Use of suburban landscapes by the Pileated Woodpecker (Dryocopus pileatus)

Authors: Tomasevic, Jorge A., and Marzluff, John M.

Source: The Condor, 120(4) : 727-738

Published By: American Ornithological Society

URL: https://doi.org/10.1650/CONDOR-17-171.1

THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 120, 2018, pp. 727–738
DOI: 10.1650/CONDOR-17-171.1

RESEARCH ARTICLE

Use of suburban landscapes by the Pileated Woodpecker (*Dryocopus pileatus*)

Jorge A. Tomasevic[1,2]* and John M. Marzluff[2]

[1] School of Environmental and Forest Sciences, University of Washington, Seattle, Washington, USA
[2] Centro de Humedales Rio Cruces, Universidad Austral de Chile, Valdivia, Chile
* Corresponding author: jorge.tomasevic@uach.cl

Submitted August 28, 2017; Accepted May 29, 2018; Published August 22, 2018

ABSTRACT

Urban areas continue to expand, with cities now containing more than half of the world's population. As cities grow, natural habitat is transformed, changing the face of the local biota and the resources available for it. Wherever woodpeckers are present, the cavities that they excavate provide an important ecological service that facilitates many other species. We studied how the Pileated Woodpecker (*Dryocopus pileatus*) uses suburban areas. From 2009 to 2013, we used radio-telemetry to determine the annual home range size and habitat use of 13 individuals in 9 suburbs that varied in their level of urbanization (ranging from 5% to 90% forest remaining). We used concentration of use and resource utilization functions to examine vegetative characteristics used by woodpeckers at relatively large (i.e. 1 km^2) and more local (i.e. ⅓ ha) scales. The average home range of suburban Pileated Woodpeckers was significantly smaller than expected based on previous studies. Pileated Woodpeckers concentrated their use of the landscape in native coniferous and deciduous forest, as well as in lightly and moderately urbanized areas. Highly urbanized areas were seldom used. For males, resource use increased with increasing mean diameter of dominant hardwood species. Our results suggest that maintaining forest cover above 20% and retaining large deciduous trees and snags in public green spaces and yards may improve the suitability of suburban areas for woodpeckers and the biodiversity that they facilitate.

Keywords: Picidae, resource utilization function, urban, suburban, utilization distribution, home range

Uso de paisajes suburbanos por *Dryocopus pileatus*

RESUMEN

Las áreas urbanas se siguen expandido y ahora albergan más de la mitad de la población mundial. En la medida que las ciudades crecen los paisajes naturales son transformados, cambiando la biota local y los recursos disponibles para ella. Donde los pájaros carpinteros están presentes facilitan a otras especies mediante la provisión de las cavidades que excavan. Estudiamos cómo *Dryocopus pileatus* usa áreas suburbanas. Desde 2009 al 2013 usamos radio telemetría para determinar el ámbito de hogar y uso de hábitat de 13 individuos en 9 suburbios que variaron en su nivel urbanización (5 a 95% de bosque remanente). Usamos concentración de uso y funciones de uso de recursos para examinar las características del paisaje usados por los pájaros carpinteros a pequeña (1/3 ha) y gran (1 km^2) escala. El tamaño promedio del ámbito de hogar de los pájaros carpinteros en los suburbios fue considerablemente más pequeño que lo esperado comparado con estudios previos. Los pájaros carpinteros concentraron significativamente su uso del paisaje en los bosques nativos del sector (coníferas y latifoliadas), como también en lugares con urbanización leve y moderada. Las áreas con alta urbanización rara vez fueron usadas. Los machos usaron más los bosques que contenían árboles latifoliados con troncos de gran diámetro. Nuestros resultados indican que mantener una cobertura boscosa de al menos 20% junto con la mantención de grandes árboles latifoliados y árboles muertos en jardines y espacios verdes públicos podrían mejorar la calidad de las áreas suburbanas para estos pájaros carpinteros y potencialmente para las otras especies que ellos benefician.

Palabras clave: Picidae, función de utilización de recursos, urbano, suburbano, distribución de uso, ámbito de hogar

INTRODUCTION

More than half of the world's population now lives in cities (United Nations 2008) and ~67 million people are added to urban areas each year (Pickett et al. 2011). Given that cities expand in size at a much faster rate than their populations increase (Blair 2004, Aronson et al. 2014), this massive increase in urban population is resulting in an unprecedented rate of urban area expansion (Cohen 2006).

Urbanization and sprawl of cities are complex and dynamic processes. They not only change vegetation composition, cover, and structure (Donnelly and Marzluff

2006), but also microclimatic conditions, biotic interactions (e.g., increased predation by domestic animals, competition with exotic species, transmission of diseases; Chace and Walsh 2006, Endlicher 2011), and connectivity within and between surrounding natural areas (Fernández-Juricic 2000). These altered conditions usually produce a gradient of land cover between natural and urbanized areas (urban–wildland or urban–rural gradient; Blair 1996) wherein habitats are less modified with increasing distance from foci of urban development (Alberti et al. 2001). Once an area is developed it rarely goes back to its natural habitat state (Marzluff and Ewing 2001, McKinney 2006), although native vegetation may be retained or incorporated by developers, planners, managers, or residents (Aronson et al. 2014). Different vegetation structure and composition, altered disturbance regimes, novel predators, deadly obstructions, and supplemental food and water create novel habitat conditions for wildlife and plants, favoring species with the ability to exploit these changes (Chace and Walsh 2006, Robb et al. 2008, Clucas and Marzluff 2011, Kowarik 2011, Loss et al. 2013, 2014, Marzluff 2014). In general, there is consensus that highly urbanized bird communities are less diverse (typically dominated by few native or exotic species) and support more biomass than adjacent natural communities (Beissinger and Osborne 1982, Blair 1996, Melles et al. 2003, Chace and Walsh 2006, Chapman and Reich 2007, Møller 2009, MacGregor-Fors et al. 2012, Aronson et al. 2014, Sol et al. 2014).

The presence and abundance of many woodpecker species, as with many other cavity-nesting birds, may be limited by the availability of snags for foraging, roosting, and nesting (Newton 1998, Bull and Jackson 2011). Because snags are normally removed when natural forests are developed (Blewett and Marzluff 2005, Blair and Johnson 2008, Davis et al. 2014, LaMontagne et al. 2015), urbanization may result in woodpecker population declines (Blair 1996). These declines may cascade to other species that are connected to the resources that woodpeckers provide, potentially amplifying the negative effects onto other species (Martin and Eadie 1999, Aubry and Raley 2002, Morrison and Chapman 2005). Given the recent extinctions of the Ivory-billed Woodpecker (*Campephilus principalis*) and Imperial Woodpecker (*Campephilus imperialis*), formerly the largest woodpecker species in North America, we were interested in the potential challenges that urban sprawl could pose to the largest woodpecker remaining in North America, the Pileated Woodpecker (*Dryocopus pileatus*). We characterized the size and land cover composition of Pileated Woodpecker territories in suburban areas around Seattle, Washington, USA, to examine whether the birds made differential use of available land cover types in this heterogeneous suburban setting. We also compared our home range size estimates from this setting with those from previous studies of Pileated Woodpeckers throughout North America.

METHODS

Focal Species

Pileated Woodpeckers occupy expansive home ranges (Renken and Wiggers 1989, Mellen et al. 1992, Bull and Holthausen 1993, Bonar 2001). The cavities that this species create facilitate many other species (Raley and Aubry 2006). The Pileated Woodpecker has been described as a mature or late-successional coniferous or deciduous forest specialist (Mellen et al. 1992, Bull and Holthausen 1993, Renken and Wiggers 1993, Aubry and Raley 2002) that benefits from high abundance of trees larger than 30 cm in diameter at breast height (DBH; Mellen et al. 1992, Renken and Wiggers 1993). The species also uses younger forests (Bull and Jackson 2011) and suburban areas (Hoyt 1957, Blewett and Marzluff 2005, Erskine 2008). Although there is evidence that this species is sensitive to habitat degradation due to forest loss and fragmentation (Bull et al. 2007, Bull and Jackson 2011), there is little information on how it responds to urbanization. Pileated Woodpeckers can be found in urban and suburban areas (Blewett and Marzluff 2005, Erskine 2008), although their densities tend to be low (Beissinger and Osborne 1982, Blewett and Marzluff 2005). In fact, Pileated Woodpecker density is positively associated with the percentage of forest remaining (at a 1 km^2 scale) in urbanizing landscapes, and the species' density in suburban areas (forested and built areas combined) can be reduced by 85% compared with natural areas (Blewett and Marzluff 2005).

Study Area

We monitored Pileated Woodpeckers in 9 sites within 3 general areas along the urban–wildland gradient in the Greater Seattle area of Washington, USA (47.61°N, 122.33°W; Figure 1). These sites were selected from a set of 23 randomly chosen study sites described in detail elsewhere (Marzluff et al. 2016). The northern area was close to the town of Maltby, the central area was close to Redmond, and the southern area was close to Bellevue. All 3 areas were similar in their percentage of deciduous forest, but Redmond had less coniferous forest and more medium and heavy urban cover than Bellevue and Maltby (Table 1). Similarly, Redmond had less edge (between forested and lightly or moderately urbanized areas) than the other 2 general areas. The 9 sites found in these areas were representative of different levels and configurations of forest remaining (ranging from 5% to 90% at the 1 km^2 scale; Hepinstall et al. 2008), which we used as a proxy for the level of urbanization.

Historically, western Washington was forested, with the lowlands dominated by western hemlock (*Tsuga hetero-*

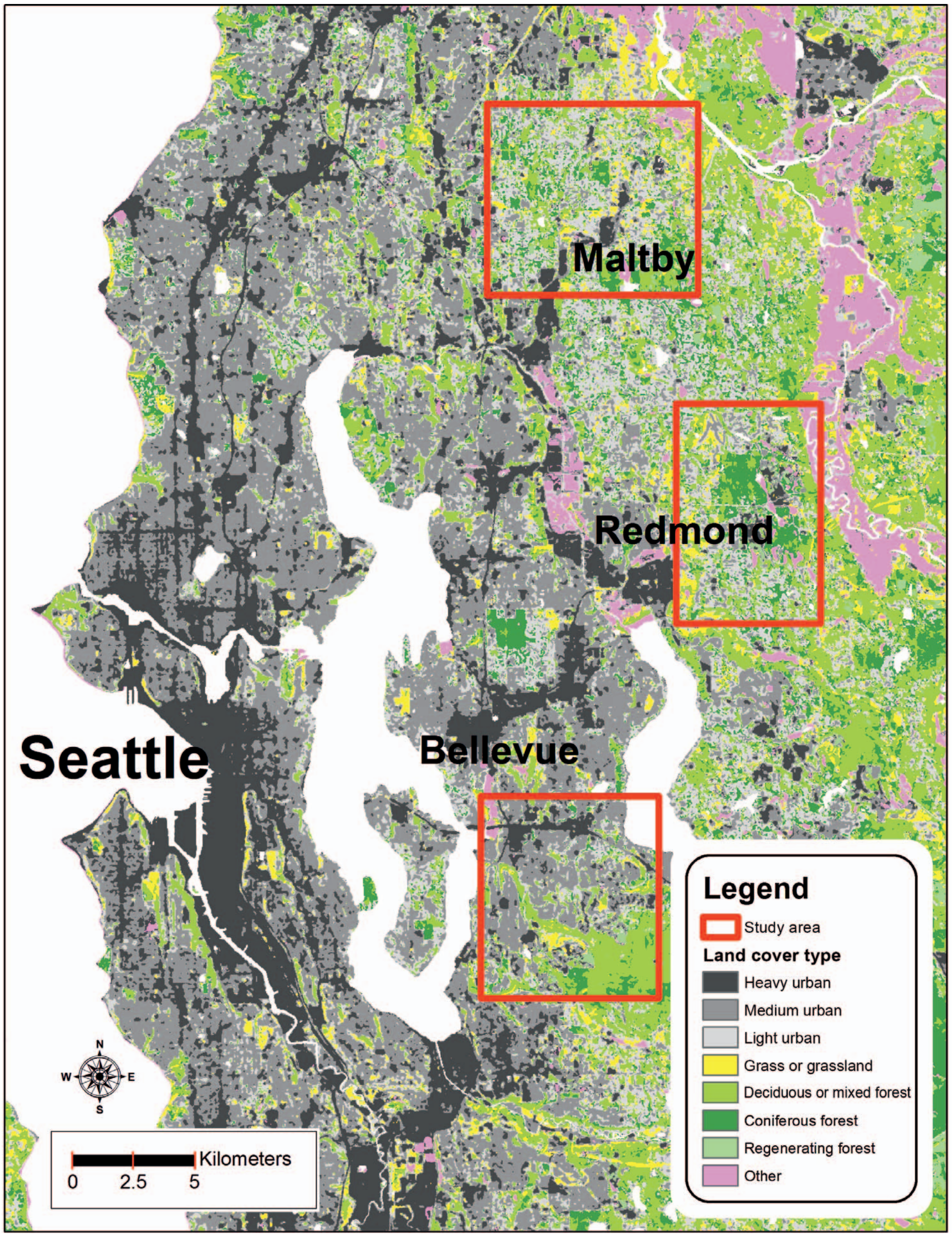

FIGURE 1. Study areas in Greater Seattle, Washington, USA, where we studied how Pileated Woodpeckers used suburban areas that varied in their level of urbanization. Land cover types follow Alberti et al. (2006).

phylla), western redcedar (*Thuja plicata*), and, as a subclimax species, Douglas-fir (*Pseudotsuga menziesii*; Franklin and Dyrness 1988). Hardwood species were not common, except in recently disturbed sites and riparian areas, where bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), and black cottonwood (*Populus balsamifera trichocarpa*) were the most prevalent tree species (Franklin and Dyrness 1988). However, these forests have undergone extensive change in the last ~170 yr. As European settlers colonized the area in the mid-1800s, the coniferous forest was logged, regrew, and was logged again for ~100 yr (Cuo et al. 2009). In the last few decades these changes have been accentuated and accelerated as populated areas have expanded and transformed the land cover from forest to urban and suburban areas (MacLean and Bolsinger 1997, Alberti et al. 2004). Projections indicate that this trend will continue and that more land will be transformed into some level of urban use (Hepinstall et al. 2008). These changes will continue to affect the amount, composition, and structure of the forests in the general area (Donnelly and Marzluff 2006), as urban and suburban forests are dominated by early successional species (mostly the

TABLE 1. Characterization of the 3 main areas in Greater Seattle, Washington, USA, in 2009–2013, where we conducted this study examining how Pileated Woodpeckers used suburban areas that varied in their level of urbanization. Land cover types are defined in Table 2. Contrast-weighted edge density quantifies the amount of edge between forested and moderately or lightly urbanized areas.

	Total area (ha)			Contrast-weighted edge density (m ha^{-1})		
Land cover type	Maltby	Redmond	Bellevue	Maltby	Redmond	Bellevue
Native forest or woodlands						
Coniferous forest	965.43 (14%)	308.43 (5%)	932.04 (17%)	24.97	7.91	23.71
Deciduous and mixed forest	1,455.75 (21%)	1,475.46 (24%)	1,309.86 (24%)	43.18	27.83	38.97
Regenerating forest	159.93 (2%)	124.02 (2%)	119.97 (2%)	N/A	N/A	N/A
Clear-cut forest	1.35 (<1%)	1.17 (<1%)	10.26 (<1%)	N/A	N/A	N/A
Urbanized lands						
Light urban	2,333.52 (34%)	873.45 (14%)	1,517.40 (28%)	63.54	29.49	57.54
Medium urban	786.24 (12%)	2,153.07 (35%)	581.04 (11%)	4.61	6.25	5.14
Heavy urban	315.81 (5%)	589.95 (10%)	153.45 (3%)	N/A	N/A	N/A
Cleared for development	1.62 (<1%)	0.72 (<1%)	6.12 (<1%)	N/A	N/A	N/A
Other						
Grass or grassland	538.02 (8%)	207.81 (3%)	414.36 (8%)	N/A	N/A	N/A
Agriculture	117.99 (2%)	2.43 (<1%)	145.71 (3%)	N/A	N/A	N/A
Unforested wetlands	70.47 (1%)	52.56 (1%)	123.39 (2%)	N/A	N/A	N/A
Open water	65.97 (1%)	318.69 (5%)	95.22 (2%)	N/A	N/A	N/A
Snow or bare rock	0.00 (0%)	0.09 (<1%)	0.00 (0%)	N/A	N/A	N/A
Grand total	6,812.10 (100%)	6,107.85 (100%)	5,408.82 (100%)	136.30	71.48	125.36

hardwoods described above and Douglas-fir), thus also changing the composition and structure of the biological communities present in the area (Gavareski 1976).

Radio-telemetry and Home Range Estimation

We trapped Pileated Woodpeckers year-round using mist nets, call playback, and a decoy (York et al. 1998). We also trapped close to suet feeders (present in neighborhoods in the study sites) during fall and winter when the birds were harder to attract using playback. Once we captured a bird, we banded it and attached a radio-tag (model A1250 from Advanced Telemetry Systems, Isanti, Minnesota, USA; expected battery life 12 mo) using a Teflon backpack harness modified from Buehler et al. (1995). We used 2-mm-wide copper rings to secure the harness. A transmitter plus harness weighed 11.5 g, <5% of the weight of an adult Pileated Woodpecker. We released captured birds back into the same area from which we captured them. Our processing time was typically ~30–45 min. We custom-fitted the transmitter to each bird to reduce potential negative effects (Ruder et al. 2012, Noel et al. 2013). We used an R-1000 telemetry receiver (Communications Specialists, Orange, California, USA) and a handheld 3-element Yagi antenna to relocate each radio-tagged bird opportunistically, aiming to have at least 1 location per week. Two birds dropped their transmitters, but we recaptured them (after 69 and 174 days of losing their transmitters, respectively) and replaced their transmitters. Both sexes participated in territorial defense, which allowed us to capture both males and females.

We recorded all locations of each bird on custom-made field sheet maps based on current aerial photographs available online (Google Maps, Google, Mountain View, California, USA) at ~1:10,000 scale. In cases in which the location was not obvious from the map, we used a GPS to mark a reference point and measured distance and bearing to the woodpecker location with a laser rangefinder (TruPulse 360B, Laser Technologies, Centennial, Colorado, USA). We then mapped all locations using ArcGIS (9.x and 10.x, ESRI, Redlands, California, USA).

Based on these locations, we estimated home ranges using 2 different techniques. First, we used the minimum convex polygon method, using all locations (100% MCP) for comparison with other studies that calculated Pileated Woodpecker home ranges. Second, we used fixed-kernel estimation to estimate the area used by each woodpecker (KDE; Worton 1989). We determined differential use of areas within the home range by constructing a utilization distribution (UD; Marzluff et al. 2004). The UD is a probability density function that quantifies the probability of an individual occurring at each location within the home range (Marzluff et al. 2004). Therefore, the volume under the UD adds to 1. We found a weak positive correlation between sample size and MCP home range size (linear regression: $F_{1,10} = 4.69$, $P = 0.06$) but not KDE home range (linear regression: $F_{1,10} = 0.77$, $P = 0.40$), which indicates that our sampling effort was sufficient to estimate home range using the latter technique, and that the number of locations did not affect our KDE.

Habitat Use

We related different degrees of use (UD) to habitat characteristics using 2 approaches: (1) concentration of use (Neatherlin and Marzluff 2004), to characterize the use

TABLE 2. Land cover types that were used in this study, as defined by Alberti et al. (2006).

Land cover type	Definition
Heavily urbanized ('Heavy urban')	>80% impervious area
Moderately urbanized ('Medium urban')	50–80% impervious area
Lightly urbanized ('Light urban')	20–50% impervious area
Grass or grassland	Developed grass or grassland
Deciduous and mixed forest	10–80% deciduous or mixed forest
Coniferous forest	>80% coniferous forest
Clear-cut forest	Recently clear-cut area
Regenerating forest	Regenerating forest
Agriculture	Row crops and pastures
Other	Unforested wetlands, open water, shorelines, bare rock or snow

of different land cover types in relation to their presence within each home range; and (2) resource utilization functions (RUFs; Marzluff et al. 2004), to assess the use of local resources and habitat structural characteristics at a finer scale within the most frequently used land cover types. Concentration of use is the ratio between the volume of use (from the UD) found in each cover type and the occurrence of each land cover type within the home range, analogous to other selectivity measures that relate use to occurrence (Neatherlin and Marzluff 2004). We used 30-m resolution land cover data based on 2007 Landsat TM satellite imagery classified into 14 habitat categories (heavily urbanized, moderately urbanized, lightly urbanized, cleared for development, grass or grassland, deciduous and mixed forest, coniferous forest, clear-cut forest, regenerating forest, agriculture, unforested wetlands, open water, snow or bare rock, and shorelines) for these analyses (Table 2; Alberti et al. 2006).

RUFs are multiple regression analyses that relate use (derived from the UD on a cell-by-cell basis) to resources accounting for spatial autocorrelation (Marzluff et al. 2004). For this approach, we used 30-m resolution landscape data from the 2012 Gradient Nearest Neighbor (GNN) mapping of existing vegetation for the Northwest Forest Plan Effectiveness Monitoring for Western Washington (modeling region 221; http://lemma.forestry.oregonstate.edu/data/structure-maps, Ohmann and Gregory 2002, Ohmann et al. 2014). This map was created using imputation procedures that combined remote sensing imagery and plot sampling. Based on previous publications regarding Pileated Woodpecker ecology, we expected woodpeckers to concentrate their use in areas with high quadratic mean diameter of dominant conifers, high quadratic mean diameter of dominant hardwoods, high volume of snags >25 cm DBH, and high volume of down wood >25 cm DBH. We also included a metric for edge to explore the significance of the forest–urban interface. To do so, we calculated contrast-weighted edge density using a 50-m moving window in FRAGSTATS v4 (McGarigal et al. 2012) for edge between forest (either coniferous, broadleaved, or mixed) and lightly or moderately urbanized areas. We preferred 50 m to other distances in order to have a fine enough scale to capture edges that were highly contrasted between these land cover types. We assessed differences in relative use of often-used land covers (i.e. coniferous and deciduous forest, lightly and moderately urbanized areas) by selecting only the locations found in these land cover types. We set the RUFs to randomly select a subsample of 1,000 pixels within these land cover types (all combined). It has been suggested that use should be transformed before conducting RUF analyses to prevent violations of the assumptions of homoscedasticity and normality of the residuals of a multiple regression (Johnston 2013). However, we graphically explored the residuals of our models and did not encounter such problems, so we analyzed raw values of use. We obtained one unstandardized β value for each independent variable that we later used to estimate the population-level effect of each, averaging these values across individuals that could be considered independent (Marzluff et al. 2004). We then used the standardized β value for each independent variable to evaluate the relative importance of each variable included in our models. We considered these β values (standardized and unstandardized) to be significant if the 95% confidence interval around them did not include zero (Marzluff et al. 2004). We explored consistency among individuals by comparing the frequency of significant negative and positive coefficients for each variable included in the model. To estimate population-level significance of these coefficients, we averaged across all individuals (using standardized and unstandardized β estimates for different groups) and used the standard error of this sample of coefficients to construct 95% confidence intervals. We calculated MCPs, KDEs, and UDs using Geospatial Modelling Environment 0.7.2.1 (Beyer 2012). We performed the RUF analysis using package ruf 1.5-2 (Handcock 2011) in R (R Core Team 2014).

We used linear regression to assess whether the mean size of the home range of the woodpeckers in our area followed the latitudinal trend revealed from other studies.

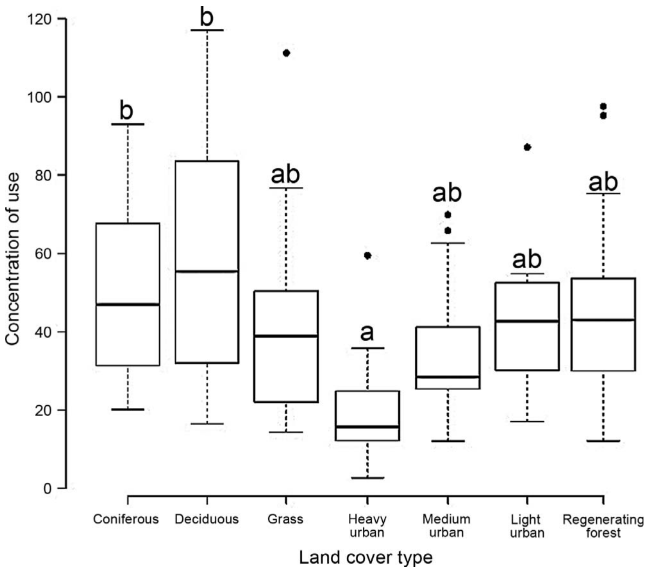

FIGURE 2. Boxplots indicating the concentration of use by male Pileated Woodpeckers of different land cover types (Coniferous = coniferous forest; Deciduous = deciduous and mixed forest; Grass = grass or grassland; Light urban = lightly urbanized; Medium urban = moderately urbanized; and Heavy urban = heavily urbanized) in the Greater Seattle area, Washington, USA. Letters indicate Tukey post hoc differences.

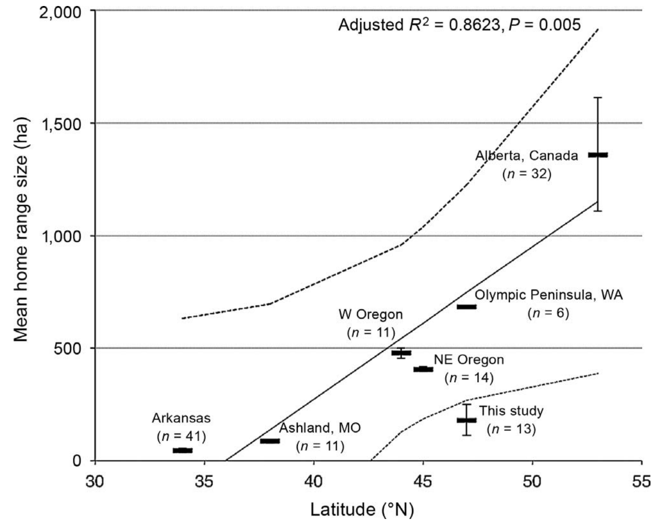

FIGURE 3. Minimum convex polygon–based home range estimates (100% MCP) for Pileated Woodpeckers in North America. Error bars indicate SE and dashed lines indicate the 95% CI for the regression. MO = Missouri, USA, WA = Washington, USA.

We used ANOVA and Tukey tests to determine significant differences among concentration of use (Zar 1999). Averages are presented ± SE.

RESULTS

We captured 16 adult Pileated Woodpeckers (9 males, 7 females) between 2009 and 2012. We discarded data for 3 females with <25 locations. For the remaining birds, we collected data for an average of 12.3 ± 1.0 mo (10/13 were followed for more than 11.5 mo) and obtained an average of 74 ± 12 locations per bird.

Home Range Estimation and Habitat Use

The average MCP home range size was 178 ± 29 ha (n = 13). Using the fixed-kernel density estimation (KDE), the average home range size was 292.6 ± 37.2 ha (99% KDE, n = 13). We found that female home ranges were not perfectly superimposed on their mate's ranges. On average, males used 73% of their female's home range (range: 51–93%, $n = 3$), while females used 62% (range: 53–71%, $n = 3$) of their male's home range, and they shared 52% (range: 46–56%, $n = 3$) of the volume under the UD (Tomasevic and Marzluff 2018).

The home ranges of suburban woodpeckers encompassed a mix of land covers (Table 3). Generally, slightly more than half of the average home range included some degree of urbanized land (~59%, including light, medium, and heavy urban) and more than a third of the area was forested (~35%). Only ~6% was grassland (where trees and snags were present), and a marginal fraction included other land cover types (i.e. unforested wetlands, open water, bare rock, and clear-cut forest). However, woodpeckers used these land cover types differently within their home ranges (ANOVA, $F_{6,77} = 3.36$, $P = 0.005$; Figure 2). They concentrated their use in forested areas more than in heavily urbanized areas (Table 4). In contrast, concentration of use of lightly and moderately urbanized areas was not significantly different from that of forested lands (Table 4, Figure 2).

The most important variable that influenced space use by woodpeckers (male and female) was the quadratic mean diameter of dominant hardwoods (β = 0.28, 95% CI = 0.00–0.56). Use by most individuals had a significant positive relationship with the diameter of hardwoods (10 individuals had a positive β, i.e. used areas with large-diameter hardwoods), although some individuals showed a significant negative relationship with the diameter of hardwoods (3 individuals had a negative β, i.e. used areas with small-diameter hardwoods). However, when examining space use by the sexes separately, for male woodpeckers, the occurrence of edge habitat (β = 0.63, 95% CI = 0.02–1.25) was more important than the diameter (i.e. size) of hardwood trees (β = 0.32, 95% CI = 0.00–0.65): The RUF coefficients for contrast-weighted edge density at 50 m were significant for 7/9 males (5 frequently used edge [positive β], while 2 used it infrequently [negative β]). The other variables had little effect on use of space.

TABLE 3. Home range composition of adult Pileated Woodpeckers in suburban areas of Greater Seattle, Washington, between 2009 and 2013. We present the area of land cover types in hectares and percentages in parentheses. Other land cover types included: unforested wetlands, agriculture, clear-cut forest, areas cleared for development, shorelines, open water, and bare rock or snow.

	Land cover type								
Bird ID	Coniferous forest	Deciduous or mixed forest	Regenerating forest	Grass or grassland	Light urban	Medium urban	Heavy urban	Other	Total
Females									
574-47011	10.7 (8)	35.2 (25)	3.1 (2)	6.9 (5)	58.8 (42)	23.9 (17)	0.7 (<1)	0.2 (<1)	139.5 (100)
574-47019	4.6 (3)	16.2 (12)	0.7 (<1)	19.2 (14)	58.5 (43)	16.0 (12)	16.2 (12)	4.1 (3)	135.5 (100)
574-47023	63.7 (19)	47.1 (14)	10.6 (3)	37.8 (11)	133.6 (41)	31.3 (10)	6.1 (2)	0.0 (0)	330.2 (100)
574-47027	5.6 (2)	19.6 (6)	2.8 (1)	3.3 (1)	61.5 (19)	213.8 (66)	17.8 (6)	0.0 (0)	324.4 (100)
Average, females	21.2 (8)	29.5 (14)	4.3 (2)	16.7 (8)	78.1 (36)	71.3 (26)	10.2 (5)	1.1 (1)	232.4 (100)
SE, females	14.2 (4)	7.2 (4)	2.2 (<1)	7.6 (3)	18.5 (6)	47.6 (13)	4.1 (3)	1.0 (1)	54.7 (0)
Males									
574-47010	39.2 (18)	29.5 (14)	5.3 (3)	17.3 (8)	98.6 (46)	23.1 (11)	0.5 (<1)	0.1 (0)	213.6 (100)
574-47012	11.7 (5)	18.8 (7)	2.0 (1)	2.6 (1)	52.1 (21)	147.5 (58)	18.6 (7)	0.1 (0)	253.4 (100)
574-47016	25.1 (13)	49.0 (25)	20.6 (11)	4.0 (2)	56.6 (29)	20.1 (10)	3.2 (2)	18.5 (<1)	197.1 (100)
574-47017	85.4 (14)	88.0 (15)	17.6 (3)	58.6 (10)	242.6 (41)	88.7 (15)	15.0 (3)	0.5 (0)	596.4 (100)
574-47018	1.3 (<1)	42.0 (16)	4.3 (2)	2.8 (1)	49.8 (19)	155.7 (60)	4.2 (2)	0.0 (0)	260.1 (100)
574-47021	4.9 (1)	157.7 (37)	39.1 (9)	22.1 (5)	68.1 (16)	102.7 (24)	27.3 (7)	0.8 (0)	422.7 (100)
574-47022	12.2 (5)	31.6 (13)	1.6 (1)	28.3 (12)	100.9 (42)	31.1 (13)	31.9 (13)	0.6 (0)	238.2 (100)
574-47028	70.1 (45)	40.5 (26)	0.5 (<1)	7.7 (5)	28.5 (18)	7.7 (5)	0.2 (<1)	1.7 (0)	156.9 (100)
574-47029	210.2 (44)	83.4 (18)	9.5 (2)	2.1 (<1)	62.6 (13)	50.6 (11)	47.3 (10)	7.3 (2)	473.0 (100)
Average, males	51.1 (16)	60.1 (19)	11.2 (3)	16.2 (5)	84.4 (27)	69.7 (23)	16.5 (5)	3.3 (<1)	312.5 (100)
SE, males	66.5 (17)	43.5 (9)	12.7 (4)	18.6 (4)	63.6 (13)	56.2 (21)	16.4 (5)	6.1 (<1)	49.6 (0)
Average, all	41.9 (14)	50.7 (18)	9.0 (3)	16.3 (6)	82.5 (30)	70.2 (24)	14.5 (5)	2.0 (<1)	287.1 (100)
SE, all	57.9 (15)	39.1 (9)	11.1 (3)	17.0 (5)	55.2 (13)	66.1 (22)	14.3 (5)	5.0 (1)	37.2 (0)

TABLE 4. Tukey pairwise comparisons of differences in the concentration of use (COU) of land cover types by 13 Pileated Woodpeckers in suburban areas of the Greater Seattle area, Washington, USA, 2009–2013. The linear hypothesis for each comparison was that the COU was equal between land cover types. Significant differences are highlighted in bold font. Land cover types are defined in Table 2.

Comparison	Estimate	SE	*t* obs	*P*
Deciduous forest vs. Coniferous forest	8.00	9.32	0.86	0.98
Grassland vs. Coniferous forest	−7.47	9.32	−0.80	0.98
Heavy urban vs. Coniferous forest	**−29.95**	**9.32**	**−3.21**	**0.03**
Medium urban vs. Coniferous forest	−14.23	9.32	−1.53	0.73
Light urban vs. Coniferous forest	−7.02	9.32	−0.75	0.99
Regenerating forest vs. Coniferous forest	−2.16	9.32	−0.23	0.99
Grassland vs. Deciduous forest	−15.47	9.32	−1.66	0.64
Heavy urban vs. Deciduous forest	**−37.95**	**9.32**	**−4.07**	**0.002**
Medium urban vs. Deciduous forest	−22.23	9.32	−2.39	0.22
Light urban vs. Deciduous forest	−15.02	9.32	−1.61	0.68
Regenerating forest vs. Deciduous forest	−10.15	9.32	−1.09	0.93
Heavy urban vs. Grassland	−22.47	9.32	−2.41	0.21
Medium urban vs. Grassland	−6.76	9.32	−0.73	0.99
Light urban vs. Grassland	0.46	9.32	0.05	1.00
Light urban vs. Heavy urban	22.93	9.32	2.46	0.19
Medium urban vs. Heavy urban	15.72	9.32	1.69	0.63
Regenerating forest vs. Heavy urban	27.79	9.32	2.98	0.06
Medium urban vs. Light urban	−7.21	9.32	−0.77	0.99
Regenerating forest vs. Light urban	4.86	9.32	0.52	0.99
Regenerating forest vs. Medium urban	12.07	9.32	1.30	0.85

Home Range Estimates across the Pileated Woodpecker's Range

We found 6 other studies that reported home range sizes for Pileated Woodpeckers (Renken and Wiggers 1989, Mellen et al. 1992, Bull and Holthausen 1993, Aubry and Raley 1996, Bonar 2001, Noel 2011) in a wide range of habitats. We found a significant positive relationship between home range size in natural areas and latitude (Figure 3; linear regression, adjusted multiple $R^2 = 0.92$, $P < 0.001$). Although our study area fell within the latitudinal range of these other studies, home ranges in our sites were smaller than expected for our latitude, falling below the 95% CI for the regression.

DISCUSSION

As expected based on previous work (Blewett and Marzluff 2005), Pileated Woodpeckers intensively used coniferous and broad-leaved forests in our study area, but they also used a large proportion of suburban areas where trees were retained. Lightly and moderately urbanized areas attracted Pileated Woodpeckers and partially complemented the resources found in the remaining native forests present in urban parks and wild parks surrounding our study sites. These resources included suet feeders, water, fruits, telephone poles, and trees (both live and dead) in backyards. The combination of native and nonnative resources may have enabled this species to exploit this altered, and novel, ecosystem. However, this environment is not exempt from risks, as Seattle's suburban areas are known to be used by avian predators as well, including Cooper's Hawks (*Accipiter cooperii*), Barred Owls (*Strix varia*), and Great Horned Owls (*Bubo virginianus*; Rullman and Marzluff 2014). We witnessed several unsuccessful predation attempts by Cooper's Hawks on Pileated Woodpeckers. In addition, there are novel risks associated with urban and suburban areas that may also result in woodpecker mortality, such as cat or other mammalian predation, window collisions (close to feeders or at buildings), attacks at feeders, or even vehicle strikes (Dunn 1993, O'Connell 2001, Chace and Walsh 2006, Loss et al. 2013, 2014). Unfortunately, we are not aware of such information for the Pileated Woodpecker, and we could not determine sources of mortality for the birds that we followed, so this is certainly a promising field of research.

Pileated Woodpeckers have traditionally been considered mature forest specialists, yet they will also use suburban habitats (Hoyt 1957, Conner et al. 1975, Blewett and Marzluff 2005, Erskine 2008, Bull and Jackson 2011). Pileated Woodpeckers were in rapid decline at the beginning of the 20th century due to significant reductions in their natural habitat, but they were able to use what was considered suboptimal habitat, including suburban areas (Hoyt 1957, Bull and Jackson 1995). By the 1950s they were using bird feeders, and they continue to colonize suburban areas that they have not used before (Hoyt 1957, Erskine 2008). Our findings suggest that their ability to use suburban areas depends in part on the incorporation of wooded areas into suburbs.

Home range size can be affected by the abundance and availability of resources that are important to woodpeckers, such as the density of snags for nesting, foraging, and roosting, or by other factors, such as territoriality (Renken and Wiggers 1989). For Pileated Woodpeckers from Arkansas, USA, to Alberta, Canada, we found a significant positive relationship between home range size and latitude. These studies were done in landscapes with less urbanization than our study sites. Our home range size estimate was much lower than expected for this latitude, and was only 30% as large as the home ranges of Pileated Woodpeckers on the heavily forested Olympic Peninsula, at the same latitude as Seattle. Our limited data do not allow us to address mechanisms for this result, but possibilities include: (1) differences in forest productivity compared with other sites; (2) a "crowding effect"; (3) supplementary resources provided by humans; and (4) the availability of snags in yards and parks.

Forest net primary productivity (NPP) differs with latitude and forest type. In general, broad-leaved forests are more productive than coniferous forests at similar latitudes, and forests closer to the equator are more productive than forests closer to the poles (Grier et al. 1989, Gillman et al. 2015). As forest productivity increases, more resources are available, supporting more individuals and species at the landscape level, and reducing home ranges at the local level (Renken and Wiggers 1989, Pautasso and Gaston 2005). We conducted our study mostly in second-growth broad-leaved forests, which may have higher productivity than forests in sites in other Pileated Woodpecker studies in western North America (Mellen et al. 1992, Bull and Holthausen 1993, Aubry and Raley 1996). This difference in productivity may also be strengthened by the fact that suburban forests benefit from the heat island effect found close to cities, which tends to lengthen the growing season for plants (Pickett et al. 2011).

Habitat loss and fragmentation can result in crowding (Debinski and Holt 2000), another mechanism that could have potentially driven the smaller home ranges found in our study. Resource reduction for animals confined to small patches eventually results in reduction of population density and occasionally local extinctions (Debinski and Holt 2000). We found little support for this hypothesis, as there was no evidence of population decline and we observed individuals moving across the landscape without interference by what we expected to be habitat barriers for Pileated Woodpeckers (e.g., roads, highways, open areas, and densely populated areas). Also, we have evidence that survivorship and reproduction in our study areas may be equal to or higher than that in more natural areas of the Pacific Northwest (Bull and Meslow 1988, Bull 2001, Bull and Jackson 2011, Tomasevic 2017).

Supplementation of resources by humans, especially bird feeders, has a great impact on bird communities (Robb et al. 2008). Typically, areas with higher bird feeder density result in higher bird density and higher species richness than areas without feeders (Fuller et al. 2008). Pileated Woodpeckers actively used suet feeders in our study area, as reported by many residents and our personal observations. Feeders may increase food supply and could have a partial compensatory effect on the decrease of resources due to habitat reduction, ultimately reducing home range sizes (Fuller et al. 2008).

As urban areas are developed, snags are removed (Blewett and Marzluff 2005). However, we found snags in suburban green spaces. In fact, 16 of 17 Pileated Woodpecker nests that we found were placed in green spaces (parks, trail buffers, rights-of-way, and large wooded lots; J. Tomasevic personal observation). We believe that being able to find nesting sites is a critical aspect of the success of Pileated Woodpeckers in suburban areas, as nesting sites are commonly a limiting factor among cavity-nesting birds (Newton 1998).

Contrary to other studies (Ruder et al. 2012, Noel et al. 2013), we did not find any evidence of mortality associated with the use of the radio-tags or the Teflon backpack on our birds. Ruder et al. (2012) and Noel et al. (2013) reported high mortality rates (12/34 birds), wherein 11/12 birds died within 12 days of capture (~8 days on average). Four birds that died in our study lived between 104 and 353 days after capture (211 ± 58 days). Also, we did not notice any effect of the radio-tags on reproduction. Even when females carried a transmitter, the antenna did not preclude them from incubating and raising young.

Management Implications

This research provides a new perspective on the Pileated Woodpecker's ecology and opens new opportunities for its conservation and that of the many species associated with it. Under this perspective, suburban areas could and should be incorporated into management and conservation plans for Pileated Woodpeckers. Our results indicate that areas with less than 20% forest (heavily urbanized areas) were used significantly less than areas with higher forest cover. Retaining greater than 20% forest cover over large suburban areas may help to sustain this species (and maybe others tied to it). This forest will be better suited for woodpeckers if dead trees are retained in green spaces. Early-successional species, such as bigleaf maple, red alder, and Douglas-fir, are easy to include in green space management. These species are used by Pileated Woodpeckers for nesting, roosting, foraging, drumming, and calling. By increasing the sustainability of snags and other resources used by large cavity-nesting species, such as the Pileated Woodpecker, cities can play an important role in the conservation of biodiversity.

ACKNOWLEDGMENTS

We thank Jon Bakker, Joshua J. Lawler, Martin G. Raphael, and Elinore J. Theobald for their invaluable comments at different stages in the development of this manuscript, and Brian Kertson for his support with the calculation of the UDs. We are grateful to Jim Ladd, Kim Holt, April Gale-Seixeiro, Sharon Shriver, Dale Griffith, and Jim Rettig for kindly allowing us to trap Pileated Woodpeckers on their properties. We are indebted to Sean Williams, Laura Farwell, Sara Wang, Lauren Walker, Ross Forbush, Ila Palmquist, Jamie Granger, Kristen Richardson, Frank Stewick, Chase O'Neil, Jack DeLap, Janice Bragg, and many others for their assistance in the field. We also thank Sean Williams, Laura Farwell, Peter Hodum, and Nathalie Hamel, who helped with transportation. We extend our gratitude to 2 anonymous reviewers who helped us to greatly improve this paper.

Funding statement: A School of Environmental and Forest Sciences (SEFS) grant to J.M.M. funded the radio-tags. A Student Technology Fee grant (#2010-131-1) at University of Washington to the SEFS funded the radio receivers and GPS units. Carol Nygren kindly provided funding to partially cover field expenses. J.A.T. conducted part of this research while on a Fulbright-Conicyt scholarship for his Ph.D. program. None of the funders had any input into the content of the manuscript. None of the funders required their approval of the manuscript before submission or publication.

Ethics statement: Permission to capture, handle, band, and radio-tag woodpeckers was approved by the University of Washington Institutional Animal Care and Use Committee (IACUC #3077-01), Washington State (IACUC #14-010), and the U.S. National Bird Banding Laboratory (permit #22489).

Author contributions: Both authors conceived the idea and designed the research. J.A.T. collected and analyzed the data and wrote the paper with edits from J.M.M. Both authors agreed to this submission.

Data deposits: The data may be available from the authors upon request.

LITERATURE CITED

Alberti, M., E. Botsford, and A. Cohen (2001). Quantifying the urban gradient: Linking urban planning and ecology. In Avian Ecology and Conservation in an Urbanizing World (J. M. Marzluff, R. Bowman, and R. Donnelly, Editors). Kluwer Academic Publishers, Norwell, MA, USA. pp. 89–115.

Alberti, M., J. M. Marzluff, P. Waddell, and M. Handcock (2006). Modeling interactions among urban development, land-cover change, and bird diversity. NSF Final Report BE/CNH 0120024.

Alberti, M., R. Weeks, and S. Coe (2004). Urban land-cover change analysis in central Puget Sound. Photogrammetric Engineering & Remote Sensing 70:1043–1052.

Aronson, M. F. J., F. A. La Sorte, C. H. Nilon, M. Katti, M. A. Goddard, C. A. Lepczyk, P. S. Warren, N. S. G. Williams, S. Cilliers, B. Clarkson, C. Dobbs, et al. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proceedings of the Royal Society B 281:20133330.

Aubry, K. B., and C. M. Raley (1996). Ecology, management, and conservation of sensitive species. Wildlife Ecology Team 1996 Annual Report, USDA Forest Service, Pacific Northwest Research Station, Olympia, WA, USA.

Aubry, K. B., and C. M. Raley (2002). The Pileated Woodpecker as a keystone habitat modifier in the Pacific Northwest. In Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests (W. F. Laudenslayer Jr., P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, Technical Coordinators). USDA Forest Service General Technical Report PSW-GTR-181. pp. 257–274.

Beissinger, S. R., and D. R. Osborne (1982). Effects of urbanization on avian community organization. The Condor 84:75–83.

Beyer, H. L. (2012). Geospatial Modelling Environment, Version 0.7.2.1. http://www.spatialecology.com/gme/

Blair, R. (2004). The effects of urban sprawl on birds at multiple levels of biological organization. Ecology and Society 9:art.2.

Blair, R. B. (1996). Land use and avian species diversity along an urban gradient. Ecological Applications 6:506–519.

Blair, R. B., and E. M. Johnson (2008). Suburban habitats and their role for birds in the urban–rural habitat network: Points of local invasion and extinction? Landscape Ecology 23:1157–1169.

Blewett, C. M., and J. M. Marzluff (2005). Effects of urban sprawl on snags and the abundance and productivity of cavity-nesting birds. The Condor 107:678–693.

Bonar, R. L. (2001). Pileated Woodpecker habitat ecology in the Alberta foothills. Ph.D. dissertation, University of Alberta, Edmonton, AB, Canada.

Buehler, D. A., J. D. Fraser, M. R. Fuller, L. S. McAllister, and J. K. D. Seegar (1995). Captive and field-tested radio transmitter attachments for Bald Eagles. Journal of Field Ornithology 66:173–180.

Bull, E. L. (2001). Survivorship of Pileated Woodpeckers in northeastern Oregon. Journal of Field Ornithology 72:131–135.

Bull, E. L., and R. S. Holthausen (1993). Habitat use and management of Pileated Woodpeckers in northeastern Oregon. The Journal of Wildlife Management 57:335–345.

Bull, E. L., and J. A. Jackson (2011). Pileated Woodpecker (*Dryocopus pileatus*), version 2.0. In The Birds of North America (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.148

Bull, E. L., and E. C. Meslow (1988). Breeding biology of the Pileated Woodpecker—Management implications. USDA Forest Service Research Note PNW-RN-474.

Bull, E. L., N. Nielsen-Pincus, B. C. Wales, and J. L. Hayes (2007). The influence of disturbance events on Pileated Woodpeckers in northeastern Oregon. Forest Ecology and Management 243:320–329.

Chace, J. F., and J. J. Walsh (2006). Urban effects on native avifauna: A review. Landscape and Urban Planning 74:46–69.

Chapman, K. A., and P. B. Reich (2007). Land use and habitat gradients determine bird community diversity and abundance in suburban, rural and reserve landscapes of Minnesota, USA. Biological Conservation 135:527–541.

Clucas, B., and J. M. Marzluff (2011). Coupled relationships between humans and other organisms in urban areas. In Urban Ecology: Patterns, Processes, and Applications (J. H. Breuste, T. Elmqvist, G. Guntenspergen, P. James, and N. E.

McIntyre, Editors). Oxford University Press, Oxford, UK. pp. 135–147.

Cohen, B. (2006). Urbanization in developing countries: Current trends, future projections, and key challenges for sustainability. Technology in Society 28:63–80.

Conner, R. N., R. G. Hooper, H. S. Crawford, and H. S. Mosby (1975). Woodpecker nesting habitat in cut and uncut woodlands in Virginia. The Journal of Wildlife Management 39:144–150.

Cuo, L., D. P. Lettenmaier, M. Alberti, and J. E. Richey (2009). Effects of a century of land cover and climate change on the hydrology of the Puget Sound basin. Hydrological Processes 23:907–933.

Davis, A., R. E. Major, and C. E. Taylor (2014). Distribution of tree-hollows and hollow preferences by parrots in an urban landscape. Emu 114:295–303.

Debinski, D. M., and R. D. Holt (2000). A survey and overview of habitat fragmentation experiments. Conservation Biology 14: 342–355.

Donnelly, R., and J. M. Marzluff (2006). Relative importance of habitat quantity, structure, and spatial pattern to birds in urbanizing environments. Urban Ecosystems 9:99–117.

Dunn, E. (1993). Bird mortality from striking residential windows in winter. Journal of Field Ornithology 64:302–309.

Endlicher, W. (2011). Introduction: From urban nature studies to ecosystem services. In Perspectives in Urban Ecology: Studies of Ecosystems and Interactions between Humans and Nature in the Metropolis of Berlin (W. Endlicher, P. Hostert, I. Kowarik, E. Kulke, J. Lossau, J. Marzluff, E. van der Meer, H. Mieg, G. Nützmann, M. Schulz, and G. Wessolek, Editors). Springer-Verlag, Berlin, Germany. pp. 1–13.

Erskine, A. J. (2008). Pileated Woodpeckers, *Dryocopus pileatus*, foraging in suburban habitats in New Brunswick. The Canadian Field-Naturalist 122:226–229.

Fernández-Juricic, E. (2000). Avifaunal use of wooded streets in an urban landscape. Conservation Biology 14:513–521.

Franklin, J. F., and C. T. Dyrness (1988). Natural Vegetation of Oregon and Washington. Oregon State University Press, Crovallis, OR, USA.

Fuller, R. A., P. H. Warren, P. R. Armsworth, O. Barbosa, and K. J. Gaston (2008). Garden bird feeding predicts the structure of urban avian assemblages. Diversity and Distributions 14:131–137.

Gavareski, C. A. (1976). Relation of park size and vegetation to urban bird populations in Seattle, Washington. The Condor 78:375–382.

Gillman, L. N., S. D. Wright, J. Cusens, P. D. McBride, Y. Malhi, and R. J. Whittaker (2015). Latitude, productivity and species richness. Global Ecology and Biogeography 24:107–117.

Grier, C. C., K. M. Lee, N. M. Nadkarni, G. O. Klock, and P. J. Edgerton (1989). Productivity of forests of the United States and its relation to soil and site factors and management practices: A review. USDA Forest Service General Technical Report PNW-GTR-222.

Handcock, M. S. (2011). Package ruf: Software to implement resource utilization function estimation. http://www.stat.ucla.edu/~handcock/ruf

Hepinstall, J. A., M. Alberti, and J. M. Marzluff (2008). Predicting land cover change and avian community responses in rapidly urbanizing environments. Landscape Ecology 23:1257–1276.

Hoyt, S. F. (1957). The ecology of the Pileated Woodpecker. Ecology 38:246–256.

Johnston, A. N. (2013). Eastern gray squirrel ecology and interactions with western gray squirrels. Ph.D. dissertation, University of Washington, Seattle, WA, USA.

Kowarik, I. (2011). Novel urban ecosystems, biodiversity, and conservation. Environmental Pollution 159:1974–1983.

LaMontagne, J. M., R. J. Kilgour, E. C. Anderson, and S. Magle (2015). Tree cavity availability across forest, park, and residential habitats in a highly urban area. Urban Ecosystems 18:151–167.

Loss, S. R., T. Will, S. S. Loss, and P. P. Marra (2014). Bird–building collisions in the United States: Estimates of annual mortality and species vulnerability. The Condor: Ornithological Applications 116:8–23.

Loss, S. R., T. Will, and P. P. Marra (2013). The impact of free-ranging domestic cats on wildlife of the United States. Nature Communications 4:art.1396.

MacGregor-Fors, I., L. Morales-Pérez, and J. E. Schondube (2012). From forests to cities: Effects of urbanization on subtropical mountain bird communities. In Urban Bird Ecology and Conservation (C. A. Lepczyk and P. S. Warren, Editors). Studies in Avian Biology 45:33–48.

MacLean, C. D., and C. L. Bolsinger (1997). Urban expansion in the forests of the Puget Sound region. USDA Forest Service Resource Bulletin PNW-RB-225.

Martin, K., and J. M. Eadie (1999). Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. Forest Ecology and Management 115: 243–257.

Marzluff, J. M. (2014). Welcome to Subirdia: Sharing Our Neighborhoods with Wrens, Robins, Woodpeckers and Other Wildlife. Yale University Press, New Haven, CT, USA.

Marzluff, J. M., and K. Ewing (2001). Restoration of fragmented landscapes for the conservation of birds: A general framework and specific recommendations for urbanizing landscapes. Restoration Ecology 9:280–292.

Marzluff, J. M., B. Clucas, M. D. Oleyar, and J. DeLap (2016). The causal response of avian communities to suburban development: A quasi-experimental, longitudinal study. Urban Ecosystems 19:1597–1621.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock (2004). Relating resources to a probabilistic measure of space use: Forest fragments and Steller's Jays. Ecology 85:1411–1427.

McGarigal, K., S. A. Cushman, and E. Ene (2012). FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps. University of Massachusetts, Amherst, MA, USA. http://www.umass.edu/landeco/research/fragstats/fragstats.html

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. Biological Conservation 127:247–260.

Mellen, T. K., E. C. Meslow, and R. W. Mannan (1992). Summertime home range and habitat use of Pileated Woodpeckers in western Oregon. The Journal of Wildlife Management 56:96–103.

Melles, S., S. Glenn, and K. Martin (2003). Urban bird diversity and landscape complexity: Species–environment associations along a multiscale habitat gradient. Conservation Ecology 7:art.5.

Møller, A. P. (2009). Successful city dwellers: A comparative study of the ecological characteristics of urban birds in the Western Palearctic. Oecologia 159:849–858.

Morrison, J. L., and W. C. Chapman (2005). Can urban parks provide habitat for woodpeckers? Northeastern Naturalist 12: 253–262.

Neatherlin, E. A., and J. M. Marzluff (2004). Responses of American Crow populations to campgrounds in remote native forest landscapes. The Journal of Wildlife Management 68:708–718.

Newton, I. (1998). Population Limitation in Birds. Academic Press, San Diego, CA, USA.

Noel, B. L. (2011). Breeding ecology of the Pileated Woodpecker (*Dryocopus pileatus*) in bottomland forests of eastern Arkansas, with reference to the conservation of the Ivory-billed Woodpecker (*Campephilus principalis*). Ph.D. dissertation, Arkansas State University, Jonesboro, AR, USA.

Noel, B. L., J. C. Bednarz, M. G. Ruder, and M. K. Keel (2013). Effects of radio-transmitter methods on Pileated Woodpeckers: An improved technique for large woodpeckers. Southeastern Naturalist 12:399–412.

O'Connell, T. J. (2001). Avian window strike mortality at a suburban office park. The Raven 72:141–149.

Ohmann, J. L., and M. J. Gregory (2002). Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, USA. Canadian Journal of Forest Research 32:725–741.

Ohmann, J. L., M. J. Gregory, and H. M. Roberts (2014). Scale considerations for integrating forest inventory plot data and satellite image data for regional forest mapping. Remote Sensing of Environment 151:3–15.

Pautasso, M., and K. J. Gaston (2005). Resources and global avian assemblage structure in forests. Ecology Letters 8:282–289.

Pickett, S. T. A., M. L. Cadenasso, J. M. Grove, C. G. Boone, P. M. Groffman, E. Irwin, S. S. Kaushal, V. Marshall, B. P. McGrath, C. H. Nilon, R. V. Pouyat, et al. (2011). Urban ecological systems: Scientific foundations and a decade of progress. Journal of Environmental Management 92:331–362.

Raley, C. M., and K. B. Aubry (2006). Foraging ecology of Pileated Woodpeckers in coastal forests of Washington. The Journal of Wildlife Management 70:1266–1275.

R Core Team (2014). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Renken, R. B., and E. P. Wiggers (1989). Forest characteristics related to Pileated Woodpecker territory size in Missouri. The Condor 91:642–652.

Renken, R. B., and E. P. Wiggers (1993). Habitat characteristics related to Pileated Woodpecker densities in Missouri. The Wilson Bulletin 105:77–83.

Robb, G. N., R. A. McDonald, D. E. Chamberlain, and S. Bearhop (2008). Food for thought: Supplementary feeding as a driver of ecological change in avian populations. Frontiers in Ecology and the Environment 6:476–484.

Ruder, M. G., B. L. Noel, J. C. Bednarz, and M. K. Keel (2012). Exertional myopathy in Pileated Woodpeckers (*Dryocopus pileatus*) subsequent to capture. Journal of Wildlife Diseases 48:514–516.

Rullman, S., and J. M. Marzluff (2014). Raptor presence along an urban–wildland gradient: Influences of prey abundance and land cover. Journal of Raptor Research 48:257–272.

Sol, D., C. González-Lagos, D. Moreira, J. Maspons, and O. Lapiedra (2014). Urbanisation tolerance and the loss of avian diversity. Ecology Letters 17:942–950.

Tomasevic, J. A. (2017). Cavity-nesting bird interactions in the urban-suburban gradient. Ph.D. dissertation, University of Washington, Seattle, WA, USA.

Tomasevic, J. A., and J. M. Marzluff (2018). Space use of suburban Pileated Woodpeckers (*Dryocopus pileatus*): Insights on the relationship between home range, core areas, and territory. Oecologia 187:15–23.

United Nations (2008). World urbanization prospects: The 2007 revision. Highlights. United Nations, Department of Economic and Social Affairs, Population Division, New York, NY, USA.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70: 164–168.

York, D. L., J. E. Davis, Jr., J. L. Cummings, and E. A. Wilson (1998). Pileated Woodpecker capture using a mist net and taped call. North American Bird Bander 23:81–82.

Zar, J. H. (1999). Biostatistical Analysis, fourth edition. Prentice-Hall, Upper Saddle River, NJ, USA.