Cavity-Nesting Bird Interactions In The Urban-Suburban Gradient

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A Dissertation
submitted in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

University of Washington
2017

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Program Authorized to Offer Degree:
Environmental and Forest Sciences

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Abstract

Cavity-Nesting Bird Relationships Along An Urban-Wildland Gradient On The Greater Seattle Area

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Urbanization brings dramatic and sudden changes to ecological conditions affecting natural communities. I studied potential effects on cavity-nesting birds, both primary and secondary (hereafter PCN and SCN, respectively), which may be limited in these novel environments because of reduced abundance of nesting sites (e.g. snags and cavities) and competition for cavities with non-native species. I addressed community-wide effects of urbanization on cavity nesting birds, and then focused on the ecology of a particular cavity-nesting species, the Pileated Woodpecker (*Dryocopus pileatus*).

Humans can potentially compensate for negative effects of urbanization by directly and indirectly providing nest sites (e.g., nest boxes, crevices on houses), especially for SCN species. I investigated whether and how PCNs and humans facilitated the cavity-nesting bird community along a gradient of urbanization. To do so, I estimated the abundance of cavity-nesting species between 1998 and 2010 at 135, 1-km2 sites that differed in the degree of urbanization (0–100% forest cover). Also, I found 367 nests on a subset of 31 sites. PCNs (n=67 nests) nested mostly on snags (98.5%), while native SCNs (n=141) used both natural (71.63%) and anthropogenic (28.37%) cavities. Non-native SCNs (n=159 nests) used mostly anthropogenic cavities (98.11%). PCN abundance facilitated native SCN abundance on sites with more than 12% forest cover at 1-km^2 scale, but not at less forested sites. There, native SCNs nested primarily (59%) in anthropogenic cavities. Human facilitation allowed native SCNs to successfully use and reproduce where snags were scarce, changing the composition and structure of the cavity-nesting bird community within the most urbanized sites. Flexible nest site selection and human facilitation provide new opportunities for native cavity-nesting birds in a rapidly changing world.

I studied how a purported sensitive species, the Pileated Woodpecker (*Dryocopus pileatus*), adapts to rapid and extensive land-cover change as urbanization reduces and isolates forest. From 2009 – 2013, I used radio-telemetry to determine the annual home range size and habitat use of 17 individuals in 9 suburbs that varied in their level of urbanization (ranging 5 – 90% forest

remaining). I used Concentration of Use and Resource Utilization Functions to examine vegetative characteristics used by woodpeckers at the landscape (i.e. 1 km^2) and local (i.e. 1/3 ha) levels. The average suburban woodpecker home range was significantly smaller than expected based on latitude. Pileated woodpeckers significantly concentrated their use of the landscape on native forest (coniferous and deciduous), as well as light and medium urbanized areas. Highly urbanized areas were seldom used. Resource use was highest along edges between forest and light and medium urbanized areas, and in forests with increasing mean diameter of dominant hardwood species. My results not only indicate the adaptability of a species that has traditionally been considered a mature forest specialist, but they also suggest that maintaining forest cover above 20%, retaining large deciduous trees and snags in public green spaces and yards, and providing feeders would improve the biodiversity of suburban areas.

Finally, home range, territory and core areas are concepts that have been used to describe space use. However, little research has been done to understand potential spatial relationships between them. And while the relative importance of different areas of the home range has been addressed with utilization distributions; there is a lack of such analysis for territories. I propose a behavior-based approach to determine areas of importance within the territories, that I defined as highly-defended areas. I studied the spatial ecology of a territorial species, the pileated woodpecker, and the relationships between their home range, territory, core areas, and highly-defended areas. I found significant spatial overlap between male and female woodpeckers of the same breeding pair, but little overlap between same sex individuals on neighboring home ranges. On average, territories represented 69.63% ± 0.06% of the home ranges, and highly-defended areas were 34.3% ± 0.03% of the home range. My definition of a highly-defended area was useful in determining the portions of the territory that were important for the birds. Though more objective that other proposed methods, my approach is contingent upon the types of behaviors surveyed. In my case, highly-defended areas contained a significant proportion of the roost sites for pileated woodpeckers, a resource that may affect survivorship, especially in winter. This approach could be useful to further incorporate behavior on the study of the spatial ecology of species.

Acknowledgements

First, I would like to thank the support and guidance provided by my committee. John Marzluff pushed me to do my very best. He always gave me with an alternative view and challenged my perspective, not only expanding, but also greatly enriching my work. Josh Lawler, Jon Bakker, Martin Raphael, Josh Tewksbury, and Raymond Huey were always there for me, always willing to help in the best way possible. I will always be grateful for your time, support and contributions to make my work better.

I would also like to acknowledge the financial support that I received throughout my studies. Fulbright and Conicyt provided me with a generous scholarship to attend to University of Washington. Without it, I doubt I would be writing these pages. The School of Environmental and Forest Sciences (formerly the College of Forest Resources) also supported me with a generous tuition waiver that accompanied my Fulbright-Conicyt scholarship. Carol Nygren was a generous private donor that partially funded my fieldwork.

The work I present here would not have been possible without the generosity of so many people that helped me in the field. I would like to thank Jim Ladd, Kim Holt, April Gale-Seixeiro, Sharon Shriver, Dale Griffith, and Jim Rettig for kindly allowing me to trap pileated woodpeckers on their property, and so many anonymous people that let me work on or around their property and neighborhoods. I would like to acknowledge Sean Williams, Laura Farwell, Sara Wang, Lauren Walker, Ross Forbush, Ila Palmquist, Jamie Granger, Kristen Richardson, Frank Stevick, Chase O'Neil, Jack DeLap, Janice Bragg, and so many others that volunteered their time and effort to achieve this.

Also, I would not have achieved this without the constant support of Michelle Trudeau, Amanda Davis, Abdallah Ben-Hamallah, George Moore, Leana de la Torre, Karen Dennean, Joseph Kobayashi, Tikvah Weiner, Celese Spencer, Jeanette Milne, Doug Ewing, Keith Possee, Karl Wirsing, Margery Cooper, Ann Corboy, David Campbell, Tom Koerber, Karina Sapunar, Marc Morrison, and so many others that truly made a difference for me and helped me on the other dimensions of what it takes pursuing a PhD.

To all my lab colleagues and friends, David Oleyar, Stan Rullman, Thomas Unfried, Heather Cornell, Vivian Bui, Laura Farwell, Ben Shryock, Melanie Colon, Scott Horton, Lauren Walker, Jack DeLap, Kaeli Swift, Carol Bogezi, Amber Mount, Leif Hansen, Michael Heimbuch, Chad Wilsey, Jorge Ramos, Betsy Bancroft, Evan Givertz, Michael Case, John Withey, Avery Meeker, Steven Walters, Ursula Valdez, Todd Mitchell, Carolina Gomez-Posada, and so many others, for all their comments, support and ideas that greatly enriched my work and life at UW.

To my wife, Vania, and my daughter, Matilda, for their constant support through this long and hard process, and for being such an inspiration for me. They give meaning to my life and fill my heart with love.

Thank you all!

Introduction

More than half of the world's population now lives in cities (United Nations 2008) and around 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 population increases (Blair 2004, Aronson et al. 2014), this massive increase in urban population is resulting in an unprecedented rate of urban area expansion (Cohen 2006). As an example, projections indicate that the USA could face a 79% increase in urban land cover between 2000 and 2025, potentially reaching 9.2% of the area of the lower 48 states (range: 6.9 – 12.1%, Alig et al. 2004) while the proportion of urban people slowly increases from 75% (1990) to 81% (2014) and potentially to 87% (2050, United Nations 2014).

Urbanization and the sprawl of cities are very complex and dynamic processes. They not only change vegetation composition, quantity and structure (Donnelly and Marzluff 2006), but also micro-climatic conditions, biotic interactions (e.g., increasing predation by domestic animals, competition with exotic species, and transmission of diseases, Chace and Walsh 2006, Endlicher 2011), and connectivity within and between surrounding natural areas (Fernández-Juricic 2000). These changed conditions usually produce a gradient of land cover between natural and urbanized areas (urban-wildland or urban-rural gradient, Blair 1996) where habitats are increasingly less modified the farther they reside 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). This, in conjunction with factors such as altered disturbance regimes (Chace and Walsh 2006) and supplemental food and water (Robb et al. 2008, Clucas and Marzluff 2011) create novel habitat conditions for wildlife and plants that bring challenges and opportunities that will favor species with the ability to adapt to them (Kowarik 2011) and extirpate those that cannot (Marzluff 2014).

In fact, changes wrought by urbanization may have profound effects on bird communities (Er et al. 2005, Chace and Walsh 2006). In general, there is consensus that highly urbanized bird communities are less diverse (typically dominated by few human-adapted species) and they can 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). At the urban cores, bird communities are normally dominated by generalist species (either native or exotic) that are able to cope with the significant changes in habitat conditions and resources (Sol et al. 2014). Similarities among urban cores around the world are resulting in a small homogenous set of species being favored (Blair 2001, McKinney 2006, Shanahan et al. 2014). Moreover, specialist species may not adapt to these novel environmental conditions, resulting in their decline and eventually their local extirpation (Farwell and Marzluff 2013).

But urban and suburban areas also provide an opportunity to study ecological relationships among species and with their environment under a set of circumstances that can be translated to the “natural” world as well. In this work, I address how cavity-nesting birds are being affected by the changes brought by urbanization. I chose cavity-nesting birds because they tend to be very sensitive to changes to their habitats, especially due to the scarcity of nesting sites (i.e. snags), which are less available as places develop for urbanization (Blewett and Marzluff 2005). First, I explore the idea that humans could potentially have positive impacts on the cavity-nesting bird community via providing artificial nesting sites directly (e.g. nest boxes) or indirectly (e.g. crevices on buildings). This potential for human facilitation could have significant effects on the composition and structure of such community along a gradient of urbanization. For the rest of my chapters, I focused on the ecology of a particular species, the Pileated Woodpecker (*Dryocopus pileatus*). I chose this species, not only for being a charismatic one and considered a candidate species for WA State, but also because of its role on the cavity-nesting bird community. I addressed aspects of its habitat use, home range size and composition, territoriality, reproduction and survivorship, which shed light on how a species that is normally considered dependent on mature forest, is adapting to deal with the novel environment of suburban areas.

Chapter 1

Cavity Nesting Birds Along An Urban-Wildland Gradient: Is Human Facilitation Structuring The Bird Community?

Urban Ecosyst (2017) 20:435–448
DOI 10.1007/s11252-016-0605-6

Cavity nesting birds along an urban-wildland gradient: is human facilitation structuring the bird community?

Jorge A. Tomasevic[1] · **John M. Marzluff**[1]

Abstract Urbanization brings dramatic and sudden changes to ecological conditions affecting natural communities. Cavity-nesting birds, both primary and secondary (hereafter PCN and SCN, respectively), may be limited in this novel environment because of reduced abundance of nesting sites (e.g. snags and cavities) and competition for cavities with non-native species. But humans can also directly and indirectly provide nest sites (e.g., nest boxes, crevices on houses), especially for SCN species, potentially partially compensating for negative effects. We investigated whether and how PCNs and humans facilitated the cavity-nesting bird community along a gradient of urbanization. To do so, we estimated the abundance of cavity-nesting species between 1998 and 2010 at 135, 1-km^2 sites that differed in the degree of urbanization (0–100 % forest cover). Also, we found 367 nests on a subset of 31 sites. PCNs (n = 67 nests) nested mostly on snags (98.5 %), while native SCNs (n = 141) used both natural (71.63 %) and anthropogenic (28.37 %) cavities. Non-native SCNs (n = 159 nests) used mostly anthropogenic cavities (98.11 %). PCN abundance facilitated native SCN abundance on sites with more than 12 % forest cover at 1-km^2 scale, but not at less forested sites. There, native SCNs nested primarily (59 %) in anthropogenic cavities. Human facilitation allowed native SCNs to successfully use and reproduce where snags were scarce, changing the composition and structure of the cavity-nesting bird community within the most urbanized sites. Flexible nest site selection and human facilitation provide new opportunities for native cavity-nesting birds in a rapidly changing world.

Keywords Stress gradient hypothesis · Nest box · Cavity-nesting birds · Non-native species

Introduction

For decades, the study of species interactions in community and population ecology has been mainly approached from the point of view of negative interactions, notably competition and predation (Butterfield 2009). However, recent considerations have shown that facilitation (i.e., any positive interaction between two species where at least one of them is benefited and neither is harmed, Hacker and Gaines 1997; Stachowicz 2001), can structure ecological communities and regulate population dynamics (Stachowicz 2001; Bruno et al. 2003; Brooker et al. 2008), especially under stressful conditions (Bertness and Callaway 1994).

The urban ecosystem is a stressful environment for native species that require native vegetation or undisturbed settings. As urbanization expands globally, novel ecosystems have emerged (Kowarik 2011) and native bird communities have been affected by habitat loss and degradation, but also by changes in the abundance of food, disease transmission, predation and other interactions with native and non-native species (Blair 1996; Marzluff 2001; Kowarik 2011; Aronson et al. 2014). As such, the influence of facilitation to animals within urban ecosystems may be investigated by considering the stress-gradient hypothesis (SGH, Bertness and Callaway 1994), which posits that the importance of facilitative interactions is greatest at high levels of stress and it is less relevant

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Electronic supplementary material The online version of this article (doi:10.1007/s11252-016-0605-6) contains supplementary material, which is available to authorized users.

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when stress levels are lower and other biotic interactions, such as competition, are more important. This shift in the form of species interactions has been documented for plants with different life histories and origins (native or non-native) in a wide variety of ecosystems and climates (He et al. 2013), yet testing of this framework in animal ecology is still lacking (Barrio et al. 2013). In fact, it seems that the common conception among animal ecologists is that competition is higher in stressful than in less stressful conditions (Barrio et al. 2013).

Urbanization is a multidimensional stress as biotic and abiotic dimensions are affected at the same time, normally on a cline between urban cores and the surrounding natural areas (Blair 1996; Marzluff 2001). Under these circumstances, it has been shown that different species respond differently to these novel habitats (Marzluff et al. 2015). Urban cores usually support high levels of avian biomass concentrated in few native and non-native species (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; Shanahan et al. 2014; Sol et al. 2014). Native species, on the other hand, may be more prevalent in middle to low levels of urbanization, where more vegetation (native and non-native) is available, reaching the highest richness at middle levels of urbanization (ca. 30–70 % forest in the landscape, Hansen et al. 2005; Marzluff 2005; Tratalos et al. 2007; Blair and Johnson 2008; Pennington and Blair 2012; Shanahan et al. 2014).

Although cities are stressful for many avian species, human supplements may facilitate the presence of others (Faeth et al. 2005). People benefit birds by providing habitat in their backyards using landscaping, bird feeders, nest boxes, and water features, among other practices (Davies et al. 2009; Clucas et al. 2011; Clucas and Marzluff 2011; Marzluff 2014), increasing bird richness (Robb et al. 2008; Clucas and Marzluff 2015) and population size (Fuller et al. 2008).

The main objective of our work was to understand facilitative interactions between humans and a particular group of birds (cavity-nesting species) on a gradient of habitat disturbance, and therefore stress, which we consider to be correlated with the degree of urbanization. Cavity-nesting birds may be particularly sensitive to urbanization because they are normally limited by the availability of dead trees for nesting (Newton 1998) and habitat (e.g. forest cover). These key resources are usually lost or significantly reduced in urban areas (Blewett and Marzluff 2005; Donnelly and Marzluff 2006; Davis et al. 2014; LaMontagne et al. 2015) affecting occurrence and abundance of cavity-nesting species and other species that may interact with them as part of the ecological community (e.g. nest web, Martin and Eadie 1999). We studied the response of cavity-nesting species richness, abundance, community structure, nesting patterns and nesting success along a gradient of urbanization, paying particular attention to direct and indirect facilitation by humans. In accordance with the stress-gradient hypothesis, we expect that the effects of human facilitation (if any) on cavity nesting birds will be strongest in sites with medium to high levels of disturbance (urban cores and suburban areas) and that humans may play a role structuring the community by favoring some species over others.

Methods

Study sites and focal species

We studied 5 primary cavity nesting bird species (e.g. woodpeckers, hereafter PCN) and 7 secondary cavity nesting bird species (hereafter SCN) between 1998 and 2010 along an urban-wildland gradient in the greater Seattle area (Table 1). This area comprises a mosaic of urban, suburban and forested land cover from the Puget Sound to the Cascade Mountain foothills (Fig. 1). We used forest cover (%, at a 1 km^2 scale) estimated based on classified 30 m resolution land cover data based on 2007 Landsat TM and ETM satellite imagery to define our urban-wildland gradient (Alberti et al. 2006). This dataset included 14 land cover categories, two of which where "forest" (coniferous forest, >80 % coniferous trees, and deciduous and mixed forest, 10–80 % deciduous or mixed forest, see Hepinstall et al. 2008 for more details). We chose forest cover as our independent variable because most of the species we studied live in the forest (so it is a direct quantification of their habitat) and sites have less forest normally because they have been converted to some level of urban use in our study area (Hepinstall et al. 2008). We used imagery from 2007 because changes to forest cover after this point were minimal, including sites that were developed during the early years of our study. All bird species are native to this area, except for European Starling (*Sturnus vulgaris*) and House Sparrow (*Passer domesticus*), both SCNs. These 12 species represent the full assemblage of diurnal land bird cavity nesters and all the woodpecker species present in the area. We did not include cavity nesting waterfowl or owls for logistical reasons.

Cavity-nesting bird community characterization

We described the cavity-nesting bird community using species presence, richness, and relative abundance of all the species mentioned. To do so, we estimated these parameters at 135, 1 km^2 square plots in sites with different levels of urbanization (0–100 % forest). On each site, we counted all birds seen and heard within 4–8 50-m-fixed-radius points for 10 min (Ralph et al. 1993). We accounted for this variation in effort by having similar number of point counts for most sites (mean ± SE, 7.05 ± 0.18 points), but also by visiting the sites multiple times during the breeding season (once a month during the breeding season, i.e. April–August) and over multiple years, resulting

Table 1 Number of nests of cavity nesting species found on the urban-wildland gradient of the Greater Seattle area between 1998 and 2010

Species	Type of substrate								
	Natural				Anthropogenic				Total nests
	Snag	Tree	Other	Total	House/ building	Nest box	Other	Total	
Primary Cavity Nesting Species (PCN)									
Downy woodpecker (*Picoides pubescens*)	5	0	0	5	0	0	0	0	5
Hairy woodpecker (*Picoides villosus*)	23	1	0	24	0	0	0	0	24
Pileated woodpecker (*Dryocopus pileatus*)	3	0	0	3	0	0	0	0	3
Red-breasted sapsucker (*Sphyrapicus ruber*)	10	7	0	17	0	0	0	0	17
Northern flicker (*Colaptes auratus*)	17	0	0	17	1	0	0	1	18
Total PCN	58	8	0	66	1	0	0	1	67
Secondary Cavity Nesting Species (SCN)									
Native species									
Black-capped chickadee (*Poecile atricapillus*)	36	6	0	42	0	6	0	6	48
Chestnut-backed chickadee (*Poecile rufescens*)	38	9	0	47	0	1	0	1	48
Bewick's wren (*Thryomanes bewickii*)	2	0	4	6	1	2	3	6	12
Red-breasted nuthatch (*Sitta canadensis*)	6	0	0	6	0	0	0	0	6
Violet-green swallow* (*Tachycineta thalassina*)	0	0	0	0	27	0	0	27	27
Total native SCN species	82	15	4	101	28	9	3	40	141
Exotic Species									
European starling (*Sturnus vulgaris*)	3	0	0	3	116	0	1	117	120
House sparrow (*Passer domesticus*)	0	0	0	0	30	9	0	39	39
Total exotic SCN species	3	0	0	3	146	9	1	156	159
Total SCN	85	15	4	104	174	18	4	196	300
Total nests	143	23	4	170	175	18	4	197	367

*Migratory species

on an average of 726.15 ± 147.14 point counts per year. The point-count stations at least 150 m apart to reduce the probability of double-counting individuals on two plots. We (and field assistants) counted birds between 05:00 and 12:00, avoiding days when weather conditions would interfere with the detectability of the birds (rain, heavy winds, etc.). All participants on this study where trained on a consistent manner on how to detect and record the species during point counts to reduce observers' bias. In sites with built and forested portions, we allocated more points to the built portion (up to 6 out of 8) to account for higher variability of habitat and the bird community (Donnelly and Marzluff 2004; Donnelly and Marzluff 2006). However, because not all sites have both forest and built portions, the total allocation of point-counts was closer to a 3:7 ratio (304 point counts in the forest vs. 726 on the built matrix). This allocation allowed us to more fully describe the diversity of birds found at each site. We then averaged the relative abundance, expressed as number of individuals per count, to the site level. We used the average relative abundance per year to account for differences in effort between sites.

We estimated relative ocurrence and relative abundance within areas of small and fixed radius because land cover within developments is not homogeneous and distance to aural detections (the majority of cases in our heavily forested and built landscapes) may be difficult to estimate accurately (Hutto 2016). Because we used naïve estimates, our determination of relative abundance in forests may be biased low relative to distance-corrected estimates. Marzluff et al. (2015) reported that the overall detectability was higher on the urban portion than the forested portion of our study sites. Therefore, we exercise caution in interpreting species responses where abundance is lowest in forest and highest in more developed sites. This situation is only expected for urban-associated species such as the European Starling and House Sparrow, however, bias in their detection is minimal because of the gregarious and conspicuous nature.

Nesting patterns and nesting success

Because cavity-nesting birds can be limited by the availability of nesting sites (Newton 1998), our first approach to study

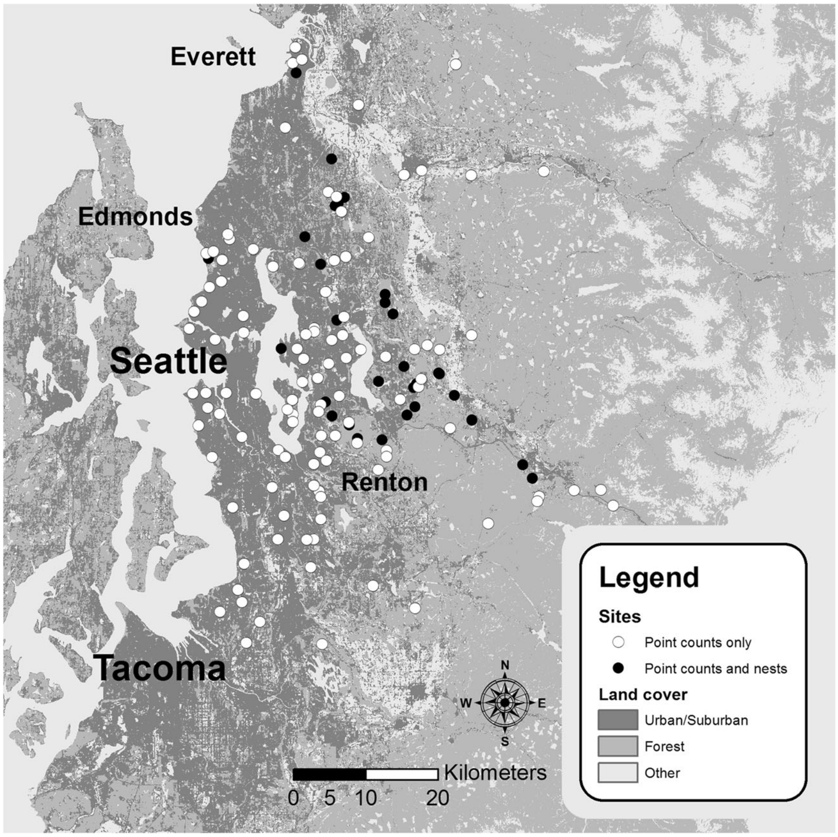

Fig. 1 Study area in Seattle, WA. Land cover types grouped as urban/suburban (in different degrees of urbanization), forest (including coniferous, deciduous or mixed) and other. Dots do not represent size of the sites

facilitation was to assess whether humans had any influence on this potentially limiting factor. We recorded nests in a subset of 31 sites that were subject to a more intensive monitoring scheme that included spot-mapping, mist-netting, and nest searching (Marzluff et al. 2015). We sampled these sites for different time spans, ranging from 1 to 10 years (mean ± SE, 6.06 ± 0.48 years). These sites represent a gradient of urbanization between urban cores and wild lands ranging from 0 to 99.8 % forest remaining (mean ± SE, 42.61 ± 4.93 %, Fig. 1). We used two nest-searching schemes: dedicated to cavity nesting birds (2000–2002, see Blewett and Marzluff 2005) and opportunistic (1998–1999, 2003–2010). The dedicated search scheme was more intensive and focused on both urban and forested portions of the study plots. The opportunistic search scheme was mostly focused on the forested portion of the study sites, but still recording nests in the urban portion where detections were easier as well. Field crews searched for nests approximately 2–3 h/site/week during the breeding season (April – August). They recorded all nests found, plus the date when they were found, the species they belonged to, and the substrate in which the nest was built. As for substrate, they recorded the species and type (e.g. tree, snag, stump, house, pole, etc.), and we later assigned its origin (natural or anthropogenic). We visited each nest found every three days to determine its fate. We considered a nest successful if at least one chick was able to fledge. If the nest attempt failed, the cause of failure was recorded when possible. Because different sites were followed for different number of years, we used nests per year (average nests) as our dependent variable.

Our second approach to study facilitation was to assess the role of PCNs on the community. PCN species are providers of natural cavities that can be used as nesting sites by SCN species when PCNs abandon them (Martin and Eadie 1999), so we tested for relationships between the abundance of PCN and SCN species, as an indicator of facilitation where nesting sites may be the limiting factor.

Statistical analyses

We used logistic regression to determine the relationship between forest cover and the presence of each individual species. We also grouped species by guild (PCN, native SCN, non-native SCN, all SCN) and looked for changes in richness patterns related to forest cover using Poisson log-linear regression, linear regression, and non-linear regression. We related other continuous data (e.g. relative abundance) to forest cover with standard linear or non-linear regression as deemed appropriate based on visual inspection of the data and quantitative model selection using the Akaike Information Criterion (AIC; Akaike 1973, Wagenmakers and Farrell 2004). We calculated AIC values using package AICcmodavg (version 2.0–4, Mazerolle 2016) and we calculated Delta AIC and AIC weights using package qpcR (version 1.4–0, Spiess 2014). We compared differences on means using paired t-test and we used Chi-squared tests to test for differences on proportions on nest success between different substrates or guilds (Zar 1999).

We looked for changes in trend or thresholds in nesting patterns related to the urban-wildland gradient using a segmented linear regression analysis (package segmented v0.2–9.4 for R, (Muggeo 2008) on the average number of nests (analyzing natural and anthropogenic nests separately) per guild. We compared this approach to other models, however our main objective was not to determine the best model of the full relationship, but rather to determine where any significant threshold in use of resources occurred (e.g., nest substrate), which may provide evidence of anthropogenic facilitation by direct or indirect provision of nest sites. For this analysis, we considered each guild (PCN, native SCN, non-native SCN) individually. In the case of native SCN, we divided our dataset, analyzing Violet-green Swallow (*Tachycineta thalassina*) separately from the other species. We took this approach because this species has significantly different habitat requirements from the others, using open areas for foraging, and its gregarious nature results in a patchy distribution on the landscape (Brown et al. 2011). Whenever we found a significant change in trend using the segmented regression analysis (which yields a point estimate and a 95 % CI for the break point), we also ran a two-sided Davies' test (package segmented v0.2–9.4 for R, Muggeo 2008) to refine the estimate. We used the results of the Davies' test as a conservative approach to inform other analyses that built upon these results.

Based on the shift in use of nesting substrates at higher levels of urbanization that we found for native SCNs, we further divided our dataset into two groups (above and below the break point). We calculated relative abundance, relative occurrence and dominance of each species for each group. We then studied differences in community structure and the effect of urbanization on each group using a multivariate approach (McCune and Grace 2002).

As suggested for community structure data (McCune and Grace 2002), we checked for rare species. We did not need to delete rare species, however, as all of the species we included were present in more than 5 % of the sites. In order to equalize the contribution of each site regardless of their total abundance of birds, we used relativization by species maxima and by site total for the SCN community data (package vegan v 2.2–1 for R, Oksanen et al. 2013). This centers the focus on the structure of the community rather than on the abundance. We used Non-Metric Multidimensional Scaling (NMDS) to visualize the differences in community structure between sites (package vegan v 2.2–1 for R, Oksanen et al. 2013). NMDS is a useful ordination technique that makes no assumptions about the form of the relationships among variables. It also relieves the "zero-truncation" problem that other ordination techniques have and it can be constructed with any distance measure (McCune and Grace 2002). In our case, we calculated differences in community structure with Bray-Curtis distance, which accounts for differences in abundance between species taking species identity into consideration (McCune and Grace 2002). We used the function metaMDS with the same parameters for all ordinations (autotransform = FALSE, distance = "Bray", tol = 1e-5, trymax =50). We tried uni-, bi- and tridimensional NMDS and selected the dimension that yielded the highest reduction in stress when comparing to the previous dimension.

We then tested for relationships between the SCN community and forest cover using PERMANOVA (McCune and Grace 2002) and the function adonis(), with Bray-Curtis distance and 1000 permutations for each run (package vegan for R). After determining significant relationships between forest cover and community structure, we plotted that relationships in ordination space with the function ordisurf() (available on package vegan). We calculated the residuals of this relationship by extracting the predicted forest cover from the generalized additive model (GAM) used by ordisurf() and the observed values for each site. We used these residuals to also interpret the potential role of human facilitation on different levels of urbanization, as we compared the predicted forest cover based on the community structure with the actual amount of forest cover of the site.

We also tested for differences in community structure above and below the threshold we found in nesting patterns by native SCN on anthropogenic substrates using Multi-response Permutational Procedure (MRPP, McCune and Grace 2002, available on package vegan). MRPP is a nonparametric technique used to test for differences among groups making no distributional assumptions about the data (such as multivariate normality and homogeneity of variances). We used Bray-Curtis distance (McCune and Grace 2002) with 1000 permutations.

We also looked for evidence of natural facilitation (i.e. by PCNs). To do so, we tested for a relationship between the abundance of PCN and SCN using Log-linear regression (Zar 1999). Our expectation was that PCN abundance should influence SCN abundance in places where nesting sites could be a limiting factor and PCNs are the main provider of such resource (Martin and Eadie 1999).

We conducted all analyses on R v3.1.0 ("Spring Dance") for Mac (R Core Team 2014) using RCommander v 2.1–7 (Fox 2005) and Rstudio v 0.98.1049 (RStudio Team 2014).

Results

Patterns of species presence and richness

Native and non-native cavity nesters responded to the gradient of urbanization in distinct ways. After evaluating different models using AIC (Table 2), we found that PCNs richness was positively associated with forest cover, which was best described with a log-linear relationship (Poisson log-linear, $z = 4.77$, $df = 131$, $p < 0.0001$, Fig. 2a). All five species were present on sites ranging from 16 to 100 % cover, but their presence declined rapidly when forest cover was less than 16 %. As a group, richness of native SCNs peaked at 37 % forest and declined with more or less forest cover (Quadratic regression, $F_{2,130} = 3.71$, $p = 0.027$, Fig. 2b; Table 2 shows alternative models evaluated). Non-native SCNs' richness was negatively related to forest cover (Linear regression, Adj. $R^2 = 0.30$, $F_{1,131} = 58.71$, $p < 0.0001$, Fig. 2c; see Table 2 for alternative models contrasted). Most of the sites with less than 40 % forest cover contained native and non-native species, but non-native species were absent on sites with 90 % or more forest cover. The results for presence at the guild level held for nearly all the individual species (Table 3). Rather than presence of all species decreasing as forest cover increased, native species were typically positively associated forest cover and non-native species were negatively associated with it (Table 3). Exceptions included species known to exploit open areas, or edges between forest and developed lands, such as Black-capped Chickadee (*Poecile atricapillus*) and Northern Flicker (*Colaptes auratus*) that yielded no significant linear relationship with forest cover (Table 3).

Species relative abundance

Relative abundance of different cavity nesting groups showed different responses to the reduction in forest cover. As expected, the average relative abundance of PCN species was lower (mean ± SE, 0.17 ± 0.01 ind/count/year) than the abundance of SCN species (mean ± SE, 3.63 ± 0.17 ind/count/year) across all sites. PCN's relative abundance was not significantly correlated with the percentage remaining forest (Linear regression, Adj, $R^2 = -0.005$, $F_{1,\ 126} = 0.40$, $p = 0.53$, Fig. 2d). However, some PCN species tended to be more abundant on either extreme of the urbanization gradient, while other species peaked at intermediate levels of urbanization. The most abundant PCN species was the Northern Flicker (mean ± SE, 0.11 ± 0.01 individuals/count/year), which was negatively related to forest cover (Table 3, Suppl1c). Hairy Woodpecker (*Picoides villosus*) abundance increased with increasing forest (Table 3, Suppl1b), while Downy (*Picoides pubescens,* Suppl1a) and Pileated Woodpecker (*Dryocopus pileatus,* Suppl1d) abundance peaked at sites with intermediate (ca. 40 %) forest cover.

Although the overall average relative abundance was not statistically different between native and non-native SCNs (1.82 vs. 1.81 ind/count/year, two-tailed paired t-test, $t_{127} = 0.06$, $p = 0.95$), their distributions along the gradient of urbanization were substantially different. Native SCN species showed a non-linear unimodal trend peaking in

Table 2 Alternative models relating richness, abundance and nesting pattern to % forest cover remaining. AIC are relevant to particular test presented. ΔAIC is relative to the best (first listed) model among the candidates

Model	ΔAIC	Relative Likelihood	w_i
Guild richness versus forest cover			
PCN			
Poisson Log-linear	0	1	0.9999
Linear	21.63	2.00E-05	2.00e-05
SCN			
Quadratic	0	1	0.923
Linear	4.97	8.32E-02	7.68E-02
Poisson Log-linear	88.33	6.59E-20	6.08E-20
Non-Native SCN			
Linear	0	1	1
Poisson Log-linear	91.62	1.27E-20	1.27E-20
Guild relative abundance versus forest cover			
SCN			
Quadratic	0	1	0.997
Linear	11.81	0.002	0.002
Average number of nests on anthropogenic substrates			
Native Secondary Cavity Nesting species (except Violet-green Swallow)			
Exponential decay	0	1	0.952
Segmented regression	5.97	5.04E-02	0.048
Multinomial regression (3rd degree)	34.47	3.27E-08	3.11E-08
Quadratic regression	52.71	3.58E-12	3.41E-12
Linear regression	67.64	2.05E-15	1.95E-15

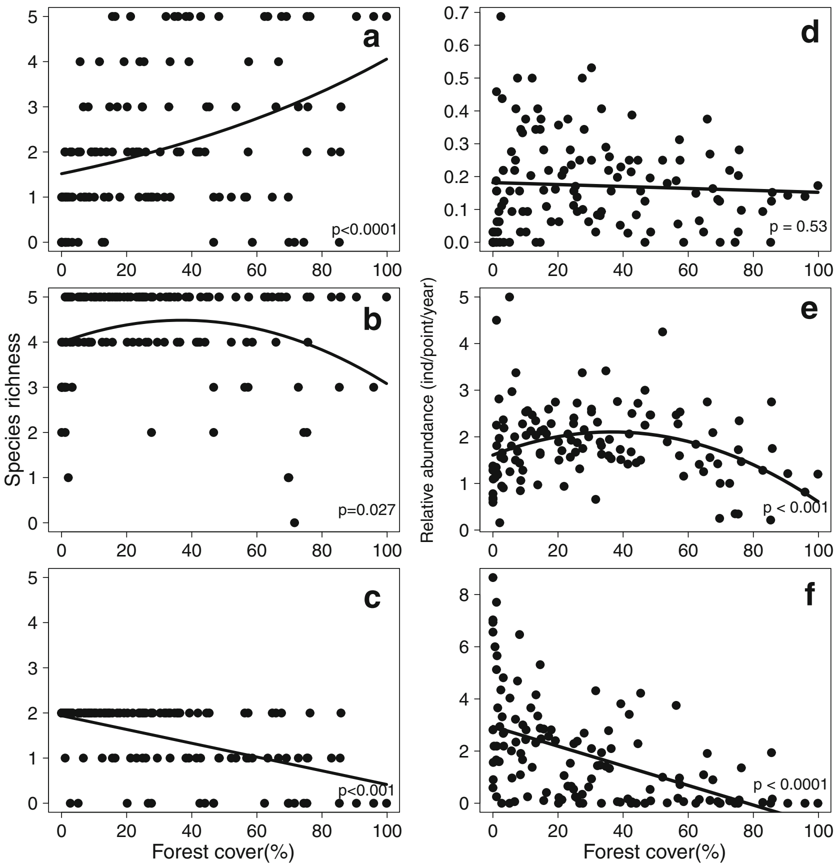

Fig. 2 Species richness and average relative abundance (respectively) by guild along the gradient of urbanization (% forest cover) between 1999 and 2010: primary cavity-nesters (**a** and **d**), native secondary-cavity nesters (**b** and **e**), and non-native secondary-cavity nesters (**c** and **f**). Regression line and significance presented. See "Results" for more details

abundance at ca. 36 % forest cover (Quadratic regression, Adj, $R^2 = 0.095$, $F_{2,\ 125} = 7.68$, $p < 0.001$, Fig. 2e, see Table 2 for alternative models). The abundance of Violet-green Swallows, which peaks at ca. 40 % forest cover, appeared to drive this pattern (Suppl 2e), but we found that the overall trend was robust even when excluding such species (Quadratic regression, Adj, $R^2 = 0.044$, $F_{2,\ 125} = 3.94$, $p = 0.022$). On the other hand, non-native SCN decreased linearly as forest cover increased (Linear regression, Adj, $R^2 = 0.27$, $F_{1,\ 126} = 47.15$, $p < 0.0001$, Fig. 2f). We also found variability in the relative abundance patterns among different SCN species (See Suppl2 and Suppl3). While some native species were more abundant as forest cover increased (e.g. Chestnut-backed Chickadee, *Poecile rufescens*, Table 3, Suppl2c); others decreased (e.g. Black-capped Chickadee, Table 3, Suppl2a). The abundance of both non-native species decreased with increase in forest cover (Table 3, Suppl3).

Nesting patterns

We found a total of 367 nests of both PCNs (*n* = 67 of 5 native species) and SCNs (*n* = 300; 141 of 5 native species, and 159 of 2 non-native species) in natural and anthropogenic substrates (Table 1). Most of the PCN nests were of Hairy Woodpeckers (*n* = 24), Red-breasted Sapsuckers (*Sphyrapicus ruber*, *n* = 18) and Northern Flickers (*n* = 17). Most of the native SCN nests belonged to Chestnut-backed Chickadees (*n* = 49) and Black-capped Chickadees (n = 49), while non-native species' nests were mostly European Starling (*n* = 120).

PCN and SCN species differed in their use of natural and anthropogenic nest substrates. PCNs relied almost exclusively on natural substrates (98.51 %, Table 1), most of them snags (86.57 %, Table 1). The only PCN species that we documented using anthropogenic substrates was the Northern Flicker. We found no PCN nests on sites with less than 6 % forest remaining.

The proportionate use of natural and anthropogenic substrates was significantly different between native and non-native SCNs ($X^2_{38} = 79.64$, p < 0.001). Native SCNs used mostly natural substrates (71.63 %). Most natural nests occurred on snags (58.16 %) and occurred along the entire extent of the gradient of urbanization (Fig. 3a) suggesting little influence of forest cover (Linear regression, $F_{1,\ 28} = 0.21$, $p = 0.65$). We did not find nests in natural substrates if the remaining forest cover was less than 9 % (Fig. 3a).

The number of nests on anthropogenic sites by native SCNs (except for Violet-green Swallow) decreased exponentially with increases of forest cover (Exponential decay model, residual std. error = 0.06, $t_{28} = 9.336$, p < 0.0001), and we

Table 3 Relationship between forest cover and presence and abundance of cavity-nesting bird species studied

Species	Presence vs. Forest cover				Abundance vs. Forest cover				
	Reg. model	Rel.	Z (df = 131)	P	Reg. model	Rel.	Adj. R^2	F or z (df = 127)	P
Primary Cavity Nesting Species (PCN)									
Downy woodpecker (*Picoides pubescens*)	Logit	+	2.411	0.0159	Linear	NS			
Hairy woodpecker (*Picoides villosus*)	Logit	+	5.048	<0.0001	Linear	+	0.22	36.65	<0.0001
Pileated woodpecker (*Dryocopus pileatus*)	Logit	+	3.068	0.0022	Linear	NS			
Red-breasted sapsucker (*Sphyrapicus ruber*)	Logit	+	3.29	<0.0001	Linear	(+)	0.02	3.837	0.0523
Northern flicker (*Colaptes auratus*)	Logit	NS			Linear	-	0.07	11	0.0012
Secondary Cavity Nesting Species (SCN)									
Native species									
Black-capped chickadee (*Poecile atricapillus*)	Logit	NS			Linear	-	0.11	16.61	<0.0001
Chestnut-backed chickadee (*Poecile rufescens*)	Logit	+	2.143	0.0321	Linear	+	0.09	13.88	<0.0003
Bewick's wren (*Thryomanes bewickii*)	Logit	-	3.864	<0.001	Linear	-	0.02	4.144	0.0446
Red-breasted nuthatch (*Sitta canadensis*)	Logit	+	2.605	0.0092	Linear	NS			
Violet-green swallow* (*Tachycineta thalassina*)	Logit	-	2.122	0.0338	Linear	NS			
Exotic Species									
European starling (*Sturnus vulgaris*)	Logit	-	4.075	<0.0001	Linear	-	0.22	37.39	<0.0001
House sparrow (*Passer domesticus*)	Logit	-	5.515	<0.0001	Poisson	-		5.883	<0.0001

found a strong break on the slope of this relationship (Segmented linear regression, Adj. $R^2 = 0.92$, $F_{3,26} = 112.5$, $p < 0.0001$, Fig. 3b, see Table 2 for alternative models evaluated) at 9.45 % forest cover (95%CI: 2.87, 16.04, Fig. 3b). This is, when forest cover was less that 9.45 %, the average number of nests decreased much faster than when forest cover was great than 9.45 %. A more conservative estimate gauging the change in slope of the relationship between use of anthropogenic cavities and forest cover yielded a significant break point at 12.78 % forest cover (Two-sided Davies test, $p < 0.0001$), which we used for subsequent analyses. And although the exponential decay model was more parsimonious than the segmented regression as shown with the AIC analysis (Table 2), the segmented model helped us answer the question of whether there was a shift in trend on this relationship and objectively determine where that threshold was. This cannot be achieved with the exponential decay model given the gradual nature of the decay. We found no significant linear relationship between average number of Violet-green Swallow nests and forest cover (Linear regression, $F_{1,\ 28} = 0.96$, $p = 0.34$). Most of the anthropogenic substrates where native SCNs (all species combined) nested were houses, buildings or other anthropogenic structures. Only 6.38 % of the nests of native SCN were placed in nest boxes. All native SCN species, except for Red-breasted Nuthatch (*Sitta canadensis*), used anthropogenic substrates when forest cover was less than 13 %.

Non-native SCNs placed almost all their nests on anthropogenic substrates (98.11 %, Table 1) with very little use of natural substrates (1.89 %, Table 1). Most (91.82 %) of the nests were placed on houses and buildings (Table 1). Non-native SCNs nested along most of the gradient (3–75 % forest cover remaining) although we found 95 % of these nests on sites with 50 % forest remaining or less (Fig. 3c). We found a tendency for nests of this group to decline with increasing forest cover (Linear regression, $F_{1,\ 28} = 3.541$, $p = 0.07$), however we found no significant break point for this relationship (Two-sided Davies test, $p > 0.85$).

Nesting success

We determined the fate of 58/67 (86.6 %) PCN nests and 296/300 (98.7 %) SCN nests. A large proportion of PCN nests were successful ($n = 48$, 71.64 %). The most common cause of failure in natural nests was eviction by European Starlings (n = 3), followed by abandonment (n = 2) and unknown (n = 2). Other causes of failure include predation (n = 1) and snag falling (n = 1). The only PCN nest we recorded in anthropogenic substrates failed also due to interference from European Starlings (Northern Flicker nest). When looking at SCNs, 266 of the nests were successful (39 native and 146 non-native nests in anthropogenic substrates and 80 native and 1 non-native nest in natural substrates, 88.67 %). In this case, nest success was significantly higher in anthropogenic structures than in natural substrates (94.4 % vs. 81 %, $X_1^2 = 13.03$, $p = 0.0003$), a trend that we also observed when looking at native SCNs in isolation (97.5 % vs. 79.2 %, $X_1^2 = 5.6$, $p = 0.018$). The most frequent cause of failure for SCN in natural nests was predation ($n = 6$),

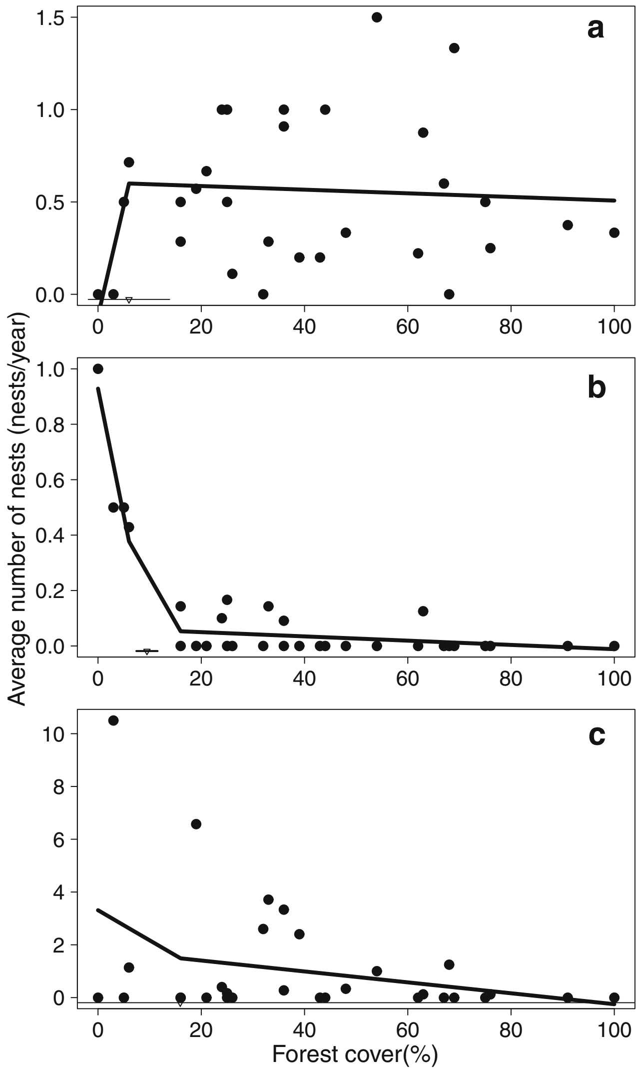

Fig. 3 Relationship (using segmented regression analysis) between average number of nests of cavity nesting birds per site and number of years surveyed and percentage of forest cover remaining along a gradient of urbanization between 1999 and 2010. **a** Native secondary cavity nesting species using natural substrates, (**b**) native secondary cavity nesting species using anthropogenic substrates, (**c**) non-native secondary cavity nesting species using anthropogenic substrates. Inverted triangle represents break point or threshold. See "Results" for more details

followed by unknown cause ($n = 5$) and abandonment ($n = 4$). The remaining 6 nests failed by causes that were observed only once (e.g. construction, logging, etc.). We could not determine the cause of failure for most failed nests in anthropogenic substrates ($n = 9$). When looking at nests in anthropogenic substrates, native SCN species had similar nest success as non-native species did (97.5 % vs. 93.6 %, $X_1^2 = 0.92$, p = 0.34).

Effects on SCN community structure

SCN community structure and composition were significantly related to forest cover (PERMANOVA, $pseudo\text{-}F_{1,\ 126} = 29.11$, $p < 0.001$). Sites on the extremes of the gradient of forest cover were also represented at either end of the ordination space along the x-axis (NMDS, Fig. 4), which reflects their dissimilarities in the structure and composition of their SCN bird community. The nature of the relationship between the SCN community and forest cover changed above 40 %. Below 40 % forest cover there is a non-linear relationship between forest cover and community structure (Fig. 4), however above this threshold there is a clear linear relationship with forest cover as indicated by the parallel isoclines in Fig. 4. In fact, below 40 % forest cover there is wide variation in the composition and structure of the community, reflected by the wide dispersion of sites along the y-axis of ordination space (Fig. 4).

We found a significant difference in the SCN community structure and composition above and below the threshold where native SCNs significantly shift to nest predominantly in anthropogenic substrates (i.e. 12 % forest. MRPP, Within-group chance-corrected agreement A = 0.0677, $p = 0.00099$, Bray-Curtis distance). In fact, the relative importance of each species in the community changed between sites below and above this threshold (Fig. 5). For example, European Starlings dominated the community on sites below 12 % followed by House Sparrow and all the native species decreasing their dominance in a linear fashion, while sites above 12 % of forest remaining were dominated by Chestnut-backed Chickadees, Violet-green Swallows, European Starlings and Black-capped Chickadees to a similar degree. Examining the location of sites in ordination space and their relationship with forest cover, we found that 61.4 % of the sites below 12 % forest where predicted to have more than 12 % forest, which means that the structure and composition of these sites was more similar to sites with more forest than what they actually had. On the other hand, only 5.95 % of the sites above 12 % forest were predicted to have less forest than that, which suggests that the community of those sites have deteriorated to be similar to sites with less forest. In fact, those individual sites had higher abundance of non-native SCN than native SCNs (average ± SE native/non-native abundance ratio of those sites was 0.35 ± 0.068, while the rest of the sites above 12 % forest had an average native/exotic abundance ratio of 9.78 ± 2.302). Sites below 12 % had an average native/non-native ratio of 2.06 ± 0.871.

Finally, we found a significant positive relationship between the abundance of PCN species and the abundance of native SCN species on sites above 12 % forest (Log-linear regression, Adj. $R^2 = 0.1387$, $F_{1,\ 82} = 14.37$, $p < 0.0003$). However, this relationship did not hold for sites below 12 % forest (Log-linear regression, Adj. $R^2 = 0.042$, $F_{1,\ 42} = 2.88$, $p = 0.10$).

Discussion

Facilitation was prevalent in our system. As expected, woodpeckers (PCNs) facilitated native SCN species (Martin and

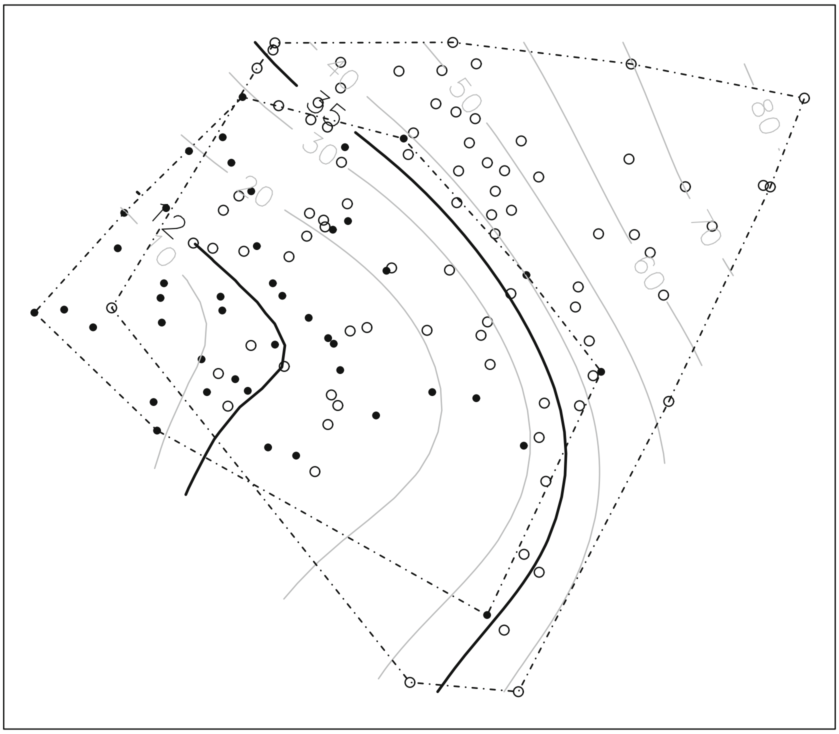

Fig. 4 Non-metric multidimensional scaling representation of the secondary cavity-nesting bird community along a gradient of urbanization between 1999 and 2010. *Open circles* represent sites that have 12 % forest cover or higher. *Black circles* represent sites with less than 12 % forest cover. Isoclines represent relationship between community structure and composition and forest cover

Eadie 1999) on sites with moderate to low levels of urbanization (specifically >12 % forest cover where snag abundance also increases; Blewett and Marzluff 2005), as suggested by the strong and positive correlation between the abundance of both groups. In addition, as urbanization increases (reducing forest cover to levels below 12 %), key nesting resources required by cavity nesting species are commonly lost (Blewett and Marzluff 2005; Harper et al. 2005; Davis et al. 2014; LaMontagne et al. 2015) and we found that in these more urban sites facilitation by humans enabled some native SCN species to overcome reductions in forest and natural cavities, by switching to nest on anthropogenic substrates. This anthropogenic facilitation reduced the dependence of SCNs on their natural facilitators in areas of moderate to extreme urbanization, as expected by the stress-gradient hypothesis (Bertness and Callaway 1994). This shift is especially important, as PCNs species started to disappear on sites with less than 16 % forest cover, which combined with the lack of snags could have jeopardized the persistence of native SCN species in urban settings. By taking advantage of the direct, and especially indirect, nesting opportunities provided by humans (Clucas et al. 2011), the composition and structure of the secondary cavity-nesting bird community changed and diversity was maintained in and beyond highly urbanized areas, as shown by richness, abundance, nesting and community structure data. The fact that ca. 60 % of the sites with less than 12 % forest had a SCN bird community that was typical of sites greater forest cover (as seen on Fig. 4) is a strong indication that native species were present on sites where the may not have been without human facilitation.

Our finding that PCN and SCN diversity did not change in a linear fashion along a gradient of urbanization, contrasts with previous findings that cavity nesting bird species richness significantly increases with forest cover (DeGraaf and Wentworth 1986; Tilghman 1987; Pidgeon et al. 2007). It is important to note that these studies analyzed PCN and SCN species together, which may obscure the guild-specific trends we report, especially because we found that people rarely provide direct nesting opportunities for PCN species (in contrast with SCN species which can use nest boxes) and they were less likely to take advantage of indirect anthropogenic nesting opportunities than SCN species, with the exception of the Northern Flicker. This adaptable woodpecker was the most abundant PCN, especially in high levels of urbanization where parks were present. This is not surprising as flickers are known to exploit open areas for foraging on the ground (Moulton and Adams 1991; Elchuk and Wiebe 2003; Wiebe and Moore 2008), and while a completely urbanized site would be unsuitable, it is favored in areas were both trees and lawns are available (e.g. parks, Tilghman 1987; Morrison and Chapman 2005). Although this species seems to have many tools to deal with the changes in the habitat due to urbanization, it also faces other challenges, such as competition with European Starlings (Ingold 1994; Ingold 1996; Fisher and Wiebe 2006).

European Starlings dominated the SCN community on the most urban sites (less than 12 % forest remaining) and

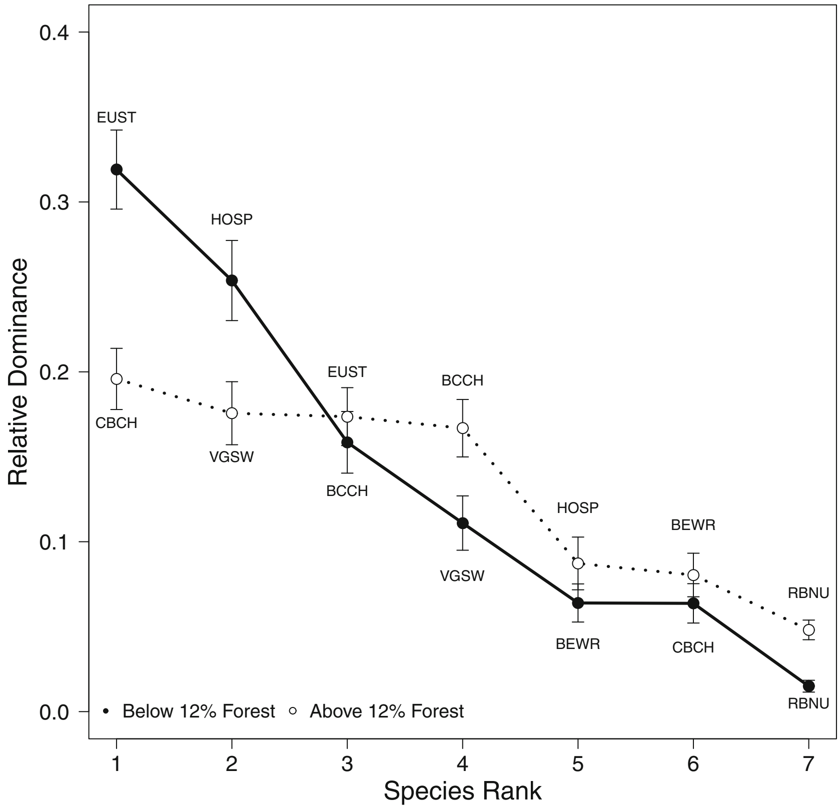

Fig. 5 Relative dominance of secondary cavity-nesting birds on sites along a gradient of urbanization between 1999 and 2010. Species (on alphabetical order): BCCH: Black-capped Chickadee, BEWR: Bewick's Wren, CBCH: Chestnut-backed Chickadee, EUSP: European Starling, HOSP: House Sparrow, RBNU: Red-breasted Nuthatch, VGSW: Violet-green Swallow. Scientific names presented on text

declined in abundance swiftly as forest cover increased. They caused nest failures among Northern Flickers (3 out of 8 failures) and Red-breasted Sapsuckers (2 out of 3 failures), but we found no evidence of competition with native SCN. Our sample size of nest failure is not large enough to make population-wide inference on the consequences of European Starlings on these species, but the pattern we found aligns with findings that Red-breasted Sapsuckers may be experiencing population reductions due to European Starlings, while the effects on Northern Flickers and SCNs are less pronounced country-wide (Koenig 2003). On the other hand, House Sparrows did not threaten nesting success among the species we studied. In fact, it seemed that both non-native SCN species were somehow constrained to areas with human presence, which is not unexpected (McKinney 2002; Blair 2004), but the fact that even when these non-native species ventured into forested settings they rarely nested in natural substrates, was surprising.

Native SCNs had higher nesting success in anthropogenic than in natural substrates suggesting lower predation and competition pressure when nesting on these novel substrates. It has been suggested that urban areas may have fewer native predators than natural areas (Adams 1994) potentially making them "safe zones" for nesting (Gering and Blair 1999). While it is often true that some natural predators are lost to urbanization (especially large species), other smaller generalist species like coyotes (*Canis latrans*), raccoons (*Procyon lotor*) or raptors (e.g. Cooper's Hawk, *Accipiter cooperii* and Barred Owl, *Strix varia*) may thrive in urbanized areas (DeStefano and DeGraaf 2003; Chace and Walsh 2006; Rullman and Marzluff 2014), and even free-ranging domestic animals, like cats (*Felis catus*) may result in significantly high rates of predation (Loss et al. 2013). So, although this "safe nesting zone" hypothesis has not been supported for open-nesters (Jokimäki et al. 2005), which may suffer greater nest predation due to high densities of corvids and sciurids in urban areas (Marzluff et al. 2007), nests in cavities are known to be safer than open-cup nests against predation (Martin and Li 1992). And, while urban areas may harbor a wide assemblage of predators (Haskell et al. 2001; Rullman and Marzluff 2014), these hunters may not have developed a reliable search image for anthropogenic nests or those nests may be hard to access.

Cavity-nesting bird abundance (lumping PCN and SCN) has been documented to decrease from natural areas into urban areas (DeGraaf and Wentworth 1986; Tilghman 1987; Blair and Johnson 2008). We found that the abundance of PCN and SCN species responded differently along the gradient, and analyzed them accordingly. SCN abundance is typically reduced in urban areas compared to natural areas as some sensitive species are lost (Blair 1996; Blair and Johnson 2008) and/or key resources are reduced (e.g. snags, Blewett and Marzluff 2005; Harper et al. 2005; Blair and Johnson 2008; Davis et al. 2014; LaMontagne et al. 2015). In our case, we did not observe a linear reduction in the abundance of native SCN, but rather a non-linear trend. This contrasted with the pattern we found for PCN, where the overall pattern was mostly driven by the abundance of Northern Flicker, the most abundant in the group; and for non-native SCN, where both species had similar abundances, but their responses to urbanization were the same. In the case of native SCN, most species had similar levels of abundance (except for the Red-breasted Nuthatch that had between half to a fifth of the average abundance of the other species), but had their peaks of abundance on different areas of the gradient. And thus, adding their abundances resulted on the hump-shaped pattern we observed.

The hump-shaped pattern of diversity along an urbanization gradient is not unexpected (Marzluff 2005). It could be the result of several factors (Graham and Duda 2011), which are not limited to: a) habitat heterogeneity found at medium levels of urbanization promotes the coexistence of synanthropic species along with early successional (e.g. Black-capped Chickadee and Bewick's Wren, (Marzluff 2005) and forest specialists species (e.g. Chestnut-backed Chickadee, Marzluff 2005), where factors such as development age, exotic shrub cover, urban land cover, and forest aggregation that affect different species in different degrees (Donnelly and Marzluff 2006) occur in different levels in close proximity; b) dynamic disturbances at intermediate levels of urbanization, which are characteristic of development (Marzluff et al. 2015), also promote the coexistence of competing species by changing habitat conditions and reducing the chance of competitive exclusion, as predicted by the Intermediate Disturbance Hypothesis (Connell 1978); c) overlap of human and PCN facilitation may augment the number of nesting sites or other resources, although we found no evidence of additive effects on the provision of nest sites where we found the peak of abundance, other forms of human facilitation (e.g. bird feeders) may have a direct contribution to the abundance of birds (Fuller et al. 2008; Robb et al. 2008) and may have a larger influence in suburban areas in Seattle (Clucas et al. 2011; Clucas and Marzluff 2012); and/or d) reduced predation pressure regulating the cavity nester population. The first three alternatives seem reasonable, but the last seems least likely as our study sites harbor a rich community of avian predators (Marzluff et al. 2007; Rullman and Marzluff 2014).

Conservation implications

In cities and their suburbs, the combination of natural resources and human subsidies may produce unexpected outcomes from the conservation perspective. In fact, urban and suburban areas are rarely conceived of as a place to practice species conservation despite their biological and social importance (Marzluff 2002; Miller and Hobbs 2002). Our data suggest that conservation can be successful in urban areas because some native species that are sensitive to habitat degradation, such as cavity-nesting birds, can use resources provided by humans (directly or indirectly). Although we only quantified a partial aspect of this facilitation (provision of nesting sites), there is evidence that the presence and success of native SCNs may also influenced by other forms of human facilitation, such as provision of food (Clucas and Marzluff 2012).

The importance of positive interactions in ecological communities may profoundly affect our understanding of nature, even changing our approach to how ecological communities are structured, how species niches and important resources are defined, and where species conservation efforts should be focused (Bruno et al. 2003; Butterfield 2009). Our study adds to the increasing realization that humans not only destroy ecological function, they can also actively facilitate it (Marzluff 2014). Broadening our facilitory role may improve the conservation of biological diversity in an increasingly urban world.

Acknowledgments Tina (Rohila) Blewett, Heather Cornell, Roarke Donnelly, Laura Farwell, Cara Ianni, David Oleyar, Stan Rullman, Thomas Unfried, Kara Whittaker, Sean Williams, and John Withey (among many others) helped collect the data we present. Jon Bakker, Carol Bogezi, Jack DeLap, Michael Heimbuch, Joshua Lawler, Loma Pendergraft, Martin Raphael, Kaeli Swift, and Lauren Walker provided invaluable comments to improve this manuscript. This research was funded by U.S. National Science Foundation (DEB-9875041, IGERT-0114351, BCS 0120024, and BCS 0508002). JAT was partially funded by a Fulbright-Conicyt scholarship and by the School of Environmental and Forest Sciences scholarship.

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Chapter 2

Pileated Woodpecker Suburban Ecology

RESEARCH ARTICLE

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

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ABSTRACT

Urban areas have expanded as more and more people live within cities, which now contain more than half the world's population. As cities grow, natural habitat is transformed changing the face of the local biota and the resources available for it. We studied how a purported sensitive species, the Pileated Woodpecker (*Dryocopus pileatus*), adapts to rapid and extensive land-cover change as urbanization reduces and isolates forest. From 2009 – 2013, we used radio-telemetry to determine the annual home range size and habitat use of 17 individuals in 9 suburbs that varied in their level of urbanization (ranging 5 – 90% forest remaining). We used Concentration of Use and Resource Utilization Functions to examine vegetative characteristics used by woodpeckers at the landscape (i.e. 1 km^2) and local (i.e. 1/3 ha) levels. The average suburban woodpecker home range was significantly smaller than expected based on latitude. Pileated woodpeckers significantly concentrated their use of the landscape on native forest (coniferous and deciduous), as well as light and medium urbanized areas. Highly urbanized areas were seldom used. Resource use was highest along edges between forest and light and medium urbanized areas, and in forests with increasing mean diameter of dominant hardwood species. Our results not only indicate the adaptability of a species that has traditionally been considered a mature forest specialist, but they also suggest that maintaining forest cover above 20%, retaining large deciduous trees and snags in public green spaces and yards, and providing feeders would improve the biodiversity of suburban areas.

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

INTRODUCTION

More than half of the world's population now lives in cities (United Nations 2008) and around 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 population increases (Blair 2004, Aronson et al. 2014), this massive increase in urban population is resulting in an unprecedented rate of urban area expansion (Cohen 2006). As an example, projections indicate that the USA could face a 79% increase in urban land cover between 2000 and 2025, potentially reaching 9.2% of the area of the lower 48 states (range: 6.9 – 12.1%, Alig et al. 2004) while the proportion of urban people slowly increases from 75% (1990) to 81% (2014) and potentially to 87% (2050, United Nations 2014).

Urbanization and the sprawl of cities are very complex and dynamic processes. They not only change vegetation composition, quantity and structure (Donnelly and Marzluff 2006), but also micro-climatic conditions, biotic interactions (e.g., increasing predation by domestic animals, competition with exotic species, and transmission of diseases, Chace and Walsh 2006, Endlicher 2011), and connectivity within and between surrounding natural areas (Fernández-Juricic 2000). These changed conditions usually produce a gradient of land cover between natural and urbanized areas (urban-wildland or urban-rural gradient, Blair 1996) where habitats are increasingly less modified the farther they reside 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 maybe retained or incorporated by developers, planners, managers or residents (Aronson et al. 2014). This, in conjunction with factors such as altered disturbance regimes (Chace and Walsh 2006) and supplemental food and water (Robb et al. 2008, Clucas and Marzluff 2011) create novel habitat conditions for wildlife and plants that bring challenges and opportunities that will favor species with the ability to adapt to them (Kowarik 2011) and extirpate those that cannot (Marzluff 2014).

In fact, changes wrought by urbanization may have profound effects on bird communities (Er et al. 2005, Chace and Walsh 2006). In general, there is consensus that highly urbanized bird communities are less diverse (typically dominated by few human-adapted species) and they can 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). At the urban cores, bird communities are normally dominated by generalist species (either native or exotic) that are able to cope with the significant changes in habitat conditions and resources (Sol et al. 2014). Similarities among urban cores around the world are resulting in a small homogenous set of species being favored (Blair 2001, McKinney 2006, Shanahan et al. 2014). Moreover, specialist species may not adapt to these novel environmental conditions, resulting in their decline and eventually their local extirpation (Farwell and Marzluff 2013).

Suburban areas represent a middle level of urbanization, where elements of urban areas and natural areas occur in close proximity and interact. Suburban areas normally offer a wide variety of conditions (e.g., housing, roads, lawns, native vegetation, riparian areas, among others) which, in temperate climes, supports a higher number of species than either end of the urban-wildland gradient (Blair 1996, Hansen et al. 2005, Marzluff 2005, Tratalos et al. 2007, Blair and Johnson 2008, Pennington and Blair 2012, Shanahan et al. 2014). This pattern is consistent with the

Intermediate Disturbance Hypothesis (Connell 1978) resulting when colonization and extinction of species depends on affinity to urban conditions (Marzluff 2005, Marzluff et al. 2016) and their disturbance regimes (Chace and Walsh 2006).

Many woodpecker species are habitat specialists and, as with many other cavity nesting birds, their presence and abundance 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 (Martin and Eadie 1999, Aubry and Raley 2002) potentially amplifying the negative effects onto the biological communities present in areas that undergo urban development (Morrison and Chapman 2005).

Puzzled by the question of whether a specialist species with such influence in the ecological community as a woodpecker may be able to adapt and succeed in a novel environment, we studied the Pileated Woodpecker (*Dryocopus pileatus*) in suburban areas around Seattle, WA, USA. Being a forest specialist and with preference for mature and old-growth forest (Bull and Jackson 2011), we expected this species to be negatively affected by habitat changes promulgated by urbanization. Given the history of recent extinctions of large woodpecker species in North America (e.g., Ivory-billed Woodpecker, *Campephilus principalis* and Imperial Woodpecker, *Campephilus imperialis*) we were interested in the potential challenges that urban sprawl could pose on the largest woodpecker remaining in the region. We tested whether

Pileated Woodpeckers made differential use of the land-cover types present in suburban areas around Seattle, and characterized their home range size and composition.

METHODS

Focal Species

The Pileated woodpecker occupies expansive home ranges (Renken and Wiggers 1989, Mellen et al. 1992, Bull and Holthausen 1993, Bonar 2001) and facilitates a large number of other species by providing nesting and roosting opportunities with the cavities it creates (Raley and Aubry 2006). This species 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 30cm in DBH (diameter at breast height, Mellen et al. 1992, Renken and Wiggers 1993). 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 Woodpeckers' density is positively associated with percentage forest remaining (at a 1 km^2 scale) in urbanizing landscapes, and their densities in suburban areas can be 8 times lower than in natural areas (Blewett and Marzluff 2005). To our knowledge, there is no information on suburban home range size and habitat use on this species.

Study Area

We monitored woodpeckers in 9 sites occupying 3 general areas along the urban-wildland gradient in the Greater Seattle, WA, USA area (47.61ºN, 122.33ºW, 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 three areas were similar in terms of percentage of deciduous forest; while 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 light or medium urban areas) than the other two general areas (Table 1). The sites found on these areas are representative of different levels and configurations forest remaining (ranging from 5–90% at the 1 km^2 scale, Hepinstall et al. 2008), which we used as a proxy for urbanization level.

Historically, Western Washington was prominently a forested land. Old-growth forests in the lowlands of Western Washington were dominated by western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*) and, as a subclimax species, Douglas-fir (*Pseudotsuga menziesii*, Franklin and Dyrness 1988). Hardwoods species were not common, except on recently disturbed sites and/or riparian areas, where big leaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), and black cottonwood (*Populus trichocarpa*) were the most prevalent tree species (Franklin and Dyrness 1988). However, these forests have undergone rapid change in the last ~170 years. As Anglo settlers colonized the area in the mid 1800s, the forest that was dominated by coniferous species was logged, regrew and logged again for ~100 years (Cuo et al. 2009). In the last few decades these changes were accentuated and accelerated as populated areas

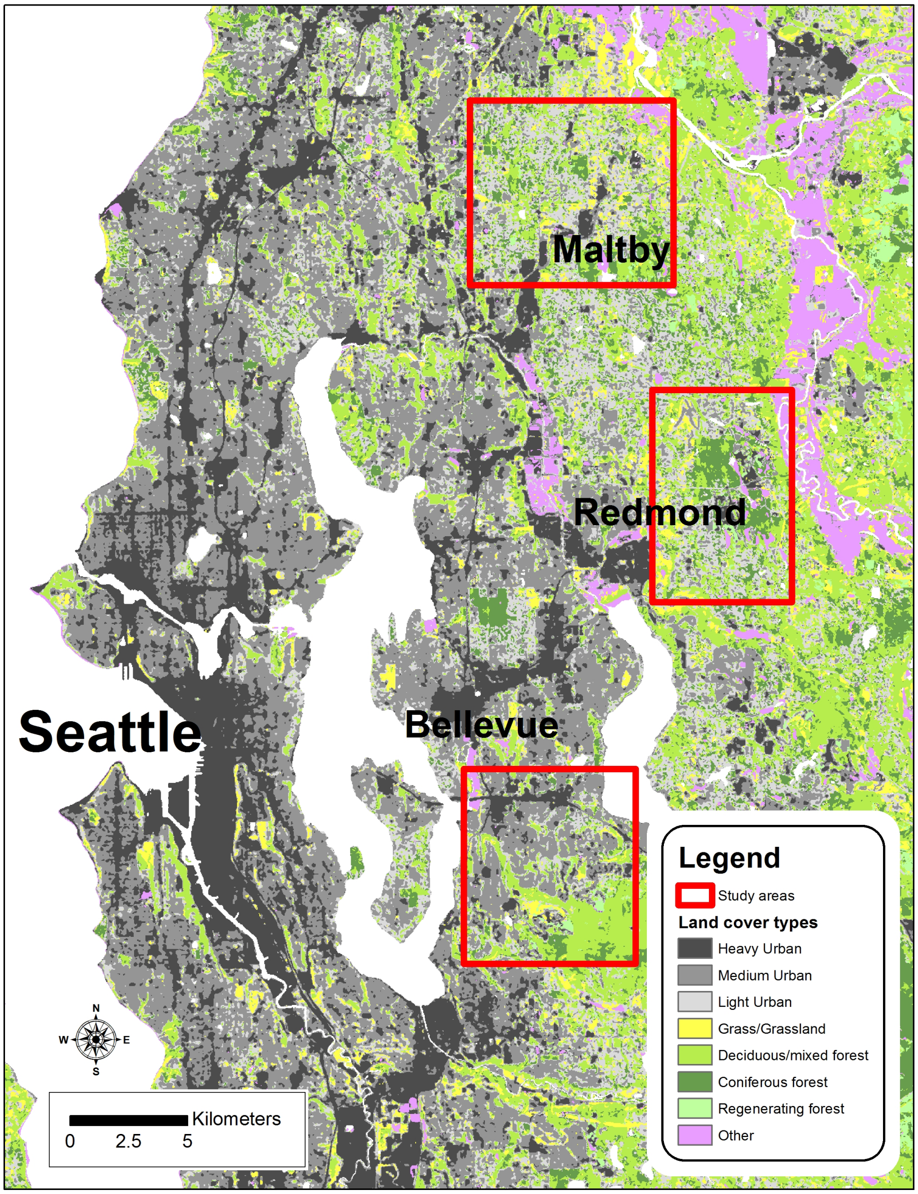

Figure 1. Study area on the Greater Seattle, WA. Land cover types are indicated according to Alberti et al. (2006).

Table 1. Characterization of the three main areas where we conducted this study. Land cover types are defined on the methods and contrast-weighted edge density quantifies the amount of edge between forested and medium and light urban areas.

Land cover type	Total area in ha (percentage)			Contrast-weighted Edge Density		
	Maltby	Redmond	Bellevue	Maltby	Redmond	Bellevue
Native forest/woodlands						
Coniferous forest	965.43 (14.17)	308.43 (5.05)	932.04 (17.23)	24.97	7.91	23.71
Deciduous/Mixed forest	1455.75 (21.37)	1475.46 (24.16)	1309.86 (24.22)	43.18	27.83	38.97
Regenerating forest	159.93 (2.35)	124.02 (2.03)	119.97 (2.22)	N/A	N/A	N/A
Clearcut forest	1.35 (0.02)	1.17 (0.02)	10.26 (0.19)	N/A	N/A	N/A
Urbanized lands						
Light Urban	2333.52 (34.26)	873.45 (14.30)	1517.40 (28.05)	63.54	29.49	57.54
Medium Urban	786.24 (11.54)	2153.07 (35.25)	581.04 (10.74)	4.61	6.25	5.14
Heavy Urban	315.81 (4.64)	589.95 (9.66)	153.45 (2.84)	N/A	N/A	N/A
Cleared for Development	1.62 (0.02)	0.72 (0.01)	6.12 (0.11)	N/A	N/A	N/A
Other						
Grass/grassland	538.02 (7.90)	207.81 (3.40)	414.36 (7.66)	N/A	N/A	N/A
Agriculture	117.99 (1.73)	2.43 (0.04)	145.71 (2.69)	N/A	N/A	N/A
Non-forested wetlands	70.47 (1.03)	52.56 (0.86)	123.39 (2.28)	N/A	N/A	N/A
Open water	65.97 (0.97)	318.69 (5.22)	95.22 (1.76)	N/A	N/A	N/A
Snow/bare rock	0 (0)	0.09 (0.00)	0 (0)	N/A	N/A	N/A
Grand Total	6812.1 (100)	6107.85 (100)	5408.82 (100)	136.31	71.49	125.36

expanded and transformed the land cover from forest to urban and suburban areas (MacLean and Bolsinger 1997, Alberti et al. 2004). Projections indicate this trend will continue and that more land will be transformed into some level of urban use (Hepinstall et al. 2008). This has affected the amount, composition and structure of the forests in the general area (Donnelly and Marzluff 2006), where mostly early successional species (mostly the hardwoods described above and Douglas-fir) dominate urban and suburban forests, changing the composition and structure of the biological communities present in the area (Gavareski 1976).

Radio-telemetry, Home Range Estimation And Habitat Use

We trapped year-round using mist-nets and playback (York et al. 1998) and used a decoy to increase responsiveness of woodpeckers. We also trapped close to suet feeders (present in neighborhoods at the study sites) during fall and winter when the birds were harder to attract using playback. Once we trapped a bird, we banded it, fitted a radio-tag (model A1250 from Advanced Telemetry Systems, Isanti, Minnesota, USA; expected battery life 12 months) using a Teflon backpack harness modified from (Buehler et al. 1995). We used 2mm wide copper rings to secure the harness. Transmitter plus harness weighed 11.5g, which is less than 5% of the weight of an adult Pileated Woodpecker. We released the birds back to the same area where we captured them. Our processing time was typically ~30–45 minutes. We used a R-1000 telemetry receiver (Communications Specialists, Orange, California, USA) and a hand-held 3-element Yagi antenna to relocate each radio-tagged bird opportunistically, aiming to have at least one location per week. Two birds dropped their transmitters, but we recaptured them (after 69 and 174 days) and replaced the transmitter. Both sexes participated on territorial defense, which allowed us to capture a similar number of males and females.

We recorded relocations of each bird on custom-made field-sheet maps based on current aerial photographs available online (Google Maps, Google Inc., Mountain View, CA) at approximately a 1:10000 scale. In cases when the location was not obvious from the map, we used a GPS to mark a reference point (GPSmap 60CSx, Garmin, Olathe, Kansas, USA) and we measured distance and bearing to the woodpecker location with a laser rangefinder (TruPulse 360B, Laser Technologies, Centennial, Colorado, USA). We then mapped all the locations using ArcGIS (9.x and 10.x, ESRI Redlands, California, USA).

Based on these relocations, we estimated home range using two different techniques. First, we used minimum convex polygon (MCP) to compare with other studies that have calculated Pileated woodpecker's home ranges. Second, we used fixed-kernel estimation (KDE, Worton 1989) to more accurately estimate the areas used by the woodpeckers, and the differential use of areas within the home range by constructing a utilization distribution (UD, Marzluff et al. 2004). The utilization distribution 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 correlation between sample size and MCP home range size (Linear regression, $F_{1,10} = 4.69$, $P = 0.06$), however we found no such relationship for our KDE home ranges (Linear regression, $F_{1,10} = 0.77$, $P = 0.40$), which indicates that our sampling effort was sufficient to estimate home range using this technique, and that the number of locations did not affect out KDE.

Then, we related different degrees of use (UD) to habitat characteristics using two approaches: concentration of use (Neatherlin and Marzluff 2004) to characterize the use of different land cover types related to their presence on each home range, and resource utilization functions (hereafter RUF, 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 on each cover type and the occurrence of each land cover type within the home range (Neatherlin and Marzluff 2004) and it is analogous to other selectivity measures that relate use to occurrence (see Neatherlin and Marzluff 2004 for more details). We used classified 30m resolution land cover data based on 2007 Landsat TM satellite imagery classified on 14 habitat categories (heavy urban, medium urban, light urban, cleared for development, grass/grassland, deciduous and mixed forests, coniferous forests, clear-cut forest, regenerating forest, agriculture, non-forested wetlands, open water, snow/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 30m 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 combining remote sensing imagery and plot sampling. Based on previous publications concerning Pileated Woodpecker ecology, we expected woodpeckers to concentrate their use in areas with high quadratic mean

Table 2. Land cover types that were used on this study as defined by Alberti et al. (2006)

Land cover type	Definition
Heavy Urban	>80% impervious area
Medium Urban	50-80% impervious area
Light Urban	20-50% impervious area
Grass/Grassland	Developed grass or grassland
Deciduous/mixed forest	10-80% deciduous or mixed forest
Coniferous forest	>80% coniferous forest
Clearcut forest	Recent clearcut area
Regenerating forest	Regenerating forest
Agriculture	Row crops and pastures
Other	Non-forested wetlands, open water, shorelines, bare rock/snow

diameter of dominant conifers, high quadratic mean diameter of dominant hardwoods, high volume of snags over 25cm in DBH, and high volume of down wood over 25cm in DBH. We also included a metric of edge to explore the significance of the forest-urban interface. To do so, we calculated contrast-weighted edge density using a 50m moving window in Fragstats (McGarigal et al. 2012) where edge between forest (either coniferous, broadleaved or mixed) and light and medium urban areas. We preferred 50m in order to have a fine-enough scale to capture edges that are highly contrasted between these land-cover types. We assessed differences in relative use within often-used land covers (i.e. coniferous and deciduous forest, light and medium urbanized) by selecting only the locations found on these land cove types. We set the RUFs to randomly select a subsample of 1000 pixels within those land cover types (all combined). It has been suggested that use should be transformed before conducting a RUF analysis to prevent violations of the assumptions of homoscedasticity and normality of the residuals of a multiple regression (Johnston 2013). However, when we graphically explored the residuals of our models and we did not encounter such problems, so we analyzed raw values of use. We obtained one un-standardized 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 (standard and un-standardized) values 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 on different groups) and used the standard error of this sample of coefficients to construct the 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 in R (Handcock 2011).

We used linear regression to compare the mean size of the home range of the woodpeckers in our area with other studies along a latitudinal gradient. We used ANOVA and Tukey tests to determine whether there were differences among concentration of use and where those differences were significant.

RESULTS

We captured 16 Pileated Woodpeckers (9 adult males, 7 adult females) between 2009 and 2012. We radio-tracked these birds for an average of 10.8 ± 1.17 months (11/17 were followed for more than 11.5 months) and obtained an average of 78 ± 12 locations per bird. 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. In fact, Ruder et al. (2012), Noel et al. (2013) reported high mortality rates (12/34 birds) where 11/12 birds died within 12 days of capture (8.2 days on average). We found that the four birds that died in our study lived between 104 and 353 days after capture (211 ± 57.76 days). Also, we did not notice any effect of transmitters on reproduction. Even when females carried the transmitter, the antenna did not preclude them from incubating and raising young.

Home Range Estimations And Habitat Use

The average MCP home range size was 180 ± 31.4 ha (*n* = 12). Using the fixed-kernel density estimation (KDE), the average home range size was 277 ± 37.0 ha (*n* = 12, 99% KDE). For the remainder of this paper, we only present results from adult males (*n* = 9) as female home ranges were correlated with their mate's ranges (Tomasevic and Marzluff, unpubl. data, see Ch. 4). In fact males used 73.29% of the females' home ranges (range: 51.42 – 93.27%, *n* = 3), while females used 61.65% (range: 53.34 – 71.16%, *n* = 3) of the male's home ranges. They shared an average 52.2% (range: 45.96 – 56.28%, *n* = 3) of the volume under the UD (Tomasevic and Marzluff, unpubl. data, see Ch. 4).

Home ranges of suburban male woodpeckers were not constrained to forested areas and the composition of their home ranges encompassed a mix of land covers (Table 3). On average, slightly over half of the average home range included some degree of urbanized land (55.05%, including light, medium and high urban); close to a third of the area was forested (29.88%); only 4.94% was grassland (where trees and snags were present) and 0.18% included other land cover types (i.e. non-forested wetlands, open water, bare rock and clear cut forest). However, woodpeckers used their habitat differently across these land cover types (ANOVA, $F_{6, 56}$ =2.67, *P* = 0.02, Figure 2). They concentrated their use in forested areas (coniferous, Tukey test, Difference = 33.42, t_8 = -3.14, *P* = 0.04 and deciduous, Tukey test, Difference = 37.55, t_8= -3.53, *P* = 0.01) more than in heavy urbanized areas.

Table 3. Home range composition for adult male Pileated Woodpeckers. We present Area in hectares and percentage on parenthesis. Other land cover types include: non-forested wetlands, agriculture, clearcut forest, cleared for development, shorelines, open water and bare rock/snow.

	Land cover type								
Bird ID	Coniferous forest	Deciduous / mixed forest	Regenerating forest	Grass / Grassland	Light Urban	Medium Urban	Heavy Urban	Other	Total
574-47010	39.15 (18.32)	29.52 (13.82)	5.31 (2.49)	17.28 (8.09)	98.64 (46.17)	23.13 (10.83)	0.54 (0.25)	0.09 (0)	213.66 (100)
574-47012	11.7 (4.62)	18.81 (7.42)	1.98 (0.78)	2.61 (1.03)	52.11 (20.56)	147.51 (58.2)	18.63 (7.35)	0.09 (0)	253.44 (100)
574-47016	25.11 (12.75)	48.96 (24.86)	20.61 (10.47)	3.96 (2.01)	56.61 (28.75)	20.07 (10.19)	3.15 (1.6)	18.45 (0.09)	196.92 (100)
574-47017	85.41 (14.32)	88.02 (14.76)	17.55 (2.94)	58.59 (9.83)	242.55 (40.68)	88.65 (14.87)	15.03 (2.52)	0.45 (0)	596.25 (100)
574-47018	1.26 (0.48)	42.03 (16.16)	4.32 (1.66)	2.79 (1.07)	49.77 (19.13)	155.7 (59.86)	4.23 (1.63)	0 (0)	260.1 (100)
574-47021	4.86 (1.15)	157.68 (37.31)	39.06 (9.24)	22.14 (5.24)	68.13 (16.12)	102.69 (24.3)	27.27 (6.45)	0.81 (0)	422.64 (100)
574-47022	12.15 (5.1)	31.59 (13.27)	1.62 (0.68)	28.26 (11.87)	100.89 (42.38)	31.05 (13.04)	31.86 (13.38)	0.63 (0)	238.05 (100)
574-47028	70.11 (44.69)	40.5 (25.82)	0.54 (0.34)	7.65 (4.88)	28.53 (18.19)	7.65 (4.88)	0.18 (0.11)	1.71 (0.01)	156.87 (100)
574-47029	210.15 (44.44)	83.43 (17.64)	9.45 (2)	2.07 (0.44)	62.55 (13.23)	50.58 (10.7)	47.34 (10.01)	7.29 (1.54)	472.9 (100)
Average	51.1 (16.21)	60.06 (19.01)	11.16 (3.4)	16.15 (4.94)	84.42 (27.25)	69.67 (22.99)	16.47 (4.81)	3.28 (0.18)	312.31 (100)
SE	66.47 (17.18)	43.49 (8.93)	12.65 (3.77)	18.59 (4.2)	63.6 (12.66)	56.17 (21.08)	16.43 (4.72)	6.13 (0.51)	148.95 (0)

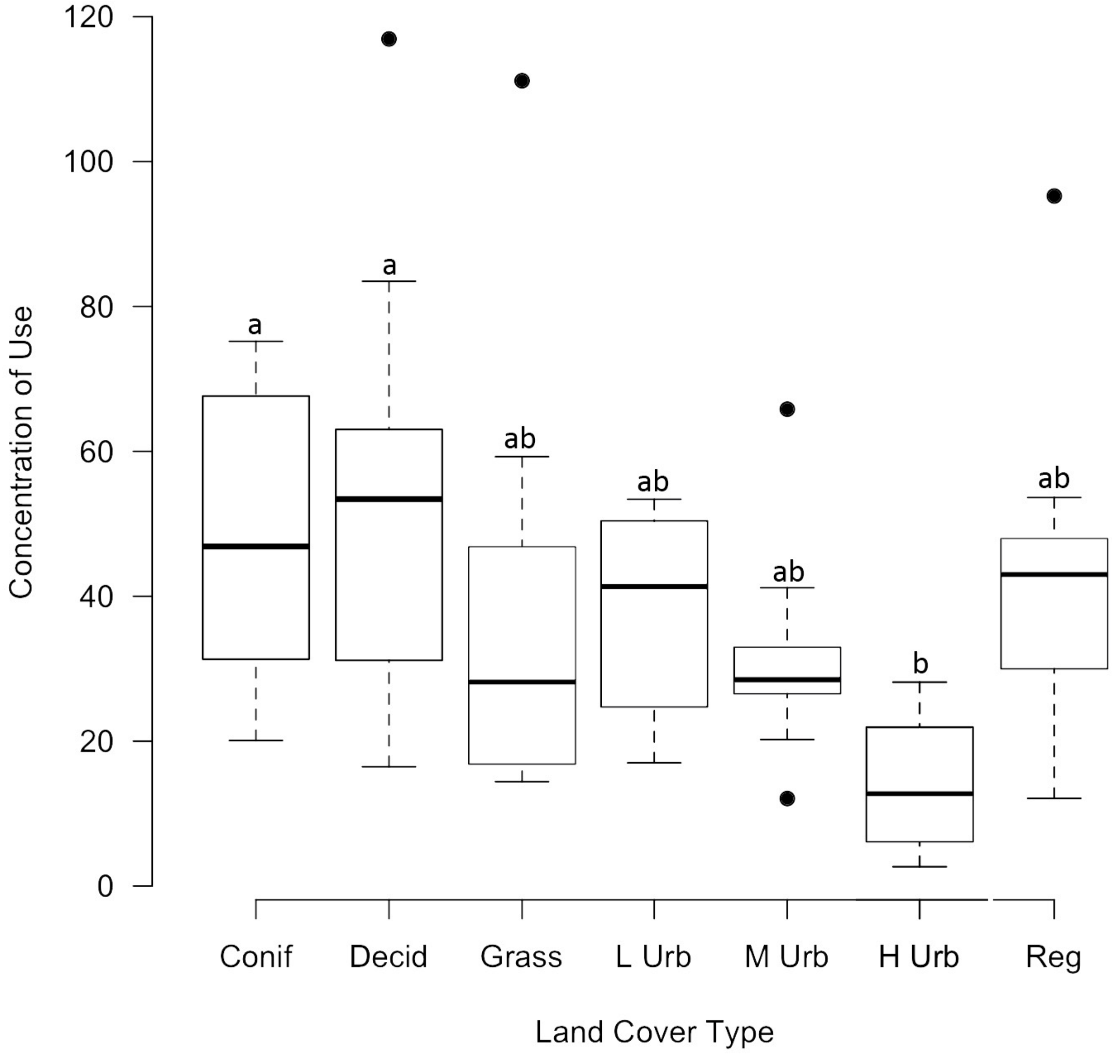

Figure 2. Boxplots indicating concentration of use by male Pileated Woodpeckers on different land cover types (Conif: coniferous forest, Decid: deciduous/mixed forest, Grass: grass/grassland, L Urb: light urban M Urb: medium urban, H Urb: heavy urban, Reg: regenerating forest) on the Greater Seattle area. Tukey test posthoc differences are presented on letters.

Concentration of use on light and medium developed areas was not significantly different from forested lands (Light Urban vs. Coniferous: Tukey test, Difference = 10.09, $t_8 = -0.95$, $P = 0.96$, Light Urban vs. Deciduous: Tukey test, Difference = 14.22, $t_8 = -1.34$, $P = 0.83$; Medium Urban vs. Coniferous: Tukey test, Difference = 16.28, $t_8 = -1.53$, $P = 0.73$, Medium Urban vs. Deciduous: Tukey test, Difference = 20.41, $t_8 = -1.92$, $P = 0.48$). Other land cover types were little used (Figure 2).

Suburban male woodpeckers consistently used edges and forests with large diameter hardwoods. The RUF coefficients for contrast-weighted edge density at 50m were significant for 7/9 birds (5 males frequently used edge (+β), while 2 used it infrequently (-β)) and it was the most significant variable at the population level (combining all woodpeckers, the population consistently frequented areas with abundant edge: $\beta = 0.63$, 95% CI 0.02 – 1.25). The second most important variable was quadratic mean diameter of dominant hardwoods, although it was half as important as edge (combining all woodpeckers, the population consistently used areas with many large diameter hardwoods: $\beta = 0.32$, 95% CI 0.00 – 0.65). This variable was significant for all 9 birds, though response to the presence of large trees was individually variable (6 used areas holding large hardwoods frequently (+β), while 3 used areas with small hardwoods (-β)). The other variables had little effect on use.

DISCUSSION

We discovered a large, specialized bird using a habitat typically considered too dynamic and hostile for such species. Pileated woodpeckers have traditionally been considered mature forest specialists (Conner et al. 1975, Mellen et al. 1992, Bull and Holthausen 1993, Renken and Wiggers 1993, Aubry and Raley 2002, Bull and Jackson 2011) yet, we found them ranging unimpeded in suburban habitats. Our study sheds light on the flexibility and resilience of this species to changes in its natural habitat when the lost of natural resources is somehow compensated. Pileated woodpeckers were in rapid decline on the beginning of the 20th Century due to significant reductions on their natural habitat (Bull and Jackson 2011). But they were able to adapt to use what was considered suboptimal habitat, including suburban areas (Hoyt 1957). It was not until the 1950s that this species started to use bird feeders (Hoyt 1957) and now they continue to colonize suburban areas that they did not use before (Erskine 2008).

As expected based on previous work (Blewett and Marzluff 2005), Pileated Woodpeckers intensively used coniferous and broadleaved forests in our area, but they also used a large proportion of suburban areas where trees were retained. Light and medium urbanized areas attract Pileated Woodpeckers and partially complement the resources they find 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, dead and live trees in backyards. The combination of native and non-native resources may enable this species to exploit this altered, and novel ecosystem.

Home range size can be affected by the abundance and availability of resources that are important to woodpeckers, such as density of snags for nesting, foraging and roosting or by other factors, such as territoriality (Renken and Wiggers 1989). When reviewing other studies (Renken and Wiggers 1989, Mellen et al. 1992, Bull and Holthausen 1993, Aubry and Raley 1996, Bonar 2001) we found a significant positive relationship between home range size in natural areas and latitude (Linear regression, Adj. Mult. $R^2 = 0.92$, $P < 0.001$, Figure 3). However, home ranges in our sites were much smaller than expected as our estimation fell below the 95% CI for the regression (Figure 3). We considered four potential non-exclusive explanations for this pattern: i) differences in forest productivity with other sites; ii) "crowding effect"; iii) supplementary resources provided by humans; and iv) availability of snags in yards and parks.

Forest net primary productivity (NPP) differs with latitude and forest type (Grier et al. 1989, Gillman et al. 2015). In general, broadleaved forests are more productive than coniferous forests at similar latitudes (Grier et al. 1989) and forests closer to the Equator are more productive than forests closer to the poles (Gillman et al. 2015). As forest productivity increases, more resources are available, supporting more individuals and species (Pautasso and Gaston 2005) at the landscape level, and individuals tend to have smaller home ranges at the local level (Renken and Wiggers 1989). We conducted our study mostly in second-growth broadleaved forests that may have higher productivity than sites where other studies on Pileated Woodpecker home range have been conducted in the west coast of 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).

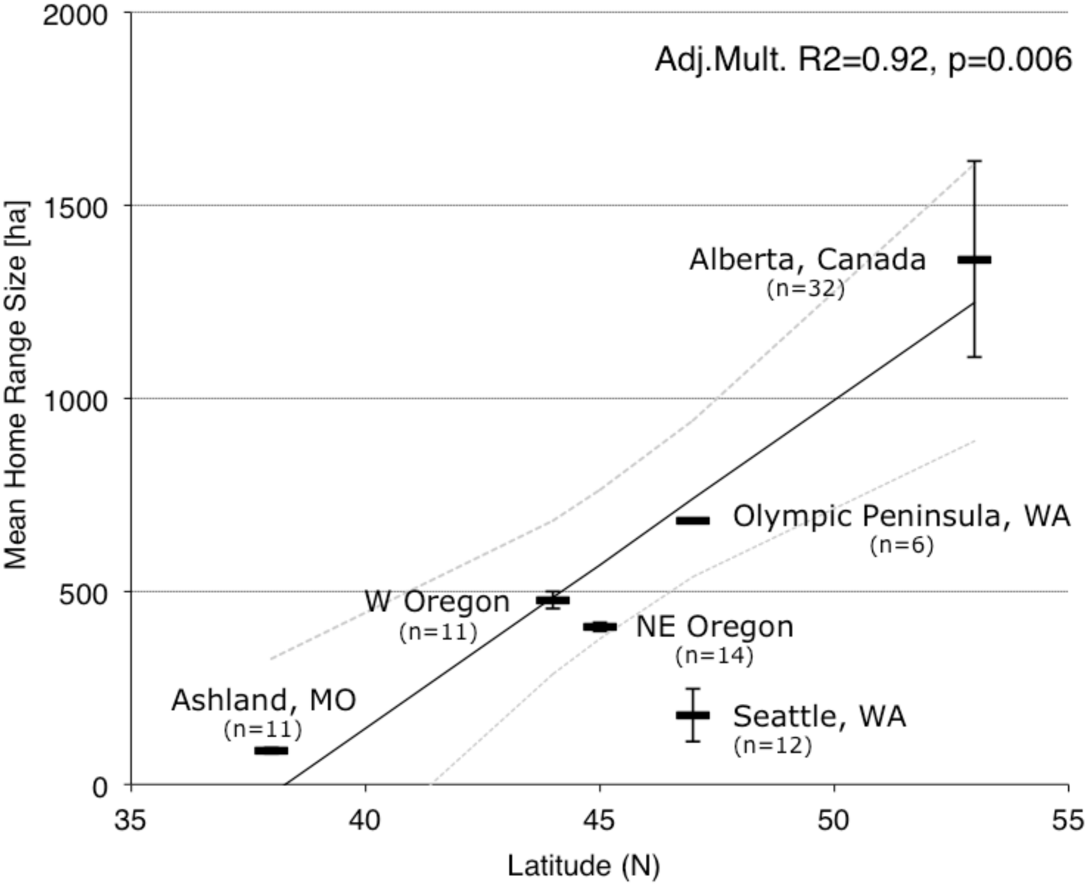

Figure 3. Minimum convex polygon-based home range estimations for Pileated Woodpecker on different studies and locations: Ashland, MO (Renken and Wiggers 1989), W Oregon (Mellen et al. 1992), NE Oregon (Bull and Holthausen 1993), Olympic Peninsula, WA (Aubry and Raley 1996), Seattle, WA (this study), and Alberta, Canada (Bonar 2001). Error bars shown on the graphic indicate SE and dashed line indicates 95% CI for the regression.

Crowding into small home ranges by other species, has been to habitat loss and fragmentation (Debinski and Holt 2000), which could be another mechanism driving the smaller home ranges in our study. The crowding effect leaves individuals in the remaining patches of habitat that are normally subject to lower productivity and survivorship due to the scarcity of resources to support populations with higher abundance than normal. This eventually results in reduction of population density and occasionally local extinctions (Debinski and Holt 2000). We found little support for this hypothesis in our area as we have no evidence of decline and we observed individuals moving across the landscape without interference of what we expected to be habitat barriers for Pileated Woodpeckers (e.g., roads, highways, open areas, densely populated areas).

Supplementation of resources by humans, especially bird feeders, has been documented to have a great impact in bird communities (Robb et al. 2008). Typically, areas with higher bird feeder density result in higher bird density and higher species richness than in areas without feeders (Fuller et al. 2008). Pileated woodpeckers actively use suet feeders commonly provided by people in our study area, as reported by many neighbors 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 (Fuller et al. 2008), which may have an effect in reducing the size of their home ranges.

As urban areas are developed, snags are removed (Blewett and Marzluff 2005). Yet, the supply of snags in suburban green spaces is similar to the supply we observe in natural areas (Blewett and Marzluff 2005). In fact, most (16/17) of the Pileated Woodpecker nests we found were placed on these green spaces (parks, trail buffers, right-of-ways, large wooded lots; Tomasevic and Marzluff, unpubl. data, also see Ch. 4). We believe that this is a critical aspect of the success of Pileated Woodpeckers in suburban areas, as they can find nesting sites, as common limiting factor among cavity nesting birds (Newton 1998).

Conservation Implications

This research gives us a new perspective on this woodpecker's ecology and opens new opportunities for its conservation and that of the myriad 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) were used significantly less than areas with higher forest cover. Retaining sufficient forest cover at the landscape level still plays a crucial part in sustaining this species (and maybe others tied to it) in a larger scale approach. This forest will be better suited for this species if dead trees are retained and managed for in green spaces. Early successional species, such as big leaf maple, red alder and Douglas fir are easy to include in green space management and they are successfully used (i.e. nesting, roosting, foraging, drumming, calling, etc.) by this species. In fact, diameter of dominant hardwood species was the second most important structural variable determining use; therefore, allowing these species to grow big will help the Pileated Woodpecker.

Biodiversity is facing great challenges today due to climate change; habitat loss, degradation and fragmentation; invasive species; and other factors. Given the urgency of the situation, conservation should not be limited to wild areas. Cities should have a role in biodiversity conservation as well.

ACKNOWLEDGMENTS

We thank Jon Bakker, Joshua J. Lawler, Martin G. Raphael, and Elinore J. Theobald for their invaluable comments at different stages of the development of this manuscript. We thank Jim Ladd, Kim Holt, April Gale-Seixeiro, Sharon Shriver, Dale Griffith, and Jim Rettig kindly for allowing us to trap Pileated Woodpeckers on their property. We thank Sean Williams, Laura Farwell, Sara Wang, Lauren Walker, Ross Forbush, Ila Palmquist, Jamie Granger, Kristen Richardson, Frank Stevick, 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.

Funding statement: A SEFS grant to JMM funded the radio-tags. A Student Technology Fee grant #2010-131-1 at University of Washington to SEFS funded the radio receivers and GPS units. Carol Nygren kindly provided funding to partially cover field expenses. JAT conducted part of this research while on a Fulbright-Conicyt scholarship for his PhD 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, and band and radio-tag woodpeckers was approved by the University of Washington (IACUC #3077-01), Washington State (14-010), and US National Bird Banding Laboratory (#22489).

Author contributions: Both authors conceived the idea, and designed the research. JAT collected and analyzed the data and wrote the paper with edits from JMM. Both authors agreed to this submission.

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Chapter 3

Suburban pileated woodpeckers (*Dryocopus pileatus*): adapting to change or falling into an ecological trap?

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† Both authors conceived the idea, and designed the research. JAT collected and analyzed the data, and wrote the paper with edits from JMM.

ABSTRACT

Urban areas have expanded as more and more people live within cities, which now contain more than half the world's population. As cities grow, natural habitat is transformed changing the face of the local biota and the resources available for it. We studied how a purported sensitive species, the Pileated Woodpecker (*Dryocopus pileatus*), adapts to rapid and extensive land-cover change as urbanization reduces and isolates forest. From 2009 – 2013, we used radio-telemetry to find their nests and roost sites, and to record nest success and adult survivorship. We found a total of 14 nests and 17 roost sites. Nests were mostly placed on dead trees or dead branches of trees. The average productivity of the nests was 2.00 young and most nests (13/14) fledged at least one young. Pileated woodpeckers roosted mostly on red alder snags or dead parts of big leaf maples. They had several roost sites that they rotated using through the year. Annual adult survivorship varied across years, but the average (86.5%) was higher than on natural sites of the Pacific Northwest. Our results suggest that fitness of suburban Pileated Woodpeckers in our area may be as good or higher than natural nearby areas. Suburban areas may be useful buffers to reduce the negative effects of heavy urbanization on the Pileated Woodpeckers and help conserve this species in addition to necessary protected areas.

Key words: reproduction, survivorship, fitness, picidae, breeding.

INTRODUCTION

More than half of the world's population now lives in cities (United Nations 2008) and around 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 population increases (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 the sprawl of cities are very complex and dynamic processes. They not only change vegetation composition, quantity and structure (Donnelly and Marzluff 2006), but also micro-climatic conditions, biotic interactions (e.g., increasing predation by domestic animals, competition with exotic species, and transmission of diseases, Chace and Walsh 2006, Endlicher 2011), and connectivity within and between surrounding natural areas (Fernández-Juricic 2000). Once an area is developed it rarely goes back to its natural habitat state (Marzluff and Ewing 2001; McKinney 2006), although native vegetation maybe retained or incorporated by developers, planners, managers or residents (Aronson et al. 2014). This, in conjunction with factors such as altered disturbance regimes (Chace and Walsh 2006) and supplemental food and water (Robb et al. 2008; Clucas and Marzluff 2011) create novel habitat conditions for wildlife and plants that bring challenges and opportunities that will favor species with the ability to adapt to them (Kowarik 2011) and extirpate those that cannot (Marzluff 2014).

Many woodpecker species are habitat specialists and, as with many other cavity nesting birds, their presence and abundance 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 (Martin and Eadie 1999; Aubry and Raley 2002) potentially amplifying the negative effects onto the biological communities present in areas that undergo urban development (Morrison and Chapman 2005).

Puzzled by the question of whether a specialist species with such influence in the ecological community as a woodpecker may be able to adapt and succeed in a novel environment, we studied demographics of the Pileated Woodpecker (*Dryocopus pileatus*) in suburban areas around Seattle, WA, USA. Being a forest specialist and with preference for mature and old-growth forest (Bull and Jackson 2011), we expected this species to be negatively affected by habitat changes promulgated by urbanization. Given the history of recent extinctions of large woodpecker species in North America (e.g., Ivory-billed Woodpecker, *Campephilus principalis* and Imperial Woodpecker, *Campephilus imperialis*) we were interested in the potential challenges that urban sprawl could pose on the largest woodpecker remaining in the region.

METHODS

Focal species

We studied the spatial ecology of the pileated woodpecker (*Dryocopus pileatus*), currently the largest woodpecker species extant in North America. Pileated Woodpecker is a forest bird, typically associated with late-successional or mature coniferous or deciduous forest (Mellen et al. 1992; Bull and Holthausen 1993; Renken and Wiggers 1993; Aubry and Raley 2002), which uses younger forests with scattered large trees (Bull and Jackson 2011) and forested suburban areas (Blewett and Marzluff 2005). It normally requires large areas of suitable habitat and it has been documented to be sensitive to habitat loss, fragmentation and degradation in natural areas (Bull et al. 2007; Bull and Jackson 2011) as well as in suburban areas, where the abundance of this species is positively associated with the percentage of forest remaining (Blewett and Marzluff 2005).

Study area

We conducted our study on three main areas in the vicinity of Seattle, Washington, USA (Fig. 1). These areas were part of 23 randomly chosen study sites described 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 (Fig. 1). These three areas were similar in terms of deciduous forest cover, while Redmond had less coniferous forest and more medium and heavy urban cover (see more details on Tomasevic and Marzluff, in prep.). The lowlands of Western Washington are naturally mostly forested lands. The climax stage of these forests is dominated by coniferous species, such as

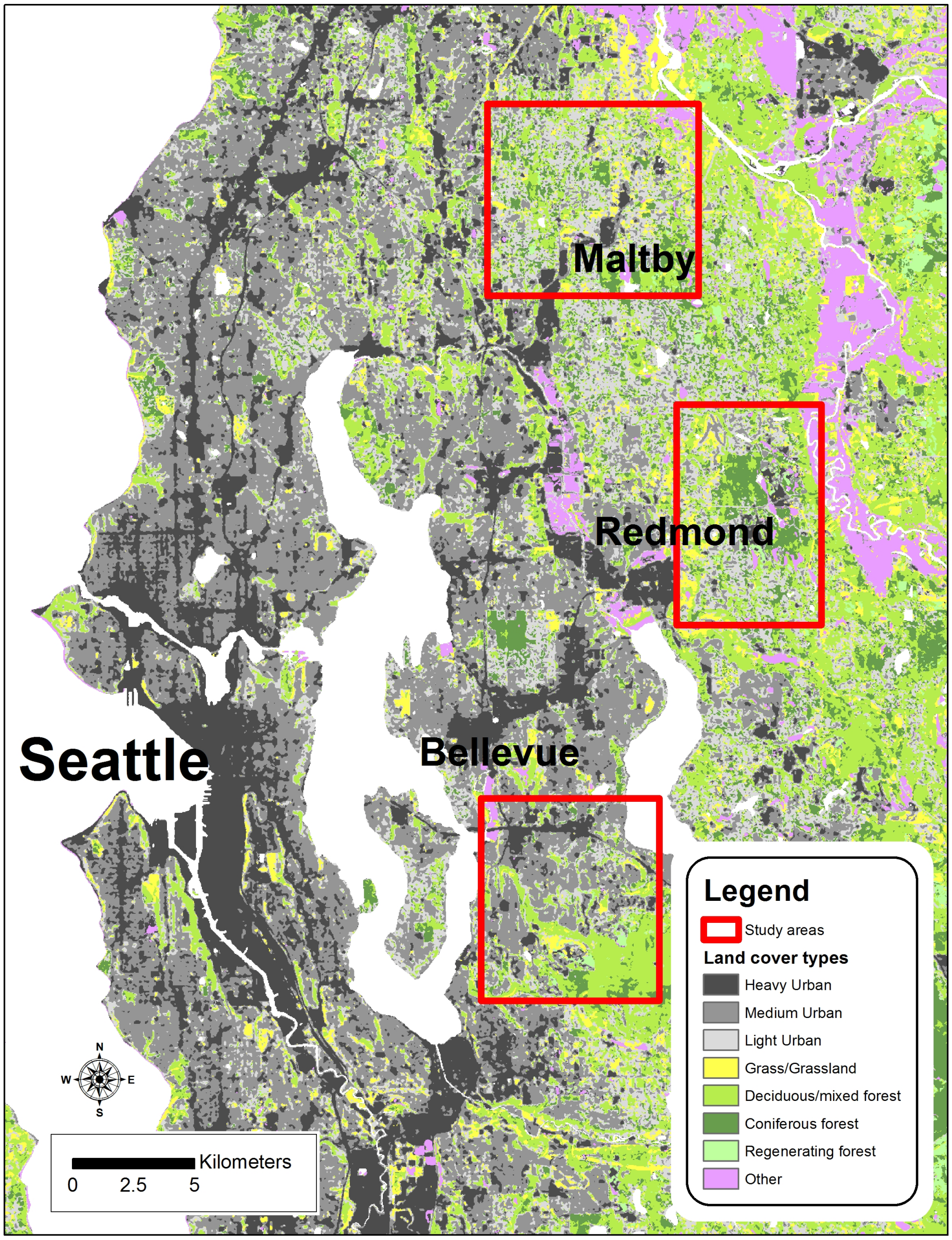

Figure 1. Study area on the Greater Seattle, WA. Land cover types are indicated according to Alberti et al. (2006).

western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) with presence on Douglas fir (*Pseudotsuga menziesii*) as subclimax species (Franklin and Dyrness 1988). Before European settlement, hardwoods were not common in this zone, except on recently disturbed or riparian areas, where big leaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*) and black cottonwood (*Populus trichocarpa*) were the most prevalent species (Franklin and Dyrness 1988). After a century and half of habitat modification (Cuo et al. 2009) and the accelerated expansion of urban and suburban areas in the region (MacLean and Bolsinger 1997; Alberti et al. 2004; Hepinstall et al. 2008), the amount, composition and structure of the forest has changed dramatically (Donnelly and Marzluff 2006), where mostly early successional species (mostly the hardwoods mentioned above and Douglas fir) dominate suburban forests.

Radiotelemetry

We trapped year-round using mist-nets and playback (York et al. 1998) and used a hand-made Styrofoam decoy (painted with the colors and patterns of a perching pileated woodpecker) with red feathers attached to its head to increase responsiveness of woodpeckers. We also trapped close to suet feeders (present in neighborhoods at the study sites) during fall and winter when the birds did not show a strong response to the playback. Once we trapped a bird, we banded it, fitted a radio transmitter (model A1250 from Advanced Telemetry Systems, Isanti, MN; expected life 12 mo) using a Teflon^{TM} backpack harness modified from (Buehler et al. 1995). We used 2mm wide copper rings to secure them in lieu of sewing. Transmitter plus harness weighed 11.5g which is less than 5% of the weight of an adult pileated woodpecker. We released the birds back to the same area where we captured them. Our processing time was typically about 30 - 45 minutes. We used a R-1000 telemetry receiver (Communications Specialists, Orange, CA) and a hand-held 3-elements Yagi antenna to relocate each radio-tagged bird opportunistically, aiming to have at least one location per week. We recaptured and re-transmittered two birds (after 69 and 174 days, respectively). Our *a priori* expectation was that our capture scheme was going to be biased towards trapping males, as they supposed to respond more aggressively to playback, but females also participated on territorial defense, as described by (Mellen et al. 1992). While handling each individual bird, we recorded its sex, weight, tail length, bill length, bill width, and bill depth. After recording this data and making sure that the harness was securely attached, we then released the birds back at their trapping location. We monitored the birds after release for 10-15 minutes and checked back on them on the following day after release to verify that there were no problems with the transmitter and that the individuals did not responded negatively to it.

We used the radio telemetry to find the bird's nests and roost sites and recorded their locations with a GPS unit (GPSmap 60CSx, Garmin, Olathe, KS). We then entered all the locations to GIS using ArcGIS (9.x and 10.x, ESRI, Redlands, CA).

Components Of Fitness: Breeding Success, Productivity And Survivorship

We assessed the reproductive output (number of chicks fledged) and annual survivorship of radio-tagged birds. To assess reproductive output, we recorded the number of offspring that fledged from each nest (*n* = 14), or when we could not find their nests (*n* = 4), we recorded presence or absence of fledglings accompanying adults during the breeding season. Given our experience, fledglings in distinct plumage (Pyle 1997) stayed with their parents for at least 3 months, thereby providing a good measure of nesting success. We considered a nest to be successful if the pair fledged at least one young. We related survivorship to characteristics of the birds and their home range using Cox proportional hazard regression (Fox and Weisberg 2011).

We present mean ± standard error (SE) throughout the text, unless otherwise noted.

RESULTS

We trapped a total of 16 adult pileated woodpeckers (9 males and 7 females) between 2009 and 2012. We captured the same number of males on all three general areas, but the number of females varied slightly (Area: #males/#females captured, Maltby: 3/4, Redmond: 3/2, Bellevue: 3/1). We captured both the male and female of 3 breeding pairs (2 pairs in consecutive years, and 1 pair in the same year). In one occasion, we trapped both male and female on the same area, but they did not breed together.

We found a total of 13 nests and 17 roost sites over this study. Pileated woodpeckers used snags (84.62%, n = 11) or dead branches on live big leaf maple trees (15.38%, n = 2) as substrate to nest. Most of the nests were located on red alder snags (69.23%, n = 9), although dead black cottonwoods (n=1) or dead Douglas firs (n=1) were occasionally used. On average, snags were 17.86 ±1.76 m in height and nests were placed at 12.37 ±2.76 m, which is in the upper third of the height of the snag (69.3%). The nests placed on trees were at similar height to the ones on snags (ca. 14 m), although since trees were taller than snags, they were at approximately in the middle of the tree (48% of the total height). Most of the snags presented either previous foraging signs by pileated or other woodpeckers (71.43%) or had signs of fungi infection (50%), although they were not foraging snags (only dedicated to foraging). Only few of these snags had other nest cavities present (37.5%). The average DBH of the nesting substrates was 46.25 ±2.99 cm (n=8).

Pileated woodpeckers roosted equally on snags and trees (52.94% vs 47.06%, respectively), but they only roosted on red alders or big leaf maples. Red alder snags and big leaf maple trees (with cavities or crevices on the trunk) had the same number of roosts (6/17 each, 35.29%), while big leaf maple snags followed with 17.65% of the roost sites (n=3). Live red alders accounted for the remaining 11.76% of the roost sites (n=2). Roosting cavities were placed on snags at an average of 13.17 ±4.75 m in height, which represented 83.86% of the snag height (on average). Roost sites placed on live trees were at an average of 8.83 ±1.14 m, which represents 43.09% of the trees height. The average DBH of the roosting substrates was 49.6 ±6.12 cm (n=10).

Breeding Success, Productivity And Survivorship

We found a total of 14 active nests, 13 of which fledged at least 1 young (92.8%). The one nest that failed did so because the female adult was preyed upon before eggs were laid. At 10 nests where we obtained accurate fledgling counts, pairs fledged a mean of 2.00 (SE = 0.69) nestlings. Considering observations of woodpecker families and nesting success we confirmed the production of 27 young fledged by 11 breeding pairs on 16 breeding attempts from 2009–2013. Over the 5 breeding seasons, we documented that only 3 adults on different territories (2 males and 1 female) failed to breed at all. One of these males was apparently paired, but never bred. The other two birds apparently were not paired. We found no relationship between the average numbers of chicks fledged and landscape characteristics of the home ranges (in terms of area or percentage of each land cover type, Appendix 1).

Adult annual survivorship rate (of males and females) varied across years (Cox Proportional Hazards Model, exp(coef) = 0.28, $z_{15} = -2.18$, df = 15, $P = 0.03$, range: 70 – 100%) being the highest in 2011 where no bird we followed died (n=8). We found no effect of bird mass or sex on survivorship (Appendix 1). On average, annual survival was 86.5 ± 0.06%. We found little relationship between survivorship and the size or percentage of different land cover types on male woodpeckers' home ranges (Appendix 1). The strongest effect was that individuals concentrating their use on coniferous forests (Cox Proportional Hazards Model, exp(coef) = 1.06, $z_8 = 1.39$, $P = 0.17$) tended to have slightly higher chance (6%) of mortality each day, and individuals that used sites with larger coniferous trees (higher quadratic mean diameter of dominant conifer) tended to reduce their daily mortality by 99% (Cox Proportional Hazards Model, exp(coef) = 0.003, $z_8 = -1.43$, $P = 0.15$). Individuals that had higher areas of heavy urban land cover on their home range tended to have lower mortality (Cox Proportional Hazards Model, exp(coef) = 0.85, $z_8 = -1.23$, $P = 0.22$).

DISCUSSION

Pileated woodpeckers successfully used the forested areas of suburban Seattle, despite these areas having few large snags (Blewett and Marzluff 2005), which is normally mentioned as a requirement for this species. For example, Pileated Woodpeckers were only found nesting on trees and snags between 65 – 154 cm DBH (mean = 101.2 cm) in western Washington (Aubry and Raley 2002) or on snags that averaged 82 cm on southeastern Vancouver Island, BC (Hartwig et al. 2004). And while there is variability on the size of nest trees or snags reported along the distribution range of this species (Bull and Meslow 1977; Mellen et al. 1992; Aubry and Raley 2002; Hartwig et al. 2004; Bull and Jackson 2011), we found that the nests on our sites were placed on snags that were significantly smaller. We found a similar pattern for roost site selection when comparing with research conducted on natural sites (Bull et al. 1992; Mellen et al. 1992; Aubry and Raley 2002).

Our results suggest that fitness of suburban Pileated Woodpeckers in our area may be as good or greater than natural areas in nearby areas. In fact, the productivity of suburban Pileated Woodpeckers was lower than that reported throughout its wide range (2.00 vs. 3.83, Bull and Jackson 2011), but similar to that reported for the Pacific Northwest (productivity: 2.26 young/nest, *t*-test, $t_1 = -0.54$, $P = 0.30$; breeding success: 83%, Bull and Meslow 1988). Mean annual adult survival in our sites was not significantly different from that reported in other studies on natural sites on the Pacific Northwest (X^2_3=1.606, $P = 0.34$, 50% in the Olympic Peninsula, Aubry and Raley cited in Bull and Jackson 2011, 64% on color-banded individuals in NE Oregon, Bull and Meslow 1988, and 47% on radio-tagged individuals in NE Oregon, Bull 2001). Although the effects were not conclusive, the evidence that individuals that used more coniferous forest had higher mortality risk, which was reduced with more use of heavy urban areas, suggests that the main mortality driver for this species may be by native raptors that may benefit from these forests and avoid more urbanized areas. There is a rich community of avian predators that use Seattle's suburban areas, including Cooper's Hawk (*Accipiter cooperi*), Barred owl (*Strix varia*), and Great horned Owl (*Bubo viriginianus*), which are known to use medium urbanized areas (Rullman and Marzluff 2014). Further study is needed to confirm the effect of these predators on suburban woodpeckers.

In summary, our results indicate that there is value on suburban areas for the conservation of a charismatic species such as the Pileated Woodpecker. This may not only provide an opportunity for the species itself, but also to engage more people on the importance of biodiversity, right here in our very back yard!

ACKNOWLEDGMENTS

We thank Jon Bakker, Joshua J. Lawler, Martin G. Raphael, and Elinore J. Theobald for their invaluable comments at different stages of the development of this manuscript. We thank Jim Ladd, Kim Holt, April Gale-Seixeiro, Sharon Shriver, Dale Griffith, and Jim Rettig kindly for allowing us to trap Pileated Woodpeckers on their property. We thank Sean Williams, Laura Farwell, Sara Wang, Lauren Walker, Ross Forbush, Ila Palmquist, Jamie Granger, Kristen Richardson, Frank Stevick, 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.

Funding statement: A SEFS grant to JMM funded the radio-tags. A Student Technology Fee grant #2010-131-1 at University of Washington to SEFS funded the radio receivers and GPS units. Carol Nygren kindly provided funding to partially cover field expenses. JAT conducted part of this research while on a Fulbright-Conicyt scholarship for his PhD 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, and band and radio-tag woodpeckers was approved by the University of Washington (IACUC #3077-01), Washington State (14-010), and US National Bird Banding Laboratory (#22489).

Author contributions: Both authors conceived the idea, and designed the research. JAT collected and analyzed the data and wrote the paper with edits from JMM. Both authors agreed to this submission.

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Appendix 1. Factors that did not show a significant effect on the average number of fledglings of Pileated Woodpeckers calculated using simple linear regression analysis, nor on survivorship of adult Pileated Woodpeckers calculated using Cox Proportional Hazards regression analysis.

	Average number of fledglings			Adult survivorship		
Factor	Adj. R-squared	F-statistic (df=1,7)	P	exp(coef)	z	P
				All birds (n = 16)		
Bird mass				0.994	-0.34	0.74
Sex				0.964	-0.04	0.97
				Males only (n = 9)		
Land cover area						
Coniferous	-0.14	0.01	0.92	0.999	-0.585	0.56
Deciduous/mixed	-0.12	0.17	0.69	0.982	-0.741	0.46
Regenerating forest	-0.14	0.04	0.84	0.995	-0.102	0.92
Grassland	0.06	1.55	0.25	0.957	-0.72	0.47
Light Urban	0.01	1.06	0.34	0.997	-0.241	0.81
Medium Urban	-0.13	0.09	0.77	0.996	-0.363	0.72
Heavy Urban	-0.14	0.01	0.95	0.851	-1.22	0.22
Other	0.21	3.16	0.12	1.106	1.182	0.24
Percentage land cover type						
Coniferous	-0.13	0.056	0.82	0.984	-0.402	0.69
Deciduous/mixed	-0.14	0.031	0.87	0.985	-0.238	0.81
Regenerating forest	-0.11	0.231	0.65	1.118	0.808	0.42
Grassland	0.11	1.952	0.21	0.929	-0.45	0.65
Light Urban	0.02	1.153	0.32	1.049	0.961	0.34
Medium Urban	-0.08	0.389	0.55	1.001	0.036	0.97
Heavy Urban	-0.13	0.076	0.79	0.639	-1.232	0.22
Other	0.21	3.163	0.12	0.299	-0.375	0.71

Chapter 4. Space use of suburban pileated woodpeckers (*Dryocopus pileatus*): insights on the relationship between home range, core areas, and territory

Space use of suburban pileated woodpeckers (*Dryocopus pileatus*): insights on the relationship between home range, core areas, and territory

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‡ Both authors conceived the idea, and designed the research. JAT collected and analyzed the data, and wrote the paper with edits from JMM.

ABSTRACT

Home range, territory and core areas are concepts that describe an animal's space use. However, little research has been done to understand potential spatial relationships between them. And while the relative importance of different areas of the home range has been addressed with utilization distributions; there is a lack of such analysis for territories. We propose an behavior-based approach to determine areas of importance within the territories, that we defined as highly-defended areas. We studied the spatial ecology of a territorial species, the pileated woodpecker, and the relationships between their home range, territory, core areas, and highly-defended areas. We found significant spatial overlap between male and female woodpeckers of the same breeding pair, but little overlap between same sex individuals of neighboring home ranges. On average, territories represented 69.63% ± 0.06% of the home ranges, and highly-defended areas were 34.3% ± 0.03% of the home range. The territory:home range size ratio for pileated woodpeckers was similar to that for nightingales (*Luscinia megarhynchos*), whereas the core areas:home range size ratio was similar to the one found for moose (*Alces alces*). Our definition of highly-defended areas was a useful and less arbitrary method than other methods available to determine the portions of the territory that were important for the birds. In this case, they contained a significant proportion of the roost sites for pileated woodpeckers, a resource that may affect survivorship, especially in winter. This approach could be useful to further incorporate behavior on the study of the spatial ecology of species.

Key words: behavior, urban ecology, territoriality, cavity-nesting birds, spatial overlap.

INTRODUCTION

Territory, home range, and core area are fundamental concepts in ecology that describe how animals use an area. Traditionally, home range has been defined as the “area traversed by an individual in its normal activities of food gathering, mating and caring for young”, while the notion that territory is “any defended area” has been used for decades (Noble 1939; Nice 1941; Burt 1943; Odum and Kuenzler 1955). Core areas, on the other hand, refer to portions of the home range that are heavily used (Samuel et al. 1985). Although the definition of core areas does not involve defense, core areas may contain important resources that may be defended or used exclusively, and could potentially overlap with territory boundaries, which may have led to the interchangeable use of these three terms by some authors (Powell 2000; Adams 2001). This muddling of terms may be clarified by linking detailed behavioral observations with modern technologies that enable close tracking of animal movements and their use of space (Marzluff et al. 2001).

Understanding animal use of an area has evolved significantly in the last few decades (Powell 2000). Kernel density estimators and utilization distributions (UD) have provided more realistic delimitation of the home range by overcoming many of the limitations of earlier methods relying on unrealistic assumptions of animal movement (e.g. circle or ellipse approaches and minimum convex polygon, hereafter MCP). These distribution-free approaches also provide insights into which areas are used most frequently and how these differences relate to the underlying resources by informing resource utilization functions (Marzluff et al. 2004) and resource selection functions (Manly et al. 1993).

However, as statistical techniques advanced, the delineation of core areas and their relationship to home range or territory boundaries has languished. For example, initial efforts to define territories and their distinction from home ranges focused on comparing abundance estimations (using mark-recapture) with territory estimations based on spot-mapping (Ferry et al. 1981), but little additional progress was made in the following 30 years. More recently, radio-tagged individuals have been used to compare the home range (based on the locations where individuals were recorded) to territory (based on singing locations) either using MCP estimates (e.g. Naguib et al. 2001) or fixed-kernel estimates of utilization distributions (e.g. Anich et al. 2009). Both approaches have advanced the understanding of the relationship between home range and territory, but they still have limitations. MCPs are known to be just a crude representation of the areas used/not used by individuals, ignoring the information provided by points or locations interior to the home range. The estimate of the used area they provide is also very sensitive to sample size and where the animals were found (Powell 2000). Kernel estimations of space use have helped overcome many of these limitations, however they have not been fully exploited in the study of the relationship between home range, core areas, and territory. For example, Anich et al. (2009) compared the relationship between size of the home ranges and territories of the Swainson's warbler (*Limnothlypis swainsonii*) based on two-dimensional, fixed-kernel representations, leaving out information about use (provided by the UD). On the other hand, core areas have been defined using arbitrary thresholds on the UD (e.g. under 25% use, Powell 2000, or more commonly, under 50% use, Chamberlain et al. 2000; Warning and Benedict 2015).

The arbitrary nature of the early reliance on UDs to define core areas reduces their biological relevance (Powell 2000; Vander Wal and Rodgers 2012). A more quantitative approach was developed for clumped distributions of locations, where core areas represented places where the probability of use was higher than what was expected by random use as determined by changes on the slope of the relationship between probability of use and the percentage of the home range with such probability of use or greater (Seaman and Powell 1990; Powell 2000). This approach was later refined by fitting an exponential regression to the relationship between use (isopleth volume) and the percent of the home range area that the isopleth represents to identify core areas (i.e., where use, indexed by isopleth volume, exceeds availability, Vander Wal and Rodgers 2012). While this approach may be useful when behavioral data are missing but locations are available (such as GPS locations), it assumes that the shape of core areas closely follow the shape of UD isopleths and that areas where relocations concentrate are important.

We studied space use of a year-round territorial species, the pileated woodpecker (*Dryocopus pileatus*), to better understand the spatial relationship between home range, territory, and core areas. We also explored territorial boundaries between adjacent woodpeckers and investigated segregation within the home range by paired individuals. In so doing, we observed defensive behaviors and used them to provide an objective description of territoriality and highly defended core areas therein.

METHODS

Focal species

The pileated woodpecker is the largest extant woodpecker in North America. It is a forest bird, typically associated with late-successional or mature coniferous or deciduous forest (Mellen et al. 1992; Bull and Holthausen 1993; Renken and Wiggers 1993; Aubry and Raley 2002) that uses younger forests with scattered large trees (Bull and Jackson 2011) and forested suburban areas (Blewett and Marzluff 2005). It normally requires large areas of suitable habitat and it has been documented to be sensitive to habitat loss, fragmentation and degradation in natural areas (Bull et al. 2007; Bull and Jackson 2011) as well as in suburban areas, where the abundance of this species is positively associated with the percentage of forest remaining (Blewett and Marzluff 2005). Pileated woodpeckers are known to be territorial year-round and both males and females participate on defense behavior (e.g. calling or drumming, Mellen et al. 1992; Bull and Jackson 2011).

Study area

We conducted our study in three main areas in the vicinity of Seattle, Washington, USA (Fig. 1). 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. These three areas were similar in terms of deciduous forest cover, while Redmond had the least coniferous forest and the most medium and heavy urban land cover.

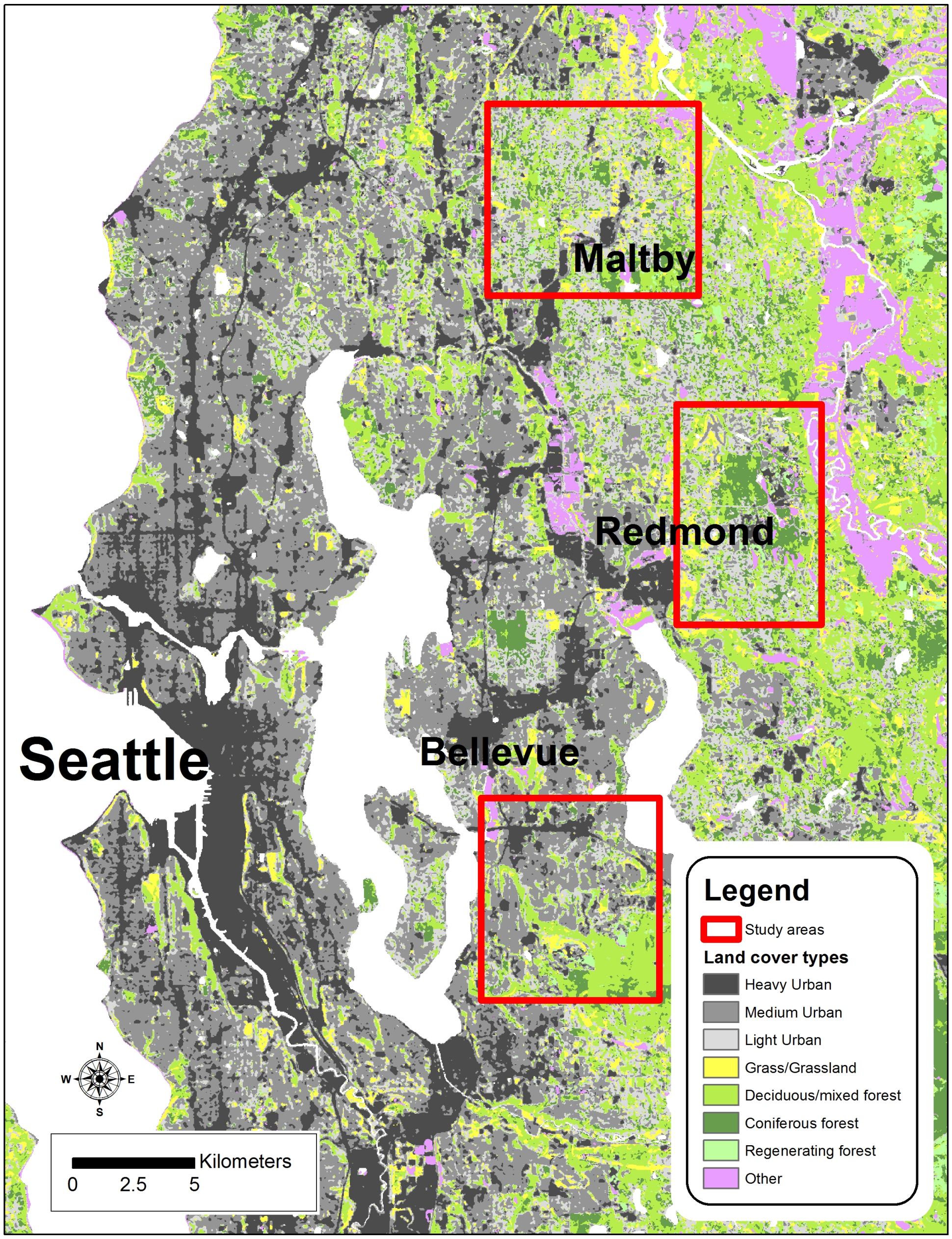

Figure 1. Study area on the Greater Seattle, WA. Land cover types are indicated according to Alberti et al. (2006).

The lowlands of Western Washington are naturally mostly forested lands dominated by coniferous species, such as western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Douglas-fir (*Pseudotsuga menziesii*, Franklin and Dyrness 1988). Before European settlement, hardwoods were not common in this zone, except on recently disturbed or riparian areas, where big leaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*) and black cottonwood (*Populus trichocarpa*) were the most prevalent species (Franklin and Dyrness 1988). After a century and half of habitat modification (Cuo et al. 2009) and the accelerated expansion of urban and suburban areas in the region (MacLean and Bolsinger 1997; Alberti et al. 2004; Hepinstall et al. 2008), the amount, composition, and structure of the forest has changed dramatically (Donnelly and Marzluff 2006), where mostly early successional hardwoods and Douglas-fir dominate suburban forests.

Radiotelemetry

We trapped woodpeckers year-round using mist-nets, decoys, and playback (York et al. 1998) throughout each study area and near bird feeders during fall and winter when the birds did not show a strong enough response to the playback. Once we trapped a bird, we banded it and fitted it with a radio transmitter (model A1250 from Advanced Telemetry Systems, Isanti, MN; expected life 12 mo) using a Teflon^{TM} backpack harness modified from Buehler et al. (1995). We used 2mm-wide copper rings to secure the harness, instead of sewing the Teflon. Transmitter plus harness weighed ca. 11.5g, which is less than 5% of the weight of an adult pileated woodpecker. We released the birds back to the same area where we captured them. Our processing time was typically about 30 - 45 minutes. We used a R-1000 telemetry receiver (Communications Specialists, Orange, CA) and a hand-held 3-elements Yagi antenna to relocate each radio-tagged bird opportunistically, aiming to have at least one location per week. We recaptured and replaced transmitters on two birds that lost their original tags (69 and 174 days after their last relocation). We monitored the birds after release for 10-15 minutes and checked back on them the following day after release to verify that there were no adverse responses to the transmitter.

We recorded relocations of each bird on custom-made field-sheet maps based on current aerial photographs available online (Google Maps, Google Inc., Mountain View, CA) at approximately a 1:10000 scale. In cases when the location could not be easily mapped, we used GPS (GPSmap 60CSx, Garmin, Olathe, KS) to mark a reference point and we measured distance and bearing to the woodpecker location with a laser rangefinder (TruPulse 360B, Laser Technologies Inc., Centennial, CO).

Home range estimation

We used individuals that had a least 30 locations to estimate their home range using a fixed-kernel density estimator (KDE) to determine their utilization distributions (UD, Marzluff et al. 2004) on Geospatial Modelling Environment v. 0.7.2.1 (Beyer 2012) and ArcGIS 10.1 (ESRI Inc., Redlands, CA). We estimated the smoothing factor (h_{pi}) for each home range with the "plug-in" method, which is considered analytically robust and appropriate compared to other smoothing factor calculating methods used in the literature (Kertson and Marzluff 2011).

Behavior and time budget

As we tracked the individual birds, we recorded and categorized their behaviors (e.g. calling, drumming, foraging, perching, other) based on our best judgment, and the initial and ending time for each of them. If calling or drumming happened only once (normally lasting a few seconds), we counted those observations as a 1-minute observation. On average, we recorded individual's behaviors during 23.56 min ± 0.09 (mean ± SE, n = 255 visits); while focal observations (i.e. less than 5 minutes spent following an individual on a single visit) comprised a minimum fraction of the total time we followed each individual (mean ± SE, 1.51% ± 0.27, n = 13 individuals). We compiled the total time spent on each behavior by each individual and expressed this time budget as a percentage of the observation period. We used compositional analysis (Aitchison 1986; Aebischer et al. 1993) to compare the relative time budget of males and females. To do so, we log-transformed the ratio of the percentage of time spent on the target behavior (i.e. calling, foraging, drumming, perching, other) to the percentage of time for which we could not determine their activity.

Territoriality, core areas, and home range

We captured individuals on three contiguous home ranges within each area. We calculated overlap between paired individuals and with individuals on adjacent home ranges using 2D overlap and Volume of Intersection (VI), which involves overlap on the amount of use of each individual (Kernohan et al. 2001; Kertson and Marzluff 2011). We calculated 2D overlap by simply dividing the area in common that two individuals shared on their 95% home range polygons by the total area of the home range at 95% use.

We used this approach to establish where overlap occurred and to compare the portion of the home range that is shared by different individuals, but also to compare with other studies (e.g. Anich et al. 2009). The VI is the level of use the two UDs have in common, which equals the sum of the minimum use values that two individuals share on a pixel-by-pixel basis within the home range (extent of home range estimated as the 99% use contour). We performed such calculations on Quantum GIS v 2.10.1 – Pisa (QGIS Development Team 2015).

We also studied the spatial relationship between core areas, territory and home range. To do so, we used a subset of individuals for which we had observed territorial behavior (i.e. calling or drumming) in at least 15 locations (an adequate number for territorial kernel estimation as determined by bootstrapping, Anich et al. 2009). We compared a new UD based only on territorial display locations with a new estimation of a home range UD based only on other behaviors (i.e. just the locations where each bird exhibited non-territorial behaviors, such as foraging, perching, and preening). We used 2D overlap of the 99% KDE to assess spatial overlap between the home ranges defined by defended and by non-defended locations (Anich et al. 2009). However, a more nuanced assessment was also possible using a gradient of use based on the difference between the UD derived from territorial locations minus that derived from other (non-defended) locations. With this approach, we were able to define "highly defended areas" as places where use involving defense was greater than use involving other non-defensive behaviors (the territorial UD minus the non-territorial UD > 0, Fig. 2). By contrast, "other important areas" are those where the use calculated based on other behaviors surpassed the use by territorial behaviors.

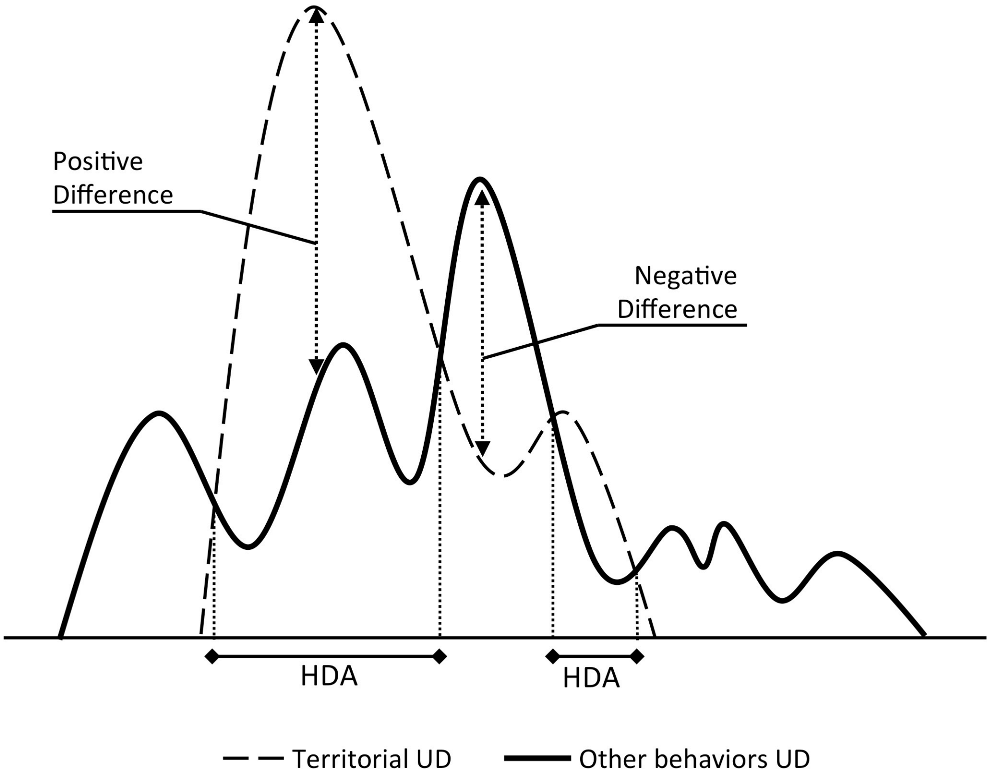

Figure 2. Calculation of highly-defended areas (HDA). The dashed line represents a hypothetical cross-section of the use volume of territorial behaviors. The solid line represents a hypothetical cross-section of the use volume of other behaviors. HDAs are areas of the home range where territorial use exceeds other behaviors use (positive difference).

To investigate habitat attributes associated with defensive behavior, we related the level of use of “highly defended areas” (hereafter HDAs) to 30 m resolution land cover data using concentration of use (Neatherlin and Marzluff 2004). Concentration of use is the ratio between the volume of use found on each cover type and the occurrence of each land cover type within the home range (Neatherlin and Marzluff 2004) and it is analogous to other selectivity measures that relate use to availability. We used classified 30 m resolution land cover data based on 2007 Landsat TM satellite imagery classified into 14 habitat categories (heavy urban, medium urban, light urban, cleared for development, grass/grassland, deciduous and mixed forests, coniferous forests, clear-cut forest, regenerating forest, agriculture, non-forested wetlands, open water, snow/bare rock, and shorelines for this analysis (Table 1, Alberti et al. 2006). We assessed differences between the concentration of use for each land cover type using ANOVA and Tukey post-hoc test as deemed necessary (Zar 1999).

Table 1. Land cover types that were used on this study as defined by Alberti et al. (2006)

Land cover type	Definition
Heavy Urban	>80% impervious area
Medium Urban	50-80% impervious area
Light Urban	20-50% impervious area
Grass/Grassland	Developed grass or grassland
Deciduous/mixed forest	10-80% deciduous or mixed forest
Coniferous forest	>80% coniferous forest
Clearcut forest	Recent clearcut area
Regenerating forest	Regenerating forest
Agriculture	Row crops and pastures
Other	Non-forested wetlands, open water, shorelines, bare rock/snow

RESULTS

We trapped 16 adult pileated woodpeckers (9 males and 7 females) between 2009 and 2012. We captured the same number of males on all three general areas, but the number of females varied slightly (Area: #males/#females captured, Maltby: 3/4, Redmond: 3/2, Bellevue: 3/1). We captured both members of three mated pairs (2 pairs in consecutive years, and 1 pair in the same year) as well as one male and female that shared an area but did not breed together. We discarded the data on 3 individuals because we had too few locations to conduct any analysis on them (fewer of 15 locations total). After following individuals for an average of 12.3 ± 0.98 months (10/13 of them we followed for more than 11.5 months), we obtained an average of 74.2 ± 12 locations per individual.

Behavior and time budget

Males and females spent their time similarly throughout the year. Assuming multivariate normality, we found no difference in the proportion of time each sex called, drummed, foraged, perched, or did otherwise (MANOVA, $F = 0.63$, $df = 5, 8$, $p = 0.68$). On average, woodpeckers spent ca. 29% of the time foraging, ca. 24% perching, ca. 9% calling and drumming, and ca. 6% on other activities. We could not confirm their activities ca. 32% of the time due to lack of visual contact with the focal individual, although it is most unlikely that the individuals were calling, drumming, or foraging because we heard none of the noises typically associated with these behaviors.

Territoriality: home-range overlap

We found significant overlap between mated males and females (Table 2). On average, males used 73.29% (2D overlap: range: 51.42 – 93.27%, n = 3) of the home range of the females, while females used 61.65% (range: 53.34 – 71.16%, n = 3) of the home ranges of the males. These values were not significantly different (Paired t-test, $t = 0.67$, $df = 2$, $p = 0.57$). The average volume of intersection between males and females was 52.2% (range: 45.96 – 56.28%, n =3).

By contrast, we found little overlap between neighboring woodpeckers. The average 2D overlap of adjacent woodpecker pairs was 4.5% (range: 0 – 21.82%), but this was significantly higher between woodpeckers of the opposite sex than between birds of same sex (One-tailed t-test, effect size = 9.5% overlap, $t = -3.35$, $df = 6.336$, $p = 0.007$). In fact, we found a significant interaction between the 2D overlap of the sex of the focal bird and the sex of the bird on the adjacent home range (Two-way ANOVA, $F = 17.95$, $df = 1,16$, $p < 0.001$) meaning that males overlapped a larger part of the adjacent female's home range than did adjacent females (Tukey HSD, effect size = 11.75%, $p = 0.008$); while females overlapped significantly more of their adjacent male's home range than did adjacent males (Tukey HSD, effect size = 6.38%, $p = 0.001$). Other combinations of 2D overlap where not significantly different. In a similar way, the average volume of intersection among birds on contiguous home ranges was only 2.08% (range: 0 – 6.98%) and it was higher between sexes than within sexes (One-tailed t-test, effect size = 3.4% overlap, $t = -2.79$, $df = 4.082$, $p = 0.02$). In this case, we found that the interaction between the sex of the focal bird and the sex of the bird on the adjacent home range was marginally significant (Two-way ANOVA, F = 5.470, $df = 1,6$, $p < 0.06$).

Table 1. Home range overlap in terms of area (2D overlap) and use (volume of intersection) between pileated woodpeckers in suburban areas of the Greater Seattle.

Sex		Total home range size (95% UD, in Ha)	Area of intersection (Ha)	2D overlap (percentage)	Volume of intersection (percentage 3D overlap)
Focal bird	Compared to				
Within breeding pairs					
M	F	169.8	120.8	71.2	54.4
F	M	235.0		51.4	
M	F	420.7	224.4	53.3	56.3
F	M	240.6		93.3	
M	F	168.6	101.9	60.5	45.9
F	M	135.5		75.2	
			Average	67.5	52.2
Between breeding pairs					
M	F	155.7	9.1	5.9	3.7
F	M	97.4		9.4	
F	F	97.4	0.0	0.0	0
F	F	240.6		0.0	
F	M	97.4	21.3	21.8	4.1
M	F	420.7		5.1	
F	F	97.4	3.3	3.4	2.3
F	F	135.5		2.4	
F	M	97.4	19.0	19.5	7.0
M	F	168.6		11.3	
M	M	351.8	5.6	1.6	2.1
M	M	112.0		5.0	
M	M	112.0	0.0	0.0	0
M	M	144.6		0.0	
M	M	169.8	0.0	0.0	0
M	M	182.7		0.0	
F	M	235.0	4.8	2.1	1.6
M	M	182.7		2.6	
M	M	297.7	0.0	0.0	0
M	M	182.7		0.0	
			Average	4.5	2.1

Home range vs. territory, core areas and highly defended areas

Pileated woodpeckers performed territorial displays (i.e. calling or drumming) mostly near but not at the edge of their home ranges. The average minimum distance between territorial displays and the edge of the home range was 129 m (±16, n=6). In addition, the 99% KDE area of territorial displays represented an average of 69.63% ± 0.06% of their home range. And the highly defended areas represented an average of 34.3% ± 0.03% of the home range, and 49.5% ± 0.01% of the territory. In terms of use, the highly defended areas represented an average of 31.8% ± 0.02% of the volume of the territorial UD. On the other hand, core areas, calculated using the method proposed by Vander Wal and Rodgers (2012), represented an average of 21.6% ± 0.02% of the home range.

We found no significant difference in the concentration of use among the different land cover types in the territories (ANOVA, F = 0.383, *df* = 6, 35, p = 0.885) or in the highly defended areas (ANOVA, F = 1.613, *df* = 6, 35, p = 0.17). Also, we found that most of the roost sites were located inside highly-defended areas (14/17), and although we found a similar number of nests inside (6/11) and outside (5/11) highly-defended areas, the overall ratio of roosts and nests did not significantly differ from expected (Chi-squared test, $X^2_3 = 5.99$, p = 0.11), indicating that most nests and roost were placed inside the HDAs (we found them on a ratio of 72:28 inside vs. out).

DISCUSSION

Use of space is central to understanding ecological relationships between species and their environments, their relationships with other organisms and how to address their conservation needs. Ecologists have addressed such questions with many different approaches and have furthered the understanding that not all space is equally important (Noble 1939; Odum and Kuenzler 1955; Samuel et al. 1985; Marzluff et al. 2004). Concepts like home range, core areas, and territories, have emerged to recognize such differences, but they have also been used interchangeably, muddling their usefulness (Powell 2000). Moreover, as ecologists are now better equipped to study animal's use of space in more detail with current technologies and quantitative tools, they have inadvertently lost track of the significance and need of behavioral observations on the definition and understanding of such concepts. But it is by coupling behavioral observations to location data that the understanding of space use and the interactions between different purposes of space use that becomes more biologically meaningful (Marzluff et al. 2001). Here we applied a more objective, behavior-based approach to define highly-defended areas, which could be interpreted as the core of an individual's territory and explored spatial relationships between home range, territory, core areas, and highly-defended areas. By determining the areas where territorial use exceeds other uses (Fig 2), we were able to distinguish areas that were defended at a higher rate than expected by occasional defense that may be correlated with space use while performing other behaviors. And, although the definition of the highly-defended areas may be dependent on the correct identification of behaviors as territorial, they are far less arbitrary than many other definitions for core areas are (Powell 2000; Chamberlain et al. 2000; Warning and Benedict 2015). Also, since HDAs are not shaped by the contours of the isopleths of all behaviors combined, but by differences on relative importance of territorial behavior relative to other behaviors, they mark the areas where important and defensible resources may be present, regardless of patterns of overall use of the home range.

Advancing our understanding of core area, territory, and home range

Even though the relationship between home range and territory in birds has gained more attention in recent years, there are still very few studies addressing such question (Ferry et al. 1981; Naguib et al. 2001; Bas et al. 2005; Anich et al. 2009). Nonetheless, we found some similarities on the ratio between the size of home range and territory compared to our study. For example, Swainson's warblers (*Limnothlypis swainsonii*) had highly variable ratios of home range to territory size, but the average was 70% (range: 21 – 130%, n=16), which is practically identical to the ratio we found between the size of the area where pileated woodpeckers conducted territorial displays (69.63 ± 0.06, mean ± SE, n=6), while territories were 54% ± 6% of the home ranges in Nightingales (*Luscinia megarhynchos*, Naguib et al. 2001). In both cases, the home ranges and territories were estimated using MCP. Early theory suggests that population density may influence the size of the home range and make it closer to the territory (Burt 1943), which is something we could not test in our area.

Our behavior-based definition of highly used areas of the territory differs from prior arbitrary definitions (e.g. 50% UD, Chamberlain et al. 2000; Warning and Benedict 2015) and from purely quantitative definitions (Seaman and Powell 1990; Powell 2000; Vander Wal and Rodgers 2012) of core areas in the sense that these behavior-based territories are delineated by observing the animal of interest. Interestingly, the quantitative approach that Vander Wal and Rodgers (2012) used for moose (*Alces alces*) relocation data defined an average core area around the 58.25% (0.78%) isopleth. This represented 27.11% (0.26%) of the home range size, which is significantly lower than our estimate of 34.30% (0.02%, One-sided t-test, effect size = 7.192, t_{obs}= 2.625, df=4.6, p = 0.021) for the highly defended areas, but just close to be significantly different to the 21.57% ratio between core areas and home range (Two-sided t-test, effect size = 5.539, t_{obs}= 2.625, df=4.6, p = 0.058). Besides this difference in value, defining the core areas using isopleths of the UD assumes that the shape of the isopleths estimated from all behaviors influences the most important areas. We found that if we used the Vander Wal and Rogers' (2012) method to define core areas, part of our HDAs was contained on them, but they were not constrained to the shape of individual isopleths (Fig 3). On the other hand, the use of spatially-explicit behavioral observations to construct behavioral-specific utilization distributions provides useful information about the mechanism that determine how and why animals use space the way they do (Marzluff et al. 2001).

Our approach estimates areas of high importance based on differences in behavior—not based on the shapes of isopleths. Thus our approach is better able to capture the shapes of territories. In our case, the shape of the HDAs did not seemed to be driven by land cover features, but by the location of important resources, like nests and roosts (especially the latter). We mapped calculated highly defended areas, but other intersections of behaviors could be used in a similar fashion. Ultimately, bridging behavioral and spatial ecology will not only expand our ecological knowledge, but can help inform conservation using a mechanistic approach based on behavior.

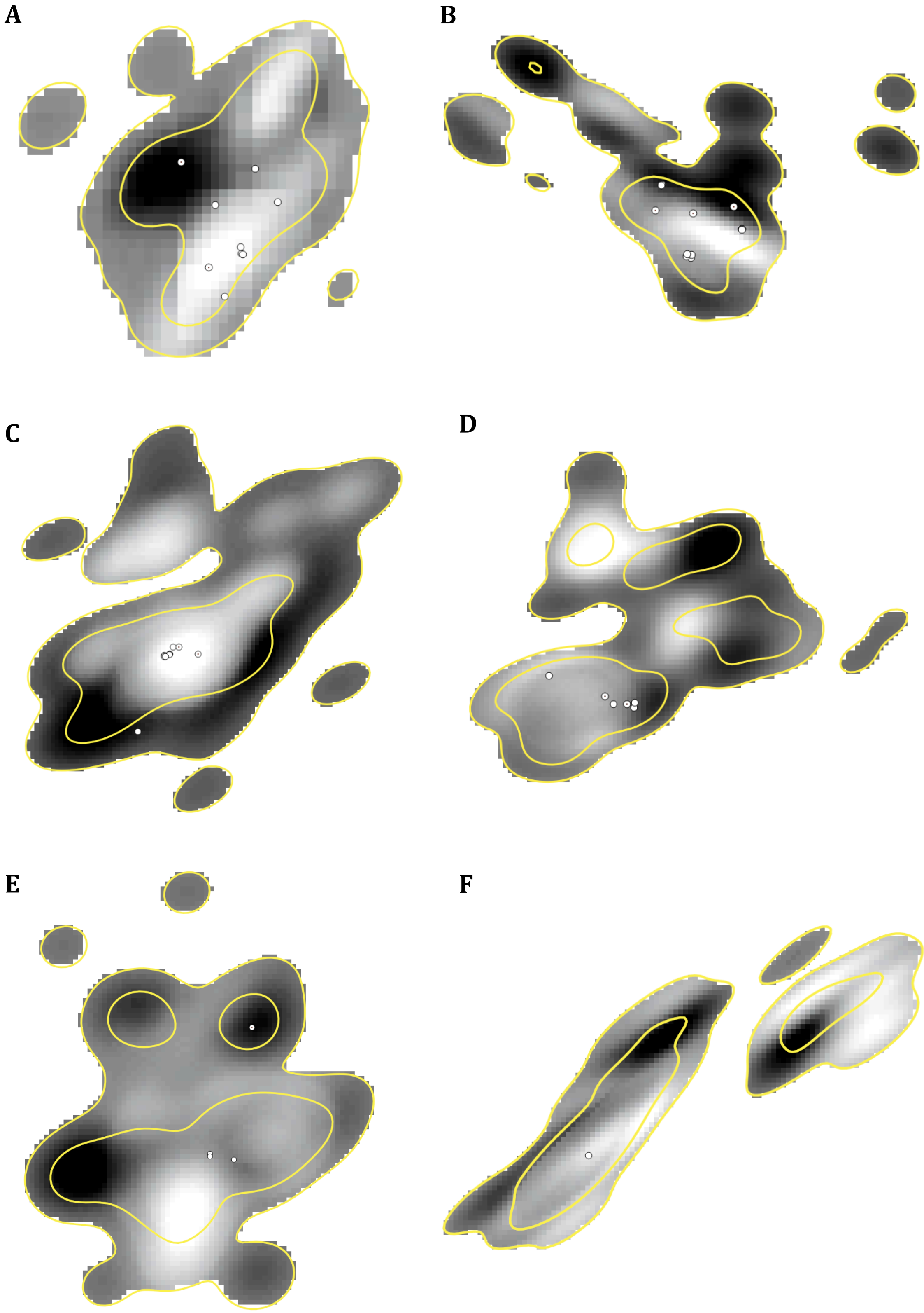
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Figure 3. Behavioral gradient for six individual pileated woodpecker home ranges (defined at 95% level). Highly-defended areas are presented in white (maximum difference) and light gray. Black indicates areas with the maximum negative difference between territorial use and other behaviors use. The individuals presented are females (A, F) and males (B, C, E, D). Individuals C and D were a breeding pair. Open white circles represent roost site locations. White circles with black dots represent nest locations. The home ranges are not presented at the same scale.

Use of Space by Pileated Woodpeckers in a Suburban Environment

Pileated woodpecker mates are known to keep their bond year-round and spend most of their time together or in close proximity (Kilham 1979; Bull and Jackson 2011), and although they may not perform the same behaviors all the time, on average they used their time in similar proportions in our area. This resulted in significant overlap of the home ranges of males and females of the same pair. The degree of overlap seems to be defined by the breeding status of the pair: when pairs successfully fledge juveniles and are feeding them outside the nest, they divide their offspring for foraging (Mellen et al. 1992; Bonar 2001) producing a smaller home range overlap than for pairs that do not have young (Mellen et al. 1992). Unfortunately, we did not have enough non-breeding pairs to assess this difference.

The pileated woodpecker is a territorial species (Hoyt 1957; Kilham 1959; Mellen et al. 1992; Bull and Jackson 2011), as expected for species that require resources that are scarce and defendable (e.g. snags, Brown 1964). As with many other cavity nesters (Newton 1994), pileated woodpeckers may be limited by the provision of snags in which to excavate their nests, roosts, and to forage; especially in built portions of urban and suburban areas, where snags are less common, if present at all, than in the their forested portions or natural areas (Blewett and Marzluff 2005). Both the male and the female have been found to defend territories (Mellen et al. 1992; Bull and Jackson 2011). Our results are consistent with this pattern. We observed both members of the pair actively defending their territories when we conducted our trapping sessions (where we used playback to lure them to the mist-net) and during the year as we followed and observed them in the field. We even found that males and females spent similar proportions of their time on territorial behaviors as well (i.e. calling, drumming), which contrasts with previous accounts that “females seem to drum far less than males” (Kilham 1959). We found further evidence of intraspecific territoriality with the little home range overlap we observed between individuals of neighbor pairs. The degree of overlap that we found between neighboring pairs is lower than the 9 – 30% overlap found on Western Oregon (Mellen et al. 1992), which we suspect was due to inadequacy in estimation, not ecology. Mellen et al. (1992) used MCP which is known to overestimate the space used by animals (Powell 2000), which could readily result on overestimating of the overlap between them as well. However, other studies have reported little to no overlap between neighboring pairs using MCP as well (Bull and Holthausen 1993; Bonar 2001). Interestingly, our data also shows intrasexual territoriality, as the overlap between members of the same sex was lower than the overlap of members of different sexes, supporting what was described by Bull and Jackson (2011) for this species, a pattern that has been shown for mammals as well, especially carnivores (Powell 2000).

Pileated woodpecker displays are loud and can be heard at great distances (Bull and Jackson 2011). And given that woodpecker auditory sensibility resembles songbirds of similar size (Lohr et al. 2013), individuals did not need to display at the edge of their home ranges to effectively defend them, potentially reducing the cost of actually displaying on a larger proportion of the home range. The minimum distance of ca. 130m between territorial display locations and the edge of the home range clearly is less than the distance individuals of this species can hear. We have some empirical evidence to support this, as we have been able draw individuals from distances greater than 200m using playback, which supports the idea that individuals could be effectively defending the edge of the home range with territorial displays at certain distance from its interior.

The similarities on territory:home range size ratios and core area:home range size ratios that we found compared with other unrelated taxa highlights the need for further exploration of potential consistency on these patterns. Such patterns may indicate potential relationships between cost and benefit of defending resources present on the home range. Also, our proposed use of a behavior-based definition of highly-defended areas also could be used to distinguish differential value of the resources present within the territory and their underlying ecological importance, something that has been done mostly at the home range level, but not for UD pertinent to specific behaviors. In a similar fashion, this approach could be used to relate resources to the relative importance of other behaviors of interest, further advancing a spatially-explicit understanding of behavioral ecology, giving us a more complete picture of the life history of species.

Acknowledgements

We thank Jon Bakker, Joshua J. Lawler, Martin G. Raphael, Kaeli Swift, Lauren Walker, Jack DeLap, Carol Bogezi, and Michael Heimbuch for their invaluable comments at different stages of the development of this manuscript. We thank Jim Ladd, Kim Holt, April Gale-Seixeiro, Sharon Shriver, Dale Griffith, and Jim Rettig for kindly allowing us to trap pileated woodpeckers on their property. We thank 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. JAT conducted this research while on Fulbright-Conicyt scholarship.

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