

EFFECTS OF URBAN SPRAWL ON SNAGS AND THE ABUNDANCE AND PRODUCTIVITY OF CAVITY-NESTING BIRDS

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Abstract. We investigated the occurrence of, and relationships among, snags and cavity-nesting birds in the rapidly urbanizing region around Seattle, Washington in 2001 and 2002. We measured the density of snags in 49 sites (1-km² “suburban landscapes” that included built and forested portions), and determined the diameter, height, decay status, and species of individual snags. We spot-mapped territories and observed nests of cavity-nesting birds at a stratified, random subsample of 13 sites. Snags, especially red alder (*Alnus rubra*), were abundant in sites’ forested portions, but rare in the built portions. Snag density was positively correlated with density of live trees. Snags in built versus forested portions were similar in all attributes except decay, which was more advanced in forested areas. In the oldest suburbs (60–80 years old), snags in forested portions were larger, more decayed, and more likely to have broken tops than those in younger suburbs (2–20 years old). Cavity-nesting bird species richness and equity of individuals per species was highest in suburban landscapes where remaining forest was not fragmented, but adjacent to highly intermixed urban and urban-forest land covers. Suburban landscapes with highly interspersed land covers had higher densities of Black-capped Chickadees (*Parus atricapillus*), Red-breasted Nuthatches (*Sitta canadensis*), Northern Flickers (*Colaptes auratus*) and Downy Woodpeckers (*Picoides pubescens*); suburban landscapes with higher percentages of forest had higher densities of Brown Creepers (*Certhia americana*), Chestnut-backed Chickadees (*Parus rufescens*), Pileated (*Dryocopus pileatus*) and Hairy Woodpeckers (*Picoides villosus*). Red-breasted Sapsucker (*Sphyrapicus ruber*) densities were positively correlated only with the density of snags. All study sites had low bird densities compared to wildlands, presumably due to the relative lack of live trees and snags. Cavity-nesting birds bred successfully in all landscapes; seven of the nine species produced fledglings in >50% of their nesting attempts. Snags important for nesting were larger in diameter, taller, and more decayed than expected based on availability. Snags with active nests also had evidence of previous use, fungal conks, broken tops, and substantial bark.

Key words: cavity-nesting birds, density, land cover, productivity, Seattle Washington, snags, urban sprawl.

Efectos de la Expansión Urbana sobre la Abundancia y la Productividad de Aves que Nidifican en Cavidades

Resumen. Durante el 2001 y 2002, investigamos la presencia de, y la relación entre, troncos muertos y aves que nidifican en cavidades en los alrededores de Seattle (Washington), una región que está urbanizándose rápidamente. Medimos la densidad de troncos en 49 sitios (1-km² de “paisajes suburbanos” que incluyeron ambientes edificados y bosques) y determinamos el diámetro, altura, estado de descomposición y especie de troncos individuales. Mapeamos los territorios mediante registros puntuales y observamos los nidos de aves que nidifican en cavidades en una sub-muestra estratificada y al azar de 13 sitios. Los troncos, especialmente de *Alnus rubra*, fueron abundantes en las áreas con bosque, pero raros en las áreas edificadas. La densidad de troncos se correlacionó positivamente con la densidad de árboles vivos. Los troncos de las áreas edificadas y de las áreas con bosque fueron similares en todos sus atributos excepto en su descomposición, que fue más avanzada en los sitios boscosos. En los suburbios más viejos (60–80 años), los troncos en las áreas con bosque fueron más grandes, estuvieron más descompuestos y presentaron mayor probabilidad de tener sus extremos rotos que aquellos presentes en los suburbios más nuevos (2–20 años). La riqueza de especies que nidifican en cavidades y la equitatividad de individuos por especie fueron mayores en los paisajes suburbanos donde el bosque remanente no estaba fragmentado, sino adyacente a coberturas con una gran mezcla de sitios urbanos y sitios en la transición bosque-ciudad. Los paisajes suburbanos con coberturas ampliamente entremezcladas presentaron mayores densidades de *Parus atricapillus*, *Sitta canadensis*,

Colaptes auratus y *Picoides pubescens*; los paisajes suburbanos con porcentajes más altos de bosque presentaron mayores densidades de *Certhia americana*, *Poecile rufescens*, *Dryocopus pileatus* y *Picoides villosus*. Las densidades de *Sphyrapicus ruber* sólo se correlacionaron positivamente con la densidad de troncos. Todos los sitios de estudio tuvieron bajas densidades de aves comparados con áreas silvestres, debido presumiblemente a la carencia relativa de árboles vivos y troncos. Las aves que nidifican en cavidades criaron con éxito en todos los paisajes; siete de las nueve especies produjeron volantones en >50% de sus intentos de nidificación. Los troncos importantes para nidificar fueron más grandes en diámetro y altura y estuvieron más descompuestos que lo esperado con relación a su disponibilidad. Los troncos con nidos activos también presentaron evidencias de uso previo, deformaciones producidas por hongos, copas rotas y bastante corteza.

INTRODUCTION

Urbanization is increasing world wide and affecting local and global ecological systems (Marzluff 2001, Pickett et al. 2001, Alberti et al. 2003, Imhoff et al. 2004). This global trend is evident in the western United States, where cities, counties, and states are among the fastest growing in the nation (Hansen et al., in press). Between 1990 and 2000, for example, the state of Washington had the 10th fastest growing population in the country (U.S. Census Bureau 2000). Incorporated land area in the four counties surrounding Seattle increased by an average of approximately 47% during this time (PSRC 2001), mostly at the expense of second growth forest (Alberti et al. 2004). In western Washington, as in much of the western US, most development occurs at the interface between existing settlements and wildlands and proceeds in a leap-frog, sprawling fashion away from the most urban areas (Robinson et al. 2005). The result is a mixture of high-density housing developments that contain few to no forest fragments and single houses on large lots that punctuate wildlands.

The expansion of cities often perforates, isolates, and degrades natural land (Meyer and Turner 1992, Matlack 1993, Marzluff and Hamel 2001, Faulkner 2004). These processes have substantial and lasting effects on bird communities (Marzluff and Ewing 2001) by altering the amount, composition, and arrangement of vegetation (Hostetler 2001, Melles et al. 2003), creating barriers to movement (Fernández-Juricic 2000) and changing local temperature, food supply, predators, and parasites (Bowman and Woolfenden 2001, Crooks et al. 2001, Marzluff 2001, Chance et al. 2003, Thorington and Bowman 2003, Sinclair et al. 2005, White et al. 2005). Richness may peak in moderately-disturbed sites where vegetation diversity is great, but bird species present in wildlands often dis-

appear as the level of urbanization increases (Blair 1996, 2001, Donnelly and Marzluff 2004).

Cavity-nesting birds may be especially sensitive to urbanization because they depend on snags for nesting, roosting, and foraging (Thomas et al. 1976, Davis 1983, Bull et al. 1997). Snags are removed from urban areas during initial construction for safety reasons, and over time by homeowners and increased exposure to wind along newly created edges. In wildlands, we know that cavity-nesting bird densities and nesting success decline if snag densities are low or snags with appropriate characteristics are not available (Cline et al. 1980, Zarnowitz and Manuwal 1985, Christman and Dhondt 1997, Aubry and Raley 2002). Cavity-nesting birds also decline in urban areas (DeGraff and Wentworth 1986, Tilghman 1987, Natuhara and Imai 1996, Rottenborn 1999, Fraterrigo and Wiens 2005), but except for a few studies that investigated competition for nest sites between woodpeckers and European Starlings (*Sturnus vulgaris*; Ingold 1989, 1994, 1996), the mechanisms accounting for declines are not known. Also, despite concern for snags and cavity-nesting birds in areas dominated by timber harvest (Brown 1985, Morrison et al. 1986, Raphael and White 1984, Ohmann et al. 1994), at the time of this study we were aware of no studies that investigated snag densities, snag characteristics, and their link to cavity-nesting birds in urban areas. This lack of basic knowledge is likely responsible for infrequent consideration of cavity-nesting bird requirements in urban snag policies (Fischer and McClelland 1983, King County 2000, Seattle Public Utilities 2000, except see Dove 1987).

To better understand snag densities and qualities as possible mechanisms controlling cavity-nesting bird densities and reproductive success in urban areas, we studied the effects of land-

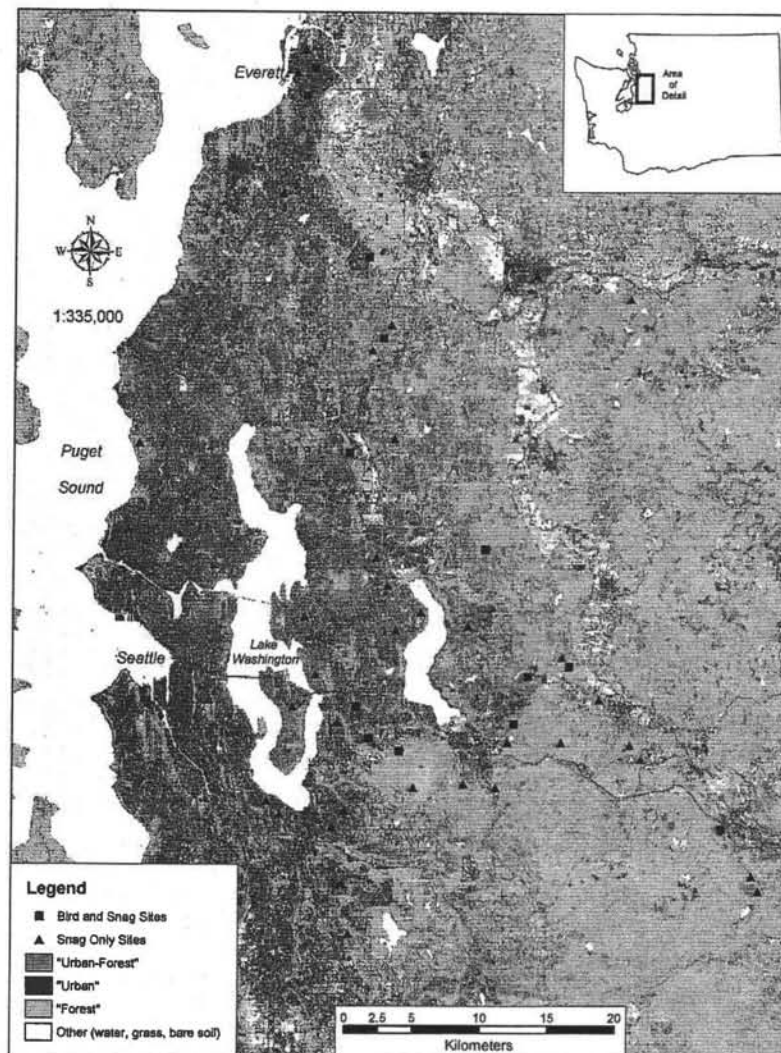


FIGURE 1. Locations of study sites in Seattle, Washington 2000–2001. Land cover data are at 30 m $\times$ 30 m resolution from a 1998 classified satellite image.

scape variables (types and amount of land covers, and their spatial relationships) and relevant site variables (mean age of built portion, vegetation attributes) on snag densities and snag characteristics (e.g., height, diameter, decay class), and compared snag densities and snag characteristics between developed and forested sections of a site. We also compared snag abundance and landscape and site variables to bird species richness and evenness, density, and reproductive success. Lastly, we investigated characteristics of snags used for nesting by cavity-nesting species.

METHODS

STUDY AREA AND SITE SELECTION

We chose 49, 1-km² “suburban landscapes” (Marzluff et al. 2001) within a 3200 km² area of temperate, moist forest around Seattle, Washington (study sites; Fig. 1). Each study site included built portions (single-family residential) and 37 sites also had forested portions. Forests were mostly coniferous, including western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), and western red cedar (*Thuja plicata*), with a few hardwoods occurring near

TABLE 1. Ranges of landscape variables among 49 study sites (100 ha each) in the greater Seattle area using classified satellite land cover data from 1998. Land cover types were considered urban, forest, and mixed urban forest (see text for details). We randomly selected study sites after stratifying the region on a per 100 ha basis using three variables: percent coverage of the dominant land cover, mean patch size of the urban and forest land cover, and a measure of land cover spatial arrangement called "contagion" (whether land cover types tend to be clumped or interspersed). A fourth variable was calculated after sites were chosen: forest aggregation (contagion calculated only using forest land cover). Contagion and forest aggregation range from 0 (maximum interspersed)–1.0 (maximum clumping). Mean patch size ranges from 0–100 ha. Bird productivity was calculated from a subset of the snag sites.

Dominant land cover	<i>n</i> (sites)	Percent cover	Contagion	Forest aggregation index	Mean patch size (ha)	
					Urban	Forest
Snag sites						
Forest	19	40–96	0.16–0.89	0.59–0.98	0.1–1.6	2.3–86.0
Urban forest	10	42–75	0.10–0.47	0.33–0.71	0.3–2.6	0.2–1.8
Urban	20	38–95	0.09–0.82	0.00–0.95	1.8–89.7	0.0–5.0
Bird productivity sites						
Forest	5	60–96	0.29–0.89	0.79–0.98	0.1–1.4	2.5–30.6
Urban and urban forest	8	60–100	0.09–0.82	0.00–0.95	0.5–91.5	0.0–5.1

riparian and disturbed areas: red alder (*Alnus rubra*), big-leaf maple (*Acer macrophyllum*), black cottonwood (*Populus trichocarpa*) and Oregon ash (*Fraxinus latifolia*; Franklin and Dyrness 1988). Elevation varied from sea level to near 300 m on the lower slopes of the Cascade Range.

We randomly selected sites after stratifying the entire area on a per km² basis by the amounts and arrangements of land cover. Botsford (2000) classified land cover from satellite imagery into "urban" (pixels containing >60% paved, or pixels containing <25% trees, >25% grass and <60% paved), "forest" (pixels with >60% trees), and mixed "urban-forest" (pixels >25% trees, and >20% but <60% paved). Stratification was based on variation in three landscape attributes: percent of land cover type in a landscape, average patch size of urban land cover, and the probability that two randomly chosen adjacent pixels belong to the same class, (contagion; Table 1). Sites varying in contagion ranged from aggregated land cover to interspersed; (Fig. 2). Calculations were done with Geographic Resource Analysis Support System (GRASS Ver. 4) with r.le add-on programs, and Fragstats (Ver 3.1) software (Baker 1997). Landscape variables may be correlated with each other, thus we selected the fewest that adequately described important characteristics of study sites (Alberti et al. 2001, Rohila 2002). We selected a subset of thirteen sites in a stratified-random fashion from the 49 sites to study cavity-nesting

bird productivity (Fig. 1). We used fewer sites because of the much greater effort necessary for territory mapping.

We quantified two additional variables after site selection for use in regression models. Forest aggregation (probability that "forest" pixels are adjacent) measured the connectivity of forested portions of the site. Mean age of the built portion of each site, determined using 2001 King and Snohomish County parcel databases and assessor's information, indicated the duration of residential development in the site. Mean ages ranged from 2 to 84 years (mean = 28.5 ± 2.8 years, $n = 49$).

The sites we chose were also representative of their immediately surrounding areas (Fig. 2). To make sure no sites where we spot-mapped birds were biased (e.g., for higher bird densities) by uncharacteristically large or small tracts of forest adjacent to the site, we correlated the amount of forest inside the 1-km² site to the amount contiguous with the sites. The amounts of forest in, and contiguous to, the sites were significantly related ($r = 0.56$, $df = 13$, $P < 0.05$). The area of additional forest measured for each site varied (0 to 31 km²), depending on the extent of the forest contiguous with that site.

DATA COLLECTION

Snags. In late summer and fall of 2000 and 2001, we completely censused the built portion of each site, and surveyed the forest portion using 3–11, randomly placed, 0.09-ha circular

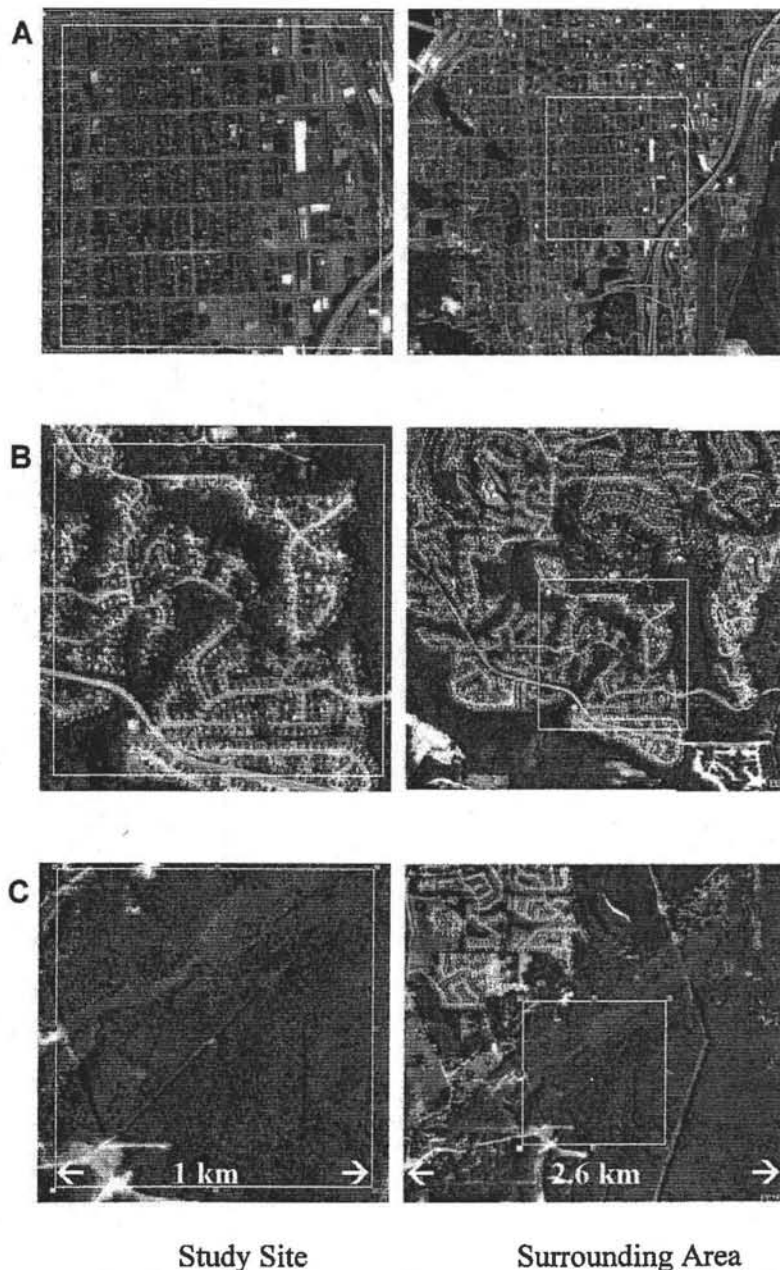


FIGURE 2. Digital orthophotos of three Seattle, Washington study sites to illustrate three landscape ecology variables: percent of forest versus urban land cover, patch size, and contagion. Low values of contagion indicate land cover types are interspersed, high values indicate land cover types are aggregated. Low values of forest aggregation indicate that forest is interspersed with other land cover types, high values indicate forest is aggregated. Variables were calculated using three land cover types: urban, forest, and urban-forest (Botsford 2000) as defined in the text. Satellite images are in two scales (study site [1-km²] and surrounding context) for (A) Highly urbanized: contagion = 0.82, forest aggregation = 0; forest = 0%, urban = 95%, urban forest = 5%; mean urban patch size = 84 ha; (B) Highly interspersed: contagion = 0.09; forest aggregation = 0.71; forest = 27%, urban = 38%, urban-forest = 35%; mean forest patch size = 3.2 ha; mean urban patch size = 3.3 ha; and (C) Highly forested: contagion = 0.44, forest aggregation = 0.89; forest = 71%, urban = 3%, urban-forest = 25%; mean forest patch size = 23 ha, mean urban patch size = 0.2 ha.

plots. If forested portions were <1 ha ($n = 5$), we censused snags. If snags in the built portions were inaccessible (behind fences) we estimated all parameters. The number of forest survey points per site was determined by obtaining a minimum number of snags ($n = 10$) in each of three size groups. We divided snags into diameter at breast height (DBH) groups based on requirements for nesting by different bird species: small snags (8–24.9 cm), medium snags (25–39.9 cm), and large snags (>40 cm).

We collected density (snags per hectare) and characteristics of all snags >8 cm DBH within the circular plot. We defined snags as completely dead trees and live trees with fewer than four live primary branches or with only live shoots. We identified the tree species, measured DBH, visually estimated height, and placed each snag in a decay class (after Bull et al. 1997) from 1 (hard) to 3 (soft). We visually estimated top condition (broken or intact), percent tree lost, remaining percentage of bark, and the presence and type of heart- and sapwood decay fungi (Bull et al. 1997). We quantified previous cavity-nesting bird use of snags by identifying and counting existing cavities excluding starts (Bull et al. 1997).

Live trees. Live trees were defined as trees >8 cm DBH with greater than four live primary branches. We surveyed live trees using four to eight randomly located 0.09-ha circular plots in the built portions, and within all survey plots in the forested portions. We counted all live trees and recorded their species, and selected a sample of eight live trees in each plot to measure DBH by taking the nearest tree to the center point in eight compass directions (N, NE, E, SE, S, SW, W and NW). We calculated live tree densities (trees ha⁻¹), percent of each species, and mean DBH.

Birds. We searched for territories and nests of eight species of native cavity-nesting birds (Black-capped and Chestnut-backed Chickadees [*Parus atricapillus* and *P. rufescens*], Red-breasted Nuthatches [*Sitta Canadensis*], Red-breasted Sapsuckers [*Sphyrapicus ruber*], Hairy [*Picoides villosus*], Downy [*P. pubescens*], and Pileated [*Dryocopus pileatus*] Woodpeckers, Northern Flickers [*Colaptes auratus*], and Brown Creepers [*Certhia americana*], a bark flake-nesting species. From April through July 2001, we used a modified behavioral mapping technique (The International Bird Census

Committee 1970), nest searching (Ralph et al. 1993), and the Vickery index (Vickery et al. 1992, Christoferson and Morrison 2001) on all nine species to sample the 1-km² site for species richness, evenness, density, and productivity. We spent equal effort (time) at each site, attempting to cover as much area as possible in both built and forested portions throughout the breeding season. Total area surveyed differed among sites (22 to 100 ha, mean = 52 ± 7 ha) because greater areas could be covered in sites with mostly built portions than in sites of mostly forest. Productivity for each species per site was determined by the average Vickery rank of all territories of that species. The Vickery method required observing bird behavior on territories to determine breeding status and success. Vickery ranks range from 1 (single bird) to 5 (successful fledging) for single-brooded species and 1 to 7 (successful fledging in two broods) for double-brooded species. If a bird species was not present at a site, we assigned the site Vickery rank of 0. We combined territory mapping with the Vickery index because nests of the larger woodpeckers were rare across the landscape, and access barriers in the urban setting prevented finding some nests but not observing parental behavior and fledglings.

We surveyed each site at least every two weeks throughout the breeding season and visited each identified bird territory a minimum of six times (International Bird Census Committee 1970). Behavior mapping and nest searching occurred between dawn and 15:00 (PST) daily, maximizing the morning hours for mapping and afternoon hours for nest searching and monitoring. For additional methodology on territory mapping and nest searching see Rohila (2002).

We gathered characteristics of snags used for nesting in 2000, when only nest-searching techniques were used, and in 2001 during territory mapping. We were able to combine data from two years because no birds ever used the same cavities more than once either between years or within the same year.

STATISTICAL ANALYSES

We completed all statistical analyses using SPSS 10.0.5 software (SPSS 1999). To meet assumptions of normality and equal variances, we transformed all percentages or proportions using arcsine square root, and transformed mean urban patch size using log 10 (Zar 1996). In cases

where assumptions of parametric tests were not met even after transformation, we used nonparametric methods and noted these accordingly. All data are reported as means $\pm$ SE.

We compared snag densities ($n = 37$ sites) and snag characteristics ($n = 33$ sites) between forest and built portions using paired t -tests. We assessed the correlations between landscape variables (percent forest, forest aggregation, mean urban patch size) and site variables (mean age of built portion, live tree density, live tree DBH) with snag densities and snag characteristics using full factorial general linear models. We reported models with the highest adjusted R^2 value, and all P -values.

We used full factorial general linear models to assess the correlations of landscape variables (contagion, percent forest, and their interaction [where land covers were interspersed, but forest remained contiguous]), and snag density with bird species richness, evenness, density (or presence and absence when samples were small), and productivity. We combined medium and large snag groups for the analyses with birds because the results were the same when analyzed individually. We report models with the highest adjusted R^2 and all P -values.

We compared the characteristics of snags used for nesting to those of all snags measured at the sites. We compared mean DBH, mean height, and mean percent bark remaining using the normal deviate (Z -score) following Zar (1996). We compared frequency of nest snags that were of each decay class, had a broken top, other cavities, conks, or other fungus using Chi-squared analysis (χ^2) with the Yates continuity correction (Zar 1996). We also tested use of snag species (red alder, other deciduous, and coniferous) using χ^2 analysis.

We first analyzed all bird species separately then combined them according to similar preferences to increase sample size. We grouped all large woodpeckers ($n = 23$ nests) except Red-breasted Sapsuckers; they appeared to select different snags than the other large primary excavators, but sample size was too small to report that species' results ($n = 6$ nests). We analyzed three species separately because they had adequate sample size: Chestnut-backed Chickadees ($n = 17$), Black-capped Chickadees ($n = 21$), and Brown Creepers ($n = 22$), and did not analyze Red-breasted Nuthatches due to small sample size ($n = 3$).

RESULTS

SNAGS AND TREES

Densities. Densities of snags and live trees in forested portions were significantly greater than in built portions, regardless of snag DBH group (Snags: small, $t_{36} = 10.2$, $P < 0.001$, medium, $t_{36} = 9.6$, $P < 0.001$, and large, $t_{36} = 9.9$, $P < 0.001$; Trees: $\bar{x}_{\text{forest}} = 28.6 \pm 1.1$, $\bar{x}_{\text{built}} = 8.9 \pm 1.0$; $t_{36} = -13.5$, $P < 0.001$; Fig. 3). In fact, densities of snags in forested portions were comparable to densities found in wildlands (Fig. 3). Snag density was consistently and positively correlated with live tree density in forested and built portions (Table 2). Densities of large snags in forested portions were positively correlated with the mean age of the built portion. The density of snags in forested portions was not strongly correlated with snag density in built portions, regardless of DBH ($P > 0.1$ in all cases). Densities of snags in all DBH groups except medium-sized snags in forest portions were correlated with landscape or site variables; however, much variation was left unexplained (Table 2).

Characteristics. Mean DBH of snags in forested portions was positively correlated with forest aggregation, mean age of the built portion, and DBH of live trees (Table 2). Mean DBH of snags in built portions was negatively correlated with percent forest and mean urban patch size. Snags in forested portions became more decayed with mean age of the built portion and percent forest. Decay of snags in built portions was positively correlated with percent forest within the 1-km² sampling site. Percentage of snags in forested portions with broken tops was positively correlated with mean age of the built portion and percent forest. Percentage bark remaining for snags in built portions was positively correlated with mean age of the built portion, and negatively correlated with percent forest.

Differences in live tree and snag characteristics between the forested and built portions were few. Snags occurred within the forested portions of all but two sites; those were completely manicured small parks. Only four sites had no snags within the built portions. Mean DBH of live trees was larger in forested portions ($40.1 \text{ cm} \pm 1.4$) than in built portions ($30.1 \text{ cm} \pm 1.5$; $t_{36} = 5.1$, $P < 0.001$). Snags in forested portions were

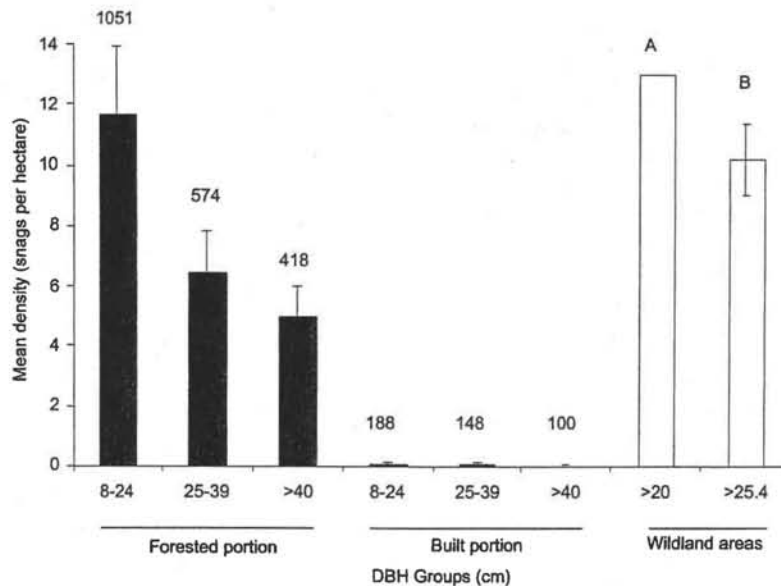


FIGURE 3. Densities of snags (number of snags per ha) in forested ($n = 37$) and built ($n = 49$) portions of Seattle area study sites for 2000–2001, data from both years combined. Snags were grouped by diameter at breast height (DBH) based on nesting requirements for different bird species: small snags (8–24.9 cm), medium snags (25–39.9 cm), and large snags (>40 cm). Numbers above bars are sample sizes (snags). For comparison, unfilled bars represent snag densities from two recent studies in wildland settings: (A) Aubry and Raley (2002), and (B) Ohmann and Waddell (1999). All data are presented as means $\pm$ 2 SE.

more decayed on average (2.0 ± 0.02) than in built portions (1.8 ± 0.07 ; $t_{32} = 2.8$, $P < 0.05$).

Sixteen different species of snags were identified. Most were red alder (50% of 977 measured snags), big-leaf maple (14%), Douglas fir (12%) and western hemlock (12%). Other species represented 5% or less of the snags surveyed.

CAVITY-NESTING BIRDS

Community composition. Richness increased with increasing interspersions of all land cover classes (decreasing contagion), if forest remained highly aggregated (Table 2). Evenness had the same relationship with landscape attributes as did richness, but much less variation was explained (Table 2). Four sites used by all nine species had 27% to 60% forest and 40% to 73% urban and urban-forest land cover, with low values of contagion (0.09 to 0.29), but high values of forest aggregation (0.69 to 0.82), similar to what is depicted in Figure 2B. The two most urban sites (0% forest, e.g., Fig. 2A.) only had two or three species (Chestnut-backed and Black-capped Chickadees, and Northern Flickers).

Densities. In 2002, we found 321 territories in both the forest and built portions of sites (Table 3). Density or occurrence of each species was significantly related to landscape or site variables (Table 2). Landscape variables were most important to eight of nine species. Interspersion of land cover (low contagion) was associated with higher densities of both chickadee species, Northern Flickers, and Red-breasted Nuthatches. Higher percent forest was associated with higher densities of Brown Creepers, Chestnut-backed Chickadees, and Hairy and Pileated Woodpeckers. Brown Creepers and woodpeckers were most abundant at the three sites with highest percentages of forest cover and largest forest patch sizes.

Cavity-nesting birds had lower densities at our sites than in forests managed for timber products far from human development (Fig. 4). Bird densities throughout our 1-km² sites (built and forested portions combined) were 2.2 times (Brown Creeper) to 8.2 times (Pileated Woodpecker) less than densities in managed forests. Within the forested portions of our sites, only Brown Creeper density was similar to managed

TABLE 2. Results of stepwise multiple regression of landscape and site variables on snag densities and snag characteristics (2000 and 2001 data combined), bird density and productivity (2001) in the greater Seattle area. Binomial logistic regression was used for Downy and Pileated Woodpeckers' presence and absence because of low sample sizes. Only significant models are reported, and variables contributing to that model are listed in their order of importance with their coefficient. Important landscape variables (percent land cover, mean patch size, contagion, forest aggregation index, and the interaction of forest and contagion; see text for details) describe the amount of land cover types and their arrangement. Important site variables (mean age of built portions, live tree density, snag density, live tree DBH) describe local conditions. We grouped snags by diameter at breast height (DBH) based on requirements for nesting by different bird species: small snags (8.0–24.9 cm), medium snags (25.0–39.9 cm), and large snags (>40 cm).

		Important variables	Model variables and coefficients	P	R ² adj.	n
Snag density						
Forest portion	small DBH	site	0.45 live tree density	0.01	0.16	37
	large DBH	site	0.11 mean age of built + 0.18 live tree density	0.02	0.16	37
Built portion	small DBH	site	0.03 live tree density	<0.01	0.18	49
	medium DBH	landscape	0.004 percent forest	<0.01	0.25	49
	large DBH	site	0.01 live tree density	<0.01	0.13	49
Snag characteristics						
Forest portion	DBH	both	0.29 live tree DBH + 0.19 forest aggregation + 0.16 mean age of built	<0.01	0.31	35
	broken top	both	0.28 mean age of development + 0.14 percent forest	0.01	0.19	35
	decay class	both	0.004 percent forest + 0.01 mean age of built	0.01	0.19	35
	percent bark remaining	both	-0.08 mean age of built + 0.11 percent forest-0.18 forest aggregation	0.05	0.15	35
	DBH	landscape	-0.24 percent forest-3.29 urban mean patch size	0.04	0.11	45
Built portion	decay class	landscape	0.01 percent forest	0.02	0.13	45
	percent bark remaining	both	0.23 mean age of built-0.15 percent forest	<0.01	0.29	45
Bird richness and evenness						
Richness		landscape	-0.12 contagion + 0.08 forest × contagion	<0.01	0.84	13
Evenness		landscape	-0.17 contagion + 0.16 forest × contagion interaction	0.05	0.33	13
Bird density or presence/absence						
Brown Creeper		both	0.003 percent forest + 0.01 snag density	<0.01	0.69	13

TABLE 2. Continued.

	Important variables	Model variables and coefficients	P	R ² adj.	n
Red-breasted Sapsucker	site	0.01 snag density	<0.01	0.58	13
Black-capped Chickadee	landscape	-0.01 contagion + 0.01 forest × contagion interaction - 0.01 percent forest	0.01	0.59	13
Chestnut-backed Chickadee	landscape	-0.002 contagion + 0.003 percent forest	0.03	0.42	13
Hairy Woodpecker	landscape	0.001 percent forest	<0.01	0.58	13
Northern Flicker	landscape	-0.002 contagion	0.04	0.26	13
Red-breasted Nuthatch	landscape	-0.002 contagion	0.01	0.42	13
Downy Woodpecker	landscape	-0.09 contagion	0.02	0.33	13
Pileated Woodpecker	landscape	2.63 percent forest	<0.01	0.58	13
Bird productivity					
Brown Creeper	both	-0.09 percent forest - 0.12 contagion + 0.17 forest × contagion interaction + 0.07 snag density	<0.01	0.88	13
Red-breasted Nuthatch	both	-0.14 percent forest - 0.12 contagion + 0.14 forest × contagion interaction + 0.33 snag density	0.04	0.52	13
Red-breasted Sapsucker	both	-0.03 contagion + 0.35 snag density	0.05	0.35	13
Northern Flicker	landscape	-0.09 contagion	<0.01	0.55	13
Pileated Woodpecker	landscape	-0.065 contagion	0.04	0.28	13

forests. Other species were 1.4 times (Northern Flicker) to 2.8 times (Pileated Woodpecker) more abundant in managed forests.

Reproductive success. Most cavity nesters in our study reproduced successfully. Overall, 211 of the 321 territories (66%, all species combined) successfully fledged young (Table 3). This number included all territories, even those with single birds only. Of the 117 nests found, 77% were successful (Table 3). Causes of nest failure were: snag fell ($n = 1$), nest trees were cut down during construction ($n = 2$), abandonment ($n = 3$), competition from European Starlings (*Sturnus vulgaris*; $n = 5$; three of the six failed Northern Flicker nests and two Red-breasted Sapsucker nests), predation ($n = 6$) and unknown ($n = 9$).

Productivity of five species was significantly associated with landscape variables and snag density (Table 2). In all five species, higher productivity was related to higher interspersed of land cover (low contagion). Productivity of Brown Creepers and Red-breasted Nuthatches was highest where the percent of forest was low but aggregated, and snag densities were high. Land cover was not related to productivity of either species of chickadee or Hairy Woodpeckers because their success was high at all sites.

Nesting substrates. All species nested most often in snags (90 of 117 nests), but some species also nested in live (defined as trees $\geq 50\%$ live) or artificial substrates (nest boxes, built structures). Nests were most common in snags of red alder (52%), big-leaf maple (11%), west-

TABLE 3. Cavity-nesting bird density (number of territories per ha), productivity (Vickery index per territory), and nest success in 13 study sites in the greater Seattle area. Territories were found in 2001 ($n = 321$) and nest data in 2000 ($n = 26$) and 2001 ($n = 91$). Unless otherwise indicated, species were observed within both the built and forested portions of each site. Downy and Pileated Woodpecker territory densities were too low to be used in analyses so presence and absence was used instead. Nests and territories where at least one fledgling was produced were classed "successful."

Species	Territories (2001)				Nests (2000 and 2001)	
	n (Number of sites)	Density (territories ha^{-1})	Percent success	Average vickery rank ^a	n	Percent success
Black-capped Chickadee	90 (13)	0.04–0.26	76	4.0 ± 0.2	29	86
Brown Creeper ^b	61 (11)	0.02–0.26	57	3.7 ± 0.2	27	59
Chestnut-backed Chickadee	79 (13)	0.01–0.32	78	4.4 ± 0.1	25	88
Hairy Woodpecker ^b	15 (10)	0.02–0.10	88	4.3 ± 0.4	9	100
Northern Flicker	23 (7)	0.02–0.18	51	3.5 ± 0.3	10	40
Red-breasted Nuthatch	27 (8)	0.03–0.13	49	3.0 ± 0.3	3	100
Red-breasted Sapsucker	8 (5)	0.02–0.07	70	4.5 ± 0.4	10	80
Downy Woodpecker ^b	6 (6)	NA	33	2.8 ± 0.7	3	100
Pileated Woodpecker	12 (11)	NA	45	3.0 ± 0.5	1	100

^a Vickery scores are based on bird behavior and range from 1 (single bird present >4 wks) to 5 (successful fledging) for single-brooded species and 1 to 7 (successful fledging in two broods) for double-brooded species. Average Vickery rank in this table is the average for all territories $\pm$ SE. For analysis, if birds were not present at a site, their Vickery rank for that site was 0.

^b Species was observed only the forested portion of each site.

ern hemlock (11%), and Douglas fir (6%). Of the 20 live trees used, 10 were big-leaf maple, a tree species that contains many natural cavities or dead branches, seven were red alder (six of these had broken tops) and three were other species with natural cavities. We observed Red-breasted Sapsuckers using live trees more frequently than other bird species: 40% of the time, in red alder ($n = 10$).

All species of birds used snags with certain characteristics more often than expected based on their occurrence in our sample of 977 snags ($P < 0.1$). All species nested in snags that were more decayed on average (mean rank = 2.09 [Woodpecker group], 2.25 [Chestnut-backed chickadees], 2.33 [Black-capped Chickadees], and 2.00 [Brown Creeper]) than those we sampled (mean rank = 1.85). Presence of previously used cavities was associated with all species except Brown Creeper. Woodpeckers nested in red alder and Chestnut-backed Chickadees nested in coniferous snags more often than other species of snags. Woodpeckers nested in snags with greater mean DBH ($38.3 \text{ cm} \pm 0.7$; expected = $27.6 \text{ cm} \pm 0.5$), and woodpeckers and Brown Creepers nested in taller snags than expected by chance. Chestnut-backed Chickadees nested in snags with more bark remaining and with more conk fungus more often than expected; both are

indicators of decay. Woodpeckers and Black-capped Chickadees nested in broken-top snags more often than expected. Brown Creepers nested in snags with any kind of fungus less often than expected by chance. Rohila (2002) provides details and test statistics not reported here.

DISCUSSION

SNAGS

Retaining portions of second growth forest in a rapidly urbanizing region appears to be an effective way to provide breeding sites for a diversity of cavity-nesting birds. Forested portions of neighborhoods provided snag densities equivalent to those in wildlands (Ohmann and Waddell 1999, Aubry and Raley 2002); some of which were of high quality to cavity-nesting birds because of their large size and advanced state of decay. On the other hand, built portions of the landscape provided few snags. Recruitment of snags in forested habitats appears functional, at least in the short-term, as density of large snags in forested portions of neighborhoods was positively correlated with mean age of built portions. However, if the death of large trees out-paces the growth of live trees, large snags may become rare. Snag recruitment in forested portions of neighborhoods appears sustain-

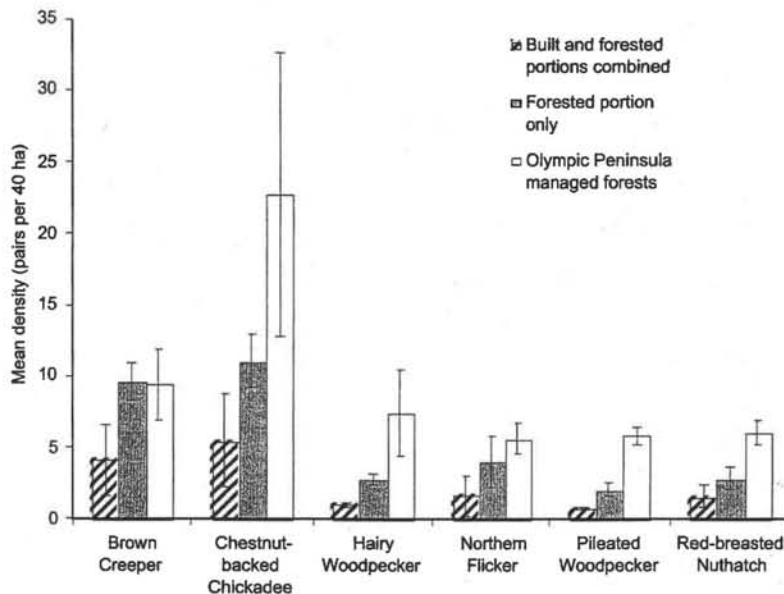


FIGURE 4. Densities of six species of cavity-nesting birds in Seattle area study sites from 2001 compared to densities in the managed forest of the Olympic Peninsula (unfilled bars; Zarnowitz and Manuwal 1985). Data are presented as mean number of pairs per 40 ha $\pm$ SE. Hatched bars represent pairs from this study from entire sites (built and forested portions combined; $n = 13$), and light grey bars represent pairs from this study from only the forest portion of sites ($n = 11$).

able: where there were trees, there were snags. This was also true in built portions interspersed with high amounts of forest; densities of medium-sized snags were higher than in built portions interspersed with less forest. However, recruitment of snags in densely built landscapes will remain very low due to the paucity of live trees.

An important tree species in our study area was a fast growing, "weedy" colonist of disturbed areas, the red alder (Franklin and Dyrness 1988). Alder was common, and was regularly and successfully used by cavity nesters. Its rapid growth and short life span quickly produced large diameter snags that may have helped maintain cavity-nesting bird populations in our study site.

Snag longevity might be a concern within forested portions. Individual snags decay and fall at differing rates depending on the species, diameter, height, cause of death, and exposure to wind (Raphael and Morrison 1987). Red alder dominated snag species, and although they provide good nesting substrates, they last only a few years before falling (McComb 1994). This may not be a problem if snag recruitment (tree death) rate matches snag fall rate, however hu-

man activity or edge effects may alter these rates. Snag demographic studies are needed to understand snag dynamics in urban areas (Morrison and Raphael 1993).

CAVITY-NESTING BIRDS

Our results confirm previous findings of lower densities of cavity-nesting birds in suburban areas (DeGraff and Wentworth 1986, Tilghman 1987, Natuhara and Imai 1996). This appears to be due to urban growth and the conversion of forest to built areas containing few trees and even fewer snags. Within forested portions of the suburban landscapes we studied, snag density and quality was high as suggested by the lack of cavity reuse, rarity of competition with exotic species, and high nesting success. However, lower density of most species in forested portions of suburbs, relative to nearby managed forests (Fig. 4), suggests suburban forests may contain too little food, too many predators, or experience too much human disturbance to support dense populations of cavity-nesting birds.

The fact that all nine species of cavity-nesting birds existed in suburban areas in and around Seattle, Washington may be a product of regional context. Although the Puget Sound region has

been growing rapidly in the last 20 years, there remain many large expanses of forest in close proximity to urban centers, potentially acting as sources (Pulliam 1988) for birds sensitive to forest loss. This may include four cavity-nesting species (Brown Creeper, Red-breasted Nuthatch, Hairy Woodpecker, and Pileated Woodpecker) whose density or productivity was closely and positively associated with the percentage of forest in the landscape (Table 2). However, the importance of the interspersed forested and built area to the density and productivity of chickadees, Northern Flickers, and perhaps Downy Woodpeckers (Table 2) suggests that distant forests are not sources for all cavity-nesting birds.

Interspersion of forested and built portions of a landscape clearly varies in its importance to different bird species. In accordance with our results, Moore (1995) found mixtures of built and forested areas important for Northern Flickers. Donnelly (2002) found little influence of contagion on native forest songbird populations (shrub- and ground-nesting guilds) in and around our study sites. Rather, the percent forest and occurrence of native vegetation was most important. Cavity-nesting birds, especially woodpeckers, may be more responsive than other songbirds to the arrangement of forested and built areas because they have relatively large home ranges and regularly commute between forest nest sites and feeders providing seeds and suet in yards.

MANAGEMENT RECOMMENDATIONS

The importance of snag density and 1-km²-scale landscape attributes (amount of remaining forest, and interspersed forest and built areas) to cavity-nesting birds differed by species, suggesting that conservation of this guild in areas of rapid urban development may need to be addressed at multiple scales and requires planners to make trade-offs between species. Fortunately, retaining forest and interspersing forest and built areas are not necessarily mutually exclusive. Sites with high interspersed forest and urban areas require at least moderate amounts of forest: one site had 27% forest and contained all nine species of birds. This site was 30-years old, which suggests that this amount of forest can maintain cavity-nesting bird populations following development.

Variety in development pattern may become increasingly important as large areas of forest are developed. To increase densities and reproductive success of all species, different patterns of developments with differing amounts of percent forest would be prudent. For example, planners in the Pacific Northwest should design some developments that retain at least 60% forest for every 100 ha developed, where mean forest patch sizes are 20–30 ha, and some that have 27% to 60% forest in a variety of patch sizes interspersed with urban areas. Forested parks (70%–96% forest; large mean forest patch sizes 23–30 ha; very small mean urban patch sizes 0.14 to 0.74 ha) would complement these urban areas for the benefit of cavity-nesting birds. When deciding which forest areas to conserve, we recommend targeting conservation efforts to areas with high densities of existing snags (>8 snags ≥ 25 cm DBH ha⁻¹), and live trees (>318 trees ha⁻¹). These management suggestions would also provide the diversity of forest conditions used by mature and early-successional forest songbirds (Donnelly 2002, Donnelly and Marzluff 2004).

Simply conserving forest may not be adequate if snags are removed or altered, or if the forest areas are degraded by human activity (Matlack 1993, Marzluff and Ewing 2001). Active management may be needed within built portions of suburban landscapes to conserve snags with characteristics important to cavity-nesters. Based on snags used by cavity-nesting birds in our study, efforts should be made to conserve all snags that are large in diameter (minimum of 30–40 cm), more decayed (class 2), red alder and coniferous species, taller (>18 m), with broken tops, with some bark remaining, with conk fungus, and containing other cavities. These recommendations are similar to those of managed forest landscapes (Harestad and Keisker 1989, Huff and Raley 1991, Dobkin et al. 1995, McClelland and McClelland 2000).

Conserving cavity-nesting birds in urbanizing areas ultimately will require the efforts of a diverse public. Planners, developers, policy makers, and managers could provide the landscapes and conserve the snags in forests as we suggest, but individual homeowners and homeowner organizations also need to know about the importance of snags. These individuals often manage forests within and near built areas that support many cavity-nesting bird species. Retaining un-

sightly, recently dead trees that pose little safety risk, allowing snags to decay and fall where they will not harm property or endanger people, trimming dead trees near valuable property to reduce the chances and consequences of deadfall, and replacing lost snags with appropriate nest boxes would all increase our ability to safely live with dead trees and enhance the productivity of cavity-nesting birds.

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LITERATURE CITED

- ALBERTI, M., E. BOTSFORD, AND A. COHEN. 2001. Quantifying the urban gradient: linking urban planning and ecology, p. 89–115. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston, MA.
- ALBERTI, M. A., J. M. MARZLUFF, E. SHULENBERGER, G. BRADLEY, C. RYAN, AND C. ZUMBRUNNEN. 2003. Integrating humans into ecology: opportunities and challenges for urban ecology. *BioScience* 53:1169–1179.
- ALBERTI, M., R. WEEKS, AND S. COE. 2004. Urban land-cover change analysis in central Puget Sound. *Photogrammetric Engineering & Remote Sensing* 70:1043–1052.
- AUBRY, K. B., AND C. M. RALEY. 2002. Selection of nest and roost trees by Pileated Woodpeckers in coastal forests of Washington. *Journal of Wildlife Management* 66:392–406.
- BAKER, W. [ONLINE] 1997. The rle programs. University of Wyoming, Laramie. <<http://www.Baylor.edu/~grass/gdp/terrain/rle.22.html>> (5 April 1998).
- BLAIR, R. B. 1996. Land use and avian species diversity along an urban gradient. *Ecological Applications* 6:506–519.
- BLAIR, R. B. 2001. Creating a homogenous avifauna, p. 461–488. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston, MA.
- BOTSFORD, E. R. 2000. Development of a modified land composition classification methodology utilizing LANDSAT thematic mapping and ancillary data. M.Sc. thesis, University of Washington, Seattle, WA.
- BOWMAN, R., AND G. E. WOOLFENDEN. 2001. Nest success and timing of nest failure of Florida Scrub-Jays in suburban and wildland habitats, p. 383–402. *In* J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston, MA.
- BROWN, E. R. 1985. Management of wildlife and fish habitats in forests of western Oregon and Washington. USDA Forest Service, Portland, OR.
- BULL, E. L., C. G. PARKS, AND T. R. TORGENSEN. 1997. Trees and logs important to wildlife in the interior Columbia River basin. USDA Forest Service General Technical Report PNW-GTR-391.
- CHANCE, J. F., J. J. WALSH, A. CRUZ, J. W. PRATHER, AND H. M. SWANSON. 2003. Spatial and temporal activity patterns of the brood parasitic Brown-headed Cowbird at an urban/wildland interface. *Landscape and Urban Planning* 64:179–190.
- CHRISTMAN, B. J., AND A. A. DHONDT. 1997. Nest predation in Black-capped Chickadees: how safe are cavity nests? *The Auk* 114:769–773.
- CHRISTOFERSON, L. L., AND M. L. MORRISON. 2001. Integrating methods to determine breeding and nesting status of 3 western songbirds. *Wildlife Society Bulletin* 29:688–696.
- CLINE, S. P., A. B. BERG, AND H. M. WIGHT. 1980. Snag characteristics and dynamics in Douglas fir forests, western Oregon. *Journal of Wildlife Management* 44:773–786.
- CROOKS, K. R., A. V. SUAREZ, D. T. BOLGER, AND M. E. SOULE. 2001. Extinction and colonization of birds on habitat islands. *Conservation Biology* 15:159–172.
- DAVIS, J. W. 1983. Snags are for wildlife. *Proceedings of the Snag Habitat Management Symposium*, Flagstaff, AZ. USDA Forest Service General Technical Report GTR-RM-99.
- DEGRAFF, R. M., AND J. M. WENTWORTH. 1986. Avian guild structure and habitat associations in suburban bird communities. *Urban Ecology* 9:399–412.
- DOBKIN, D. S., A. C. RICH, J. A. PRETARE, AND W. H. PYLE. 1995. Nest-site relationships among cavity-nesting birds of riparian and snowpocket aspen woodlands in the northwestern Great Basin. *Condor* 97:694–707.
- DONNELLY, R. E. 2002. Design of habitat reserves and settlements for bird conservation in the Seattle metropolitan area. Ph.D. dissertation, University of Washington, Seattle, WA.
- DONNELLY, R. E., AND J. M. MARZLUFF. 2004. Importance of reserve size and landscape context to urban bird conservation. *Conservation Biology* 18:733–745.
- DOVE, L. E. 1987. Saving snags for urban wildlife. *Urban wildlife manager's notebook* 12:1–8.
- FAULKNER, S. 2004. Urbanization impacts on the structure and function of forested wetlands. *Urban Ecosystems* 7:89–106.
- FERNÁNDEZ-JURICIC, E. 2000. Avifaunal use of wooded streets in an urban landscape. *Conservation Biology* 14:513–521.
- FISCHER, W. C., AND B. R. MCCLELLAND. 1983. A cavity nesting bird bibliography—including related titles on forest snags, fire, insects, disease, and de-

- cay. USDA Forest Service General Technical Report GTR-INT-140.
- FRANKLIN, J. F., AND C. T. DYRNES. 1988. Natural vegetation of Washington and Oregon. Oregon State University Press, Corvallis, OR.
- FRATERRIGO, J. M., AND J. A. WIENS. 2005. Bird communities of the Colorado Rocky Mountains along a gradient of exurban development. *Landscape and Urban Planning* 71:263–275.
- HANSEN, A. J., R. L. KNIGHT, J. M. MARZLUFF, S. POWELL, K. BROWN, P. HERNANDEZ, AND K. JONES. In press. Effects of exurban development on biodiversity: patterns, mechanisms, research needs. *Ecological Applications*.
- HARESTAD, A. S., AND D. G. KEISKER. 1989. Nest tree use by primary cavity-nesting birds in south central British Columbia. *Canadian Journal of Zoology* 67:1067–1073.
- HOSTETLER, M. 2001. The importance of multi-scale analyses in avian habitat selection studies in urban environments, p. 139–154. In J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston, MA.
- HUFF, M. M., AND C. M. RALEY. 1991. Regional patterns of diurnal breeding bird communities in Oregon and Washington, p. 177–206. USDA Forest Service General Technical Report PNW-GTR-285.
- IMHOFF, M. L., L. BOUNOUA, R. DEFRIES, W. T. LAWRENCE, D. STUTZER, C. J. TUCKER, AND T. RICKETTS. 2004. The consequences of urban land transformation on net primary productivity in the United States. *Remote Sensing of Environment* 89:434–443.
- INGOLD, D. J. 1989. Nesting phenology and competition for nest sites among Red-headed and Red-bellied Woodpeckers and European Starlings. *The Auk* 106:209–217.
- INGOLD, D. J. 1994. Influence of nest-site competition between European Starlings and woodpeckers. *Wilson Bulletin* 106:227–241.
- INGOLD, D. J. 1996. Delayed nesting decreased reproductive success in Northern Flickers: implications for competition with European Starlings. *Journal of Field Ornithology* 67:321–326.
- THE INTERNATIONAL BIRD CENSUS COMMITTEE. 1970. An international standard for a mapping method in bird census work recommended by the International Bird Census Committee. *Audubon Field Notes* 24:722–726.
- KING COUNTY. 2000. King County comprehensive plan. King County Office of Regional Policy and Planning, Seattle, WA.
- MARTIN, T. E., AND P. LI. 1992. Life history traits of open- versus cavity-nesting birds. *Ecology* 73: 579–592.
- MARZLUFF, J. M. 2001. Worldwide urbanization and its effects on birds, p. 19–47. In J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston, MA.
- MARZLUFF, J. M., R. BOWMAN, AND R. E. DONNELLY. 2001. A historical perspective on urban bird research: trends, terms, and approaches, p. 1–17. In J. M. Marzluff, R. Bowman, and R. Donnelly [EDS.], *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston, MA.
- MARZLUFF, J. M., AND K. EWING. 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. *Restoration Ecology* 9:280–292.
- MARZLUFF, J. M., AND N. HAMEL. 2001. Land use issues, p. 659–673. In S. A. Levin [ED.], *Encyclopedia of biodiversity*. Vol. 3. Academic Press, San Diego, CA.
- MATLACK, G. R. 1993. Sociological edge effects: spatial distribution of human impact in suburban forest fragments. *Environmental Management* 17: 829–835.
- MCCLELLAND, B. R., AND P. T. MCCLELLAND. 2000. Red-naped Sapsucker nest trees in northern Rocky Mountain old-growth forest. *Wilson Bulletin* 112: 44–50.
- MCCOMB, W. C. 1994. Red alder: interactions with wildlife, p. 131–138. In D. E. Hibbs, D. S. DeBell, and R. F. Tarrant [EDS.], *The biology and management of red alder*. Oregon State University Press, Corvallis, OR.
- MELLES, S., S. GLENN, AND K. MARTIN. [ONLINE] 2003. Urban bird diversity and landscape complexity: species-environment associations along a multi-scale habitat gradient. *Conservation Ecology* 7 <<http://www.consecol.org/vol7/iss1/art5>> (3 February 2004).
- MEYER, W. B., AND B. L. TURNER II. 1992. Human population growth and global land-use/cover change. *Annual Review of Ecology and Systematics* 23:39–61.
- MOORE, W. S. 1995. Northern Flicker, *Colaptes auratus*. In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 166. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- MORRISON, M. L., M. F. DEDON, M. G. RAPHAEL, AND M. P. YODER-WILLIAMS. 1986. Snag requirements of cavity-nesting birds: are USDA Forest Service guidelines being met? *Western Journal of Applied Forestry* 1:38–40.
- MORRISON, M. L., AND M. G. RAPHAEL. 1993. Modeling the dynamics of snags. *Ecological Applications* 3:322–330.
- NATUHARA, Y., AND C. IMAI. 1996. Spatial structure of avifauna along urban-rural gradients. *Ecological Research* 11:1–9.
- OHMANN, J. L., W. C. MCCOMB, AND A. A. ZUMRAWL. 1994. Snag abundance for primary cavity-nesting birds on non-federal forest lands in Oregon and Washington. *Wildlife Society Bulletin* 22:607–620.
- OHMANN, J. L., AND K. L. WADDELL. 1999. Regional pattern of dead wood in forested habitats of Oregon and Washington. *Proceedings of the conference on ecology and management of dead wood in western forests*. Reno, NV.

- PICKETT, S. T. A., M. L. CADENASSO, J. M. GROVE, C. H. NILON, R. V. POUYAT, W. C. ZIPPERER, AND R. COSTANZA. 2001. Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Annual Review of Ecology and Systematics* 32:127-157.
- PUGET SOUND REGIONAL COUNCIL. 2001. Decennial change in population and land area of cities, towns, and counties in the central Puget Sound: 1990 to 2000. Census 2000. Puget Sound Regional Council, Seattle, WA.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 32:652-661.
- RALPH, C. J., G. R. GEUPEL, P. PYLE, T. E. MARTIN, AND D. F. DESANTE. 1993. Handbook of field methods for monitoring landbirds. USDA Forest Service General Technical Report GTR-PSW-144.
- RAPHAEL, M. G., AND M. L. MORRISON. 1987. Decay and dynamics of snags in the Sierra Nevada, California, USA. *Forest Science* 33:774-783.
- RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildlife Monographs* 86:1-66.
- ROBINSON, L., J. P. NEWELL, AND J. M. MARZLUFF. 2005. Twenty-five years of sprawl in the Seattle region: growth management responses and implications for conservation. *Landscape and Urban Planning* 71:51-72.
- ROHILA, C. M. 2002. Urbanization in the greater Seattle, Washington area: impacts on vegetation, snags, and cavity-nesting birds. M.Sc. thesis, University of Washington, Seattle, WA.
- ROTTENBORN, S. C. 1999. Predicting the impacts of urbanization on riparian bird communities. *Biological Conservation* 88:289-299.
- SEATTLE PUBLIC UTILITIES. 2000. 2000 Seattle standard specifications. Seattle, WA.
- SINCLAIR, K. E., G. R. HESS, C. E. MOORMAN, AND J. M. MASON. 2005. Mammalian nest predators respond to greenway width, landscape context, and habitat structure. *Landscape and Urban Planning* 71:277-293.
- SPSS. 1999. Base 10.0.05 for windows user's guide. SPSS, Inc., Chicago, IL.
- THOMAS, J. W., R. J. MILLER, H. BLACK, J. E. RODIEK, AND C. B. K. MASER. 1976. Guidelines for maintaining and enhancing wildlife habitat: forest management in the Blue Mountains of Oregon and Washington. Transactions of the North American wildlife and natural resources conference, No. 41. Wildlife Management Institute, Washington, DC.
- THORINGTON, K. K., AND R. BOWMAN. 2003. Predation rates on artificial nests increases with human housing density in suburban habitats. *Ecography* 26:188-196.
- TILGHMAN, N. G. 1987. Characteristics of urban woodlands affecting winter bird diversity and abundance. *Forest Ecology and Management* 21:163-175.
- U.S. CENSUS BUREAU, GEOGRAPHY DIVISION. 2000. Census tract census 2000 TIGER/line files. Department of Commerce, Washington, DC.
- VICKERY, P. D., M. L. HUNTER, AND J. V. WELLS. 1992. Use of a new reproductive index to evaluate relationships between habitat quality and breeding success. *Auk* 109:697-705.
- WHITE, J. G., M. J. AMOS, J. A. FITZSIMONS, AND G. C. PALMER. 2005. Non-uniform bird assemblages in urban environments: the influence of streetscape vegetation. *Landscape and Urban Planning* 71:123-135.
- ZAR, J. H. 1996. Biostatistical analysis. 3rd ed. Simon & Schuster, Upper Saddle River, NJ.
- ZARNOWITZ, J. E., AND D. A. MANUWAL. 1985. The effects of forest management on cavity nesting birds in northwestern Washington. *Journal of Wildlife Management* 49:255-263.