001	n/a	n/a
All cavities ha <sup>-1</sup>	85.1±15.7	24.1±3.9	$21.3 \pm 5.3$	0.067	< 0.001	0.014
Excavated cavities ha-1	$20.1 {\pm} 5.1^{a}$	$1.4{\pm}0.5^{b}$	$1.4{\pm}1.0^{b}$	< 0.001	< 0.001	0.383
Natural cavities ha-1	65.0±15.4	22.7±3.6	$19.8 {\pm} 4.6$	0.151	< 0.001	0.026
Cavity trees ha-1	$59.5 \pm 9.0$	14.7±1.9	$13.0 \pm 2.7$	0.055	< 0.001	0.030
Excavated cavity trees ha <sup>-1</sup>	$14.4{\pm}3.8^{a}$	$1.2{\pm}0.4^{b}$	$1.1 {\pm} 0.6^{b}$	0.001	< 0.001	0.590
Natural cavity trees ha <sup>-1</sup>	45.1±7.7	$13.5 \pm 1.8$	$11.9 \pm 2.4$	0.116	< 0.001	0.038

<sup>a, b</sup> Letters represent significant differences between habitat types based on post-hoc Tukey tests when the main effect was significant

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**Table 2** The proportion of trees that have cavities in each of the habitats surveyed for tree cavities in the Chicagoarea. Excavated cavity trees are trees with at least one excavated cavity. Mean proportions  $\pm 95$  % confidenceintervals are shown. Letters represent significant differences between habitat types based on post-hoc Tukey testswhen the main effect was significant

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Cavity-tree group	Forest	Large park	Residential	P-value		
All Cavity trees	0.16±0.07	$0.22 \pm 0.08$	0.13±0.05	0.126		
Excavated-cavity trees	$0.04{\pm}0.02^{a}$	$0.02{\pm}0.01^{ab}$	$0.01 {\pm} 0.01^{b}$	0.022		
Natural-cavity trees	$0.12 {\pm} 0.06$	$0.20{\pm}0.08$	$0.12 {\pm} 0.04$	0.098		

natural cavities being medium size. Natural cavities were more likely to be small and large than excavated cavities (Table 3). There was not a significant difference in the orientation of cavities between cavity types ( $\chi^2$ =13.37, df=7, *P*=0.063). The mean height of excavated cavities (8.34 m±0.41 m; SE) was significantly higher than that of natural cavities (5.86 m± 0.14 m; *P*<0.001), and cavities in forest areas (7.18 m±0.26 m) were significantly higher than cavities in both park (5.57 m±0.18 m) and residential habitats (5.95 m±0.27 m; *P*<0.001). There was no significant interaction between cavity type and habitat on cavity height (*P*=0.761).

The dbh of trees that had no visible cavities of any type (control trees) compared to trees that had at least one excavated cavity (excavated cavity trees) and trees with only natural cavities (natural cavity trees), showed significant difference between the tree type (P<0.001) and between habitats (P<0.001), but there was no significant interaction (P=0.618; Fig. 2). The mean dbh of trees in forest habitat (35.77 cm±1.75 cm; untransformed data shown) was significantly smaller than trees in the other habitats (parks: 53.48 cm±1.62 cm; residential

 Table 3
 Characteristics of excavated and natural cavities in the Chicago area, with the percent of the total for each cavity type shown in parentheses. Note that the two cavity types have been pooled across the three habitat types

	Cavity Type		
	Natural	Excavated	
a) Cavity size distribution			
Small (3 cm)	56 (15 %)	3 (6 %)	
Medium (3–8 cm)	236 (63 %)	43 (90 %)	
Large (8-40 cm)	77 (21 %)	2 (4 %)	
Extra-large (>40 cm)	4 (1 %)	0 (0 %)	
b) Cavity orientation			
NW	26 (7 %)	7 (15 %)	
Ν	48 (13 %)	12 (25 %)	
NE	38 (10 %)	1 (2 %)	
Е	60 (16 %)	9 (19 %)	
SE	48 (13 %)	5 (10 %)	
S	70 (19 %)	8 (17 %)	
SW	31 (8 %)	1 (2 %)	
W	49 (13 %)	5 (10 %)	



Fig. 2 Diameter at breast height of trees with no-cavities (*control*) trees, excavated cavities, and natural cavities in each of the habitat types. Data are shown on a log-scale and the *bars* represent standard errors

51.04 cm±1.63 cm), and trees with excavated cavities (57.98 cm±3.52 cm) were significantly larger than both control trees (36.70 cm±1.38 cm) and trees with only natural cavities (54.44 cm±1.39 cm). The decay class of trees varied significantly across habitats ( $\chi^{2}$ = 108.75, df=8, *P*<0.001). Ten percent of the trees in forests were dead (decay class=4 or 5), while there were no dead trees in parks and only 1 % of trees in residential areas were dead. Trees in parks and residential areas were largely healthy or had <50 % dead branches (decay class=1 and 2). In forests, only 7 % of the trees were completely alive and healthy and 83 % of trees had some dead branches (decay class=2 or 3).

Cavity availability and landscape conditions

The density of excavated cavities was best described by a model that included a positive effect of the % canopy cover and a negative effect of road length (Table 4a). All of the models in the 90 % confidence model set included % canopy cover, half of the models included road length, while income and distance to water were not included in models that were heavily weighted. For natural cavities, the models did not perform well. The confidence set of models included 20 models, the top model had an AIC<sub>c</sub> weight of only 0.13, and the null model also appeared in the confidence set of models (Table 4b, supplementary material). Of the models, with more natural cavities in areas closer to water. The density of trees across our study sites (Table 4c) were best explained by a positive relationship with canopy cover in all models in the confidence set, and there was also a positive influence of income on tree density in most models in the set, while road length had a negative influence on the density of trees. Unlike natural cavities, distance to water appeared in very few models in the 90 % confidence set of models for tree density. The area surrounding the forest sites had significantly higher mean

**Table 4** Summary of AIC<sub>c</sub> values and the AIC<sub>c</sub> weights for the 90 % confidence sets (cumulative weight ( $w_i$ )= 0.90), presented in descending order of  $w_i$ , of regression models for the models of a) excavated cavity density, b) natural cavity density, and c) tree density. The number of parameters in each model (k, including the intercept and error) and the -2LogLikelihood (-2LL) are also shown

Model	k	-2LL	$\Delta AIC_{c}$	Wi
a) Excavated cavity density				
% Canopy cover+Road length	4	97.50	0.00	0.22
% Canopy cover	3	100.20	0.22	0.19
% Canopy cover+% Impervious	4	98.90	1.40	0.11
% Canopy cover+% Impervious+Road length	5	97.12	2.27	0.07
% Canopy cover+Distance to water+Road length	5	97.12	2.28	0.07
% Canopy cover+Distance to water	4	99.84	2.36	0.07
% Canopy cover+Income+Road length	5	97.48	2.64	0.06
% Canopy cover+Income	4	100.20	2.71	0.06
% Canopy cover+% Impervious+Distance to water	5	98.22	3.37	0.04
% Canopy cover+% Impervious+Income	5	98.86	4.01	0.03
b) Natural cavity density <sup>a</sup>				
% Canopy cover	3	115.38	0.00	0.13
% Canopy cover+Distance to water	4	113.22	0.34	0.11
% Impervious+Distance to water	4	113.74	0.86	0.08
Distance to water	3	116.74	1.36	0.06
% Impervious	3	117.14	1.76	0.05
Null model	2	119.50	1.77	0.05
% Canopy cover+% Impervious	4	115.00	2.11	0.04
% Canopy cover+% Impervious+Distance to water	5	112.40	2.17	0.04
% Canopy cover+Road length	4	115.24	2.35	0.04
% Canopy cover+Income	4	115.32	2.44	0.04
c) Tree density				
% Canopy cover+% Impervious service+Income+Road Length	6	71.32	0.00	0.26
% Canopy cover+Income	4	77.74	0.97	0.16
% Canopy cover+Income+Road Length	5	75.26	1.13	0.15
% Canopy cover+% Impervious service+Income	5	76.32	2.19	0.09
% Canopy cover+% Impervious service+Income+Road Length+Distance to water	7	71.32	2.98	0.06
% Canopy cover+Income+Distance to water	5	77.66	3.54	0.04
% Canopy cover+Road Length	4	80.48	3.71	0.04
% Canopy cover	3	83.00	3.75	0.04
% Canopy cover+Income+Road Length+Distance to water	6	75.20	3.88	0.04
% Canopy cover+% Impervious service+Income	5	78.48	4.35	0.03

<sup>a</sup> Only the top 10 models of the 90 % confidence set are shown here. See the electronic supplementary material for a full table

percent cover at 17.8 %, than the other habitats, and residential areas (3.4 %) had almost twice the percent cover of parks (2.0 %), though the latter two habitats were not significantly different (Table 5). There was no significant difference in the percentage of the area that was impervious, with means ranging from 52.2 % in forests to 60.8 % in residential areas, and while the mean income near forest areas was higher than the other habitats, there was no

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Landscape characteristic	Forest	Habitat type Large park	Residential	P-value		
% Canopy cover	$17.8 \pm 3.6^{a}$	$2.0 {\pm} 0.4^{b}$	3.4±1.1 <sup>b</sup>	< 0.001		
% Imperious Surface	$52.2 \pm 2.1$	59.0±4.3	$60.8 {\pm} 1.6$	0.066		
Distance to water (m)	$684.2{\pm}433.6^{a}$	$515.4{\pm}312.6^{a}$	$2243.2 \pm 278.2^{b}$	< 0.001		
Road length (m/km <sup>2</sup> )	$29078 {\pm} 2712^{a}$	$36081{\pm}3200^{ab}$	$42342{\pm}1308^{b}$	< 0.001		
Income (USD)	$75832 \pm 5681$	$57018 \pm 8609$	$60734 \pm 5735$	0.069		

 Table 5
 Summary of landscape characteristics (mean±standard error) within 1 km radius area around the central point of each study site for each of the three habitat types where tree cavities were surveyed in the Chicago, IL area. Letters represent significant differences between habitat types based on post-hoc Tukey tests when the main effect was significant. Note: statistical analyses were conducted on arc-sine square-root transformed proportion of canopy cover and impervious surface and log-transformed distance to water, road length and income

significant difference in income between habitats. Parks and forests were significantly closer to water than residential areas on average. We also found the mean road length was significantly greater in residential areas than in forest areas, and the road length in large parks was not significantly different than either other habitat.

# Discussion

We examined the prevalence of tree cavities in urban areas. Tree cavities represent a unique ecological resource, where few species control the creation of excavated cavities on which many other species are reliant (Robles and Martin 2011). Furthermore, this relationship is prone to pressures imposed by urbanization (Davis et al. 2013; Orchan et al. 2013). Comparing natural and excavated cavities across three habitat types in an urban area, we found that overall cavity prevalence was similar in residential areas, large parks, and forests. However, excavated cavities were more common in forest areas, whereas trees containing natural cavities were most abundant in large parks. These results were contrary to our prediction that trees in residential and park areas would be equally abundant in natural cavities. When the higher density of trees in forest habitats was accounted for, far more excavated and natural cavities occur in forest areas than in the other habitat types. Therefore, our results suggest that while cavity-nesting species may still find potential habitat in urban areas, forested areas provide the most cavities.

Our findings are consistent with Sandstrom et al. (2006) who showed that woodpeckers were more commonly found in parks and forest areas with higher tree densities and were not commonly found in residential areas or city centres. In addition, the density of all cavities and excavated cavities in the forest areas that we found was very similar to the results of a metaanalysis of tree cavity distributions in forests by Remm and Lõhmus (2011). While the residential areas included in this study were located at random distances from the city centre, we could not distinguish between the low prevalence of excavated cavities due to the lack of cavity excavators, or due to the lack of potential cavity habitat. Several studies have highlighted the specific preferences of cavity-excavators for trees. For example, Red-bellied Woodpeckers (Melanerpes carolinus) are the most common woodpecker species in Illinois and will excavate cavities in large trees situated in densely forested areas (Shackelford et al. 2000). In contrast, Red-headed Woodpeckers (Melanerpes erythrocephalus) have been shown to prefer excavating high cavities in dead or decaying trees located in open forest or along forest edges (Smith et al. 2000) and Yellow-bellied Sapsuckers (Sphyrapicus varius) are strong excavators and will excavate cavities in living trees (Kilham 1971; Harestad and Keisker 1989). We found most trees in large parks and residential areas were very healthy (showed

limited amounts of decay) which suggests that suitable cavity-creating trees are available for excavation by at least Yellow-bellied Sapsuckers in residential areas, but not likely for other species of woodpeckers. While conducting cavity surveys in residential areas, we observed sapsucker feeding holes and two foraging downy woodpeckers (*Picoides pubescens*), indicating at least the presence of woodpecker species in residential areas (J. LaMontagne and R.J. Kilgour, pers. obs.). Overall, we found trees in large parks and residential areas were larger than trees in forest habitat, with a far higher proportion of natural cavities to excavated cavities. We also found that dead trees made up 10 % of forests which is consistent with other work done in Midwestern forests (Fan et al. 2003), while dead trees were absent in parks and made up only 1 % of the trees in residential areas. While it may appear that possible habitat exists for some excavator species, the specific attributes necessary for woodpeckers may be mostly absent in most urban areas.

We did not observe any evidence of cavity 'hot spots' in any habitat in our study due to the lack of a significant correlation between the densities of excavated and natural cavities within any of the habitat types. This may be explained by the differential processes involved in the creation of excavated and natural cavities. However, cavity-nesting species might use cavity alternatives in urban areas, such as crevices in buildings or other anthropogenic structures, thereby reducing their reliance on natural or excavated tree cavities (Remacha and Delgado 2009). There is some suggestion that tree squirrels in urban areas use tree cavities less frequently for nesting than anthropogenic nesting sites (McCleery and Parker 2011).

In North America, most cavity-dwelling species that are not excavators rely on previously excavated cavities (Cockle et al. 2011). When cavities are a limited resource, as in urban areas, increased inter- and intraspecific competition can result (Davis et al. 2013). Previous research suggested that city parks may provide necessary habitat for cavity-dwelling species (Evans et al. 2009; Fernandez-Canero and Gonzales-Redondo 2010; Ikin et al. 2013; Strohbach et al. 2013), and our results support this. We found a high proportion of cavities present in large parks and residential streets, but most cavities were derived from natural decay processes. These natural cavities mostly had openings that were a similar size to excavated cavities (medium, 3–8 cm in diameter) which are large enough for arboreal squirrels (such as the fox squirrel, *Sciurus niger*, and grey squirrel, *Sciurus griseus*) to enter, which may impose a competitor bias in their occupancy. A lack of heterogeneity in cavity sizes could lead to an over-abundance of cavity occupancy by the most aggressive competitor (Koch et al. 2012). Urban bird species such as the house sparrow (*Passer domesticus*; Bennett 1990) and European starling (*Sturnus vulgaris*; Koch et al. 2012) are highly competitive, often cited as displacing or excluding native species from foraging or nesting sites (Charter et al. 2013).

Factors other than the size of a cavity opening may influence cavity suitability, because different species of cavity users require different cavity characteristics for breeding or roosting (for examples, see DeGraaf and Shigo 1985; Cockle et al. 2012; Davis et al. 2013). A variety of species-specific studies have demonstrated that individual species select cavities based on cavity dimensions (Fleming et al. 2013), tree density (Gilmer et al. 1978), cavity height (Stauffer and Best 1982), ambient cavity temperature (Bryant et al. 2012), and overall visibility (Mahon et al. 2008). Combinations of these characteristics suggest very particular ecological niches occupied by cavity-nesting species, which may not be available in urban locations given the homogeneity of both tree sizes and levels of decay outside of forest habitats.

Taking a landscape perspective that examines the levels of urbanization surrounding our study sites, we found that no landscape factors were strong predictors of the availability of natural cavities. The main landscape variable related to both the density of excavated cavities and tree density was canopy cover. Because we were examining urban forest habitat, the mean forest cover in the 1 km radius surrounding our sites was under 20 %, much lower than would

be found in continuous forest, but was still much greater than the park and residential habitats. Household income was also positively related with overall tree density in our models, which is consistent with other studies showing a typical pattern associated with urbanization in Chicago; wealthy regions tend to have higher tree cover while poorer regions have lower tree cover (Iverson and Cook 2001). Additionally, areas of higher socioeconomic levels tend to have higher biodiversity in plants and birds than areas of lower incomes (Kinzig et al. 2005).

In this study, we examined similar numbers of trees in each habitat type. When considering the urban landscape as a whole, the majority of land mass is devoted to residential areas with almost no forest habitat occupying the densest urban areas (Nowak et al. 2010). Because residential areas as a whole contain the most number of trees in Chicago (Nowak et al. 2010), and natural cavities in this habitat outnumber excavated cavities by 14-times, in the urban landscape the cavities present would be overwhelmingly natural cavities. We also examined 10 out of 12 possible large park locations, indicating that there are not many more of these parks outside of what we studied. Little is known about the suitability of natural cavities for occupancy by obligate cavity users (Cockle et al. 2011). However, one notable difference in excavated and natural cavities is that excavated cavities were located higher in trees than natural cavities, which may provide differential protection from predators. Generally, we found larger trees in parks and residential areas that were in better condition than in forest preserves. In contrast, both cavity and control trees in forest areas were smaller on average, likely due to a combination of forest regeneration processes and increased competition resulting from higher tree densities. The increased homogeneity of tree size and decay class and the lack of smaller trees in park and residential areas may have long-term impacts on tree availability, as the larger trees that are present die. Further study is needed to understand how species distributions, and specifically cavity excavators, are distributed throughout the urban landscape. Management of forest areas for cavity excavators promotes retaining a diverse stand structure in terms of tree sizes and decay classes (Fan et al. 2003). The preservation of forest habitat is essential for the integrity of excavated cavities and the species that rely on them. However, in urban areas frequented by people, the challenge is to balance a diverse structure of urban trees with public safety.

Acknowledgments We gratefully thank H. Cooke, M. Fidino, L. Lehrer, and J. Pollock for advice during the design of this study, and to R. Wenkus and G. McNickle for assistance in the field. We also thank the two anonymous reviewers and the associate editor for their comments that improved the manuscript. Funding for this project came from the Department of Biological Sciences and the College of Science and Health at DePaul University, and from the Davee Foundation.

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