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RAPTOR PRESENCE ALONG AN URBAN–WILDLAND GRADIENT: INFLUENCES OF PREY ABUNDANCE AND LAND COVER

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ABSTRACT.—Native animals are affected differently by urbanization. Some species respond favorably and thrive in human-dominated landscapes, but others are extirpated. Raptors are often sensitive to changes in land cover and prey abundance. We therefore used a combination of broadcast surveys and incidental observations while spot-mapping to evaluate the influences of these two variables on the presence of raptors at 21 sites from 2004–2008 along an urban-to-wildland gradient in western Washington, U.S.A. We detected three species of hawks: Sharp-shinned Hawk (*Accipiter striatus*), Cooper's Hawk (*Accipiter cooperii*), and Red-tailed Hawk (*Buteo jamaicensis*); and five species of owls: Northern Pygmy-Owl (*Glaucidium gnoma*), Western Screech-Owl (*Megascops kennicottii*), Barred Owl (*Strix varia*), Great Horned Owl (*Bubo virginianus*) and Barn Owl (*Tyto alba*). Models that included specific land-cover elements as independent variables explained presence for all species better than models including only prey abundance. Cooper's Hawks and Barred Owls showed a positive response to human-altered landscapes, specifically the edges between deciduous-mixed forest and light intensity urban land cover. Raptor species richness was consistent across the gradient of urbanization ($\bar{x}$ = 3.67 species/site) and not correlated with land-cover diversity, songbird species richness, or total forest cover.

KEY WORDS: *prey; abundance; raptors; suburban; survey; urban; urban–wild gradient.*

PRESENCIA DE RAPACES A LO LARGO DE UN GRADIENTE URBANO–RURAL: INFLUENCIAS DE LA ABUNDANCIA DE PRESAS Y DE LA COBERTURA DEL SUELO

RESUMEN.—Los animales nativos son afectados de manera diferente por la urbanización. Algunas especies responden favorablemente y prosperan en paisajes dominados por humanos, pero otras desaparecen. Las rapaces a menudo son sensibles a los cambios en la cobertura del suelo y a la abundancia de presas. Por lo tanto, utilizamos una combinación de censos de emisión y observaciones incidentales; al mismo tiempo, mapeamos los resultados para evaluar las influencias de estas dos variables en la presencia de rapaces en 21 sitios durante 2004–2008 a lo largo de un gradiente urbano-rural en el oeste de Washington, EEUU. Detectamos tres especies de halcones: *Accipiter striatus, A. cooperii* y *Buteo jamaicensis*; y cinco especies de búhos y lechuzas: *Glaucidium gnoma, Megascops kennicottii, Strix varia, Bubo virginianus* y *Tyto alba.* Los modelos que incluyeron elementos específicos de cobertura del suelo como variables independientes explicaron la presencia de todas las especies de forma más precisa que los modelos que sólo incluyeron la abundancia de presas. *A. cooperii* y *S. varia* evidenciaron una respuesta positiva a los paisajes alterados por humanos, específicamente en los bordes entre los bosques deciduos mixtos y las coberturas de tierra urbana con intensidad lumínica. La riqueza de especies de rapaces fue consistente a lo largo del gradiente de urbanización ($\bar{x}$ = 3.67 especies/sitio) y no estuvo correlacionada con la diversidad de la cobertura de suelo, la riqueza de especies de aves canoras o la cobertura boscosa total.

[Traducción del equipo editorial]

Urbanization profoundly affects wildlife populations throughout the world (Czech et al. 2000). Urbanization may affect wildlife through loss and fragmentation of native habitat (Wilcove et al. 1986, Theobald et al. 1997), affecting interior forest species negatively while providing abundant habitat for species associated with forest edges, lawns, and artificial structures (Marzluff 2001, Fahrig 2003). The introduction of nonnative vegetation may change the availability of natural food resources (Beissinger and Osborne 1982, Marzluff and Ewing 2001). Roads fragment the landscape and create areas of high risk for volant and non-volant species (Forman and Alexander 1998, Sherwood et al.

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2002). Urbanization also alters natural predator regimes. In most urban areas, large native predators are replaced by domestic dogs and house cats (Churcher and Lawton 1987, Marzluff 1997), but smaller generalists like raccoons (*Procyon lotor*) and coyotes (*Canis latrans*) may adapt to increased urbanization and thrive in these developed areas (DeStefano and DeGraaf 2003).

As members of the collective predator guild, raptors (Falconiformes and Strigiformes) also may be influenced by urbanization. Their sensitivity to disturbance may make many raptor species among the first to respond to changes in the landscape and human activity (Craighead and Craighead 1969, Stalmaster and Newman 1978, Newton 1979). As representatives of the upper trophic levels of local food chains, raptors may be particularly susceptible to the biomagnified effects of pesticides, herbicides, fertilizers, petrochemicals, and other toxic substances prevalent in urbanized and agricultural areas (Cade et al. 1968, Newton 1979, Sheffield 1997, Chandler et al. 2004), or other direct hazards (Hager 2009). In Tucson, Arizona, trichomoniasis from dove populations (*Zenaida* sp.) and collisions with windows were determined to be two significant sources of mortality within an urban population of Cooper's Hawks (*Accipiter cooperii*; Boal and Mannan 1999, Mannan et al. 2008). Despite these particular threats, raptors may find urban landscapes to be good places to establish residency (Newton 1979 and review in Bird et al. 1996). Firearm regulations in urban areas may dramatically reduce the killing of raptors, a risk still present in many rural landscapes.

Urban and suburban landscapes provide many raptor species with their two primary requirements for maintaining successful populations: sufficient food resources and nesting habitat (Newton 1979, Bird et al. 1996, Love and Bird 2000). Urban and suburban landscapes may promote a higher diversity of avian species (Beissinger and Osborne 1982, Estes and Mannan 2003, Marzluff 2005), which are prey for many raptor species. Perhaps more importantly for raptors than species richness, these urban areas may have higher densities of birds and rodents (Emlen 1974, Beissinger and Osborne 1982, Tomialojc and Gehlbach 1988), resulting in a net higher biomass of potential prey items for raptors than may be found within the native habitats of the region. Many prey resources also may be available at these high densities on a year-round basis, with the potential of allowing some historically migratory raptors to remain on or near their breeding territory throughout the winter (Powers 1996). This availability of high densities of prey may increase both functional and numerical responses of raptors (Solomon 1949, Boal and Mannan 1998, Curtis et al. 2006, Stout 2009). Urban landscapes also may provide unique and abundant nesting structure and habitat for a variety of raptor species (Henny and Kaiser 1996, Cade et al. 1996, Meyburg et al. 1996, Marti et al. 2005), including many woodland raptors in North America (Trexel et al. 1999, Dykstra et al. 2000, Coleman et al. 2002).

Prey abundance and habitat characteristics have historically been incorporated into habitat selection theory (Lack 1933, MacArthur and Pianka 1966, Janes 1985). In addition, landscape characteristics are frequently the focus in assessments of raptor habitat use in general (Titus and Mosher 1981, Reynolds et al. 1982, Mazur et al. 1998, Grossman et al. 2008), and under the influence of urbanization in particular (Sodhi and Oliphant 1992, Mannan and Boal 2000, Mannan et al. 2000, Coleman et al. 2002, Dykstra et al. 2012). However, prey abundance rarely has been included in raptor habitat occupancy assessments. In the few cases where prey and vegetative aspects of a raptor's habitat are considered, both have been found to be interactive and important (Southern and Lowe 1968, Newton 1986, Preston 1990).

In this report we evaluate the presence of eight species of raptors (three species of hawks and five species of owls) along an urban to wildland gradient in the lowlands of western Washington, U.S.A. We model raptor presence as a function of prey abundance (as a direct measure of an important resource), coarse-scale land-cover characteristics (as a more indirect measure of resources), and the combination of both. We expect that explanatory variables will vary with species based on sensitivities to specific land-cover associations as well as prey selection and foraging preferences. These two variables drive much of the habitat selection of birds in general (Lack 1933) and raptors in particular (Newton 1979, Janes 1985, Bird et al. 1996). Although prey abundance is inexorably related to land cover, in assessing which of these categories of variables best explain raptor presence, we contribute to our understanding of raptor habitat selection in general, and provide some guidance in the management of these species within an urbanizing landscape. Recent development trends in the lowlands of western Washington suggest that a marked decrease in forest land cover (coniferous, mixed and deciduous) from 60 to 38% will occur throughout the region over the next 25 yr (Hepinstall et al. 2008). Assuming this projection of significant land-cover conversion in the region, such planning tools may provide guidance to ensure the long-term presence of these species in the region.

Methods

Study Area. We selected 26 1-km^2 study sites (with forest fragments ranging from 0.96 to 18.7 ha in size) near Seattle in western Washington, U.S.A. (described in Donnelly and Marzluff 2004a; (47°35′N, 122°9′W; Fig. 1). We selected sites to represent varying proportions of percent forest and percent residential (urban) land cover, as well as aggregation indexes associated with these two land use classes. These sites lie within the Western Hemlock zone (Franklin and Dyrness 1988), with Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*) making up the main native species within this moist, temperate forest. Site elevations ranged from sea level to 400 masl in the foothills of the Cascade Mountains.

Raptor Presence. We determined raptor presence within each 1-km^2 site in two ways: raptor-specific broadcast surveys (2004) and weekly spot mapping efforts (2004–2008). Both methods were conducted during the passerine breeding season, from early April through early August.

In 2004, we adapted multispecies broadcast surveys from the methods described in Fuller and Mosher (1981, 1987), Rosenfield et al. (1985), Mosher et al. (1990), Takats et al. (2001), and the Cornell Lab of Ornithology (2000) to assess the presence of three species of hawks (Sharp-shinned Hawk [*Accipiter striatus*], Cooper's Hawk, and Red-tailed Hawk [*Buteo jamaicensis*]; and five species of owls (Northern Pygmy-Owl [*Glaucidium gnoma*], Northern Saw-whet Owl [*Aegolius acadicus*], Western Screech-Owl [*Megascops kennicottii*], Barred Owl [*Strix varia*], and Great Horned Owl [*Bubo virginianus*]). Broadcast surveys were conducted at 26 study sites for diurnal raptors and at 21 of the study sites for nocturnal raptors. Given this unequal sampling effort, inter-site comparisons incorporating raptor species richness were based on the 21 sites at which we conducted both diurnal and nocturnal broadcast surveys. Assessments of land cover and prey abundance effects (below) were based on all 26 sites for diurnal species, including Barred Owls, which were detected frequently during diurnal spot-mapping efforts.

We created an audio CD for each broadcast survey (diurnal and nocturnal) with preset tracks of silence for consistency. We started broadcasts with the smallest of the target species and worked up to the largest to reduce the chance of a smaller, potentially prey-sized species being lured into the proximity of a larger, previously attracted predator. During diurnal surveys, we broadcast surveyed for the three focal hawk species, followed by a Northern Pygmy-Owl sequence, which are primarily diurnal as well. We concluded diurnal broadcast surveys with a Great Horned Owl sequence. This approach has proven effective at eliciting a response from incubating or brooding Cooper's Hawks when conspecific broadcasts tend to be ineffective (Fuller and Mosher 1987).

Nocturnal surveys followed a similar protocol, starting with the smallest species (Northern Saw-whet Owls) and working up toward the largest (Great Horned Owls). We broadcast calls through a Johnny Stewart Game Caller speaker mounted on a lightweight tripod at a height of 1 m. Using a Radio Shack sound level meter (Cat. Number 33-2050, Radio Shack), we set the volume of the playback system to broadcast at 90–95 dba (at 1 m) and maintained that volume level for all surveys.

We conducted broadcast surveys from early April to mid-August 2004, from 0.5 hr before sunrise to 1600 H for diurnal species and 0.5 hr after sunset to 0300 H for the nocturnal species. The speaker was oriented to each of three directions (120° apart) with a 1-min pause between bearings and a 2-min pause between species (Table 1). We divided each 1-km^2 site into a three by three grid, and a survey point was established near the center of each subsquare, resulting in survey points ~333 m apart. Both diurnal and nocturnal surveys took approximately 55 min for each point. For all nocturnal surveys, a volunteer spotter accompanied us, and at each point, we would stand back-to-back to better detect owls approaching silently in response to the broadcast.

Broadcast surveys were not conducted during periods of steady rain or with winds exceeding three on the Beaufort scale (Mosher et al. 1990). Before each broadcast survey, we stood silently listening for any unsolicited vocalizations for 5 min. If a focal species approached the broadcast station in response to the playback (or responded vocally nearby), the survey was halted for 20 min before

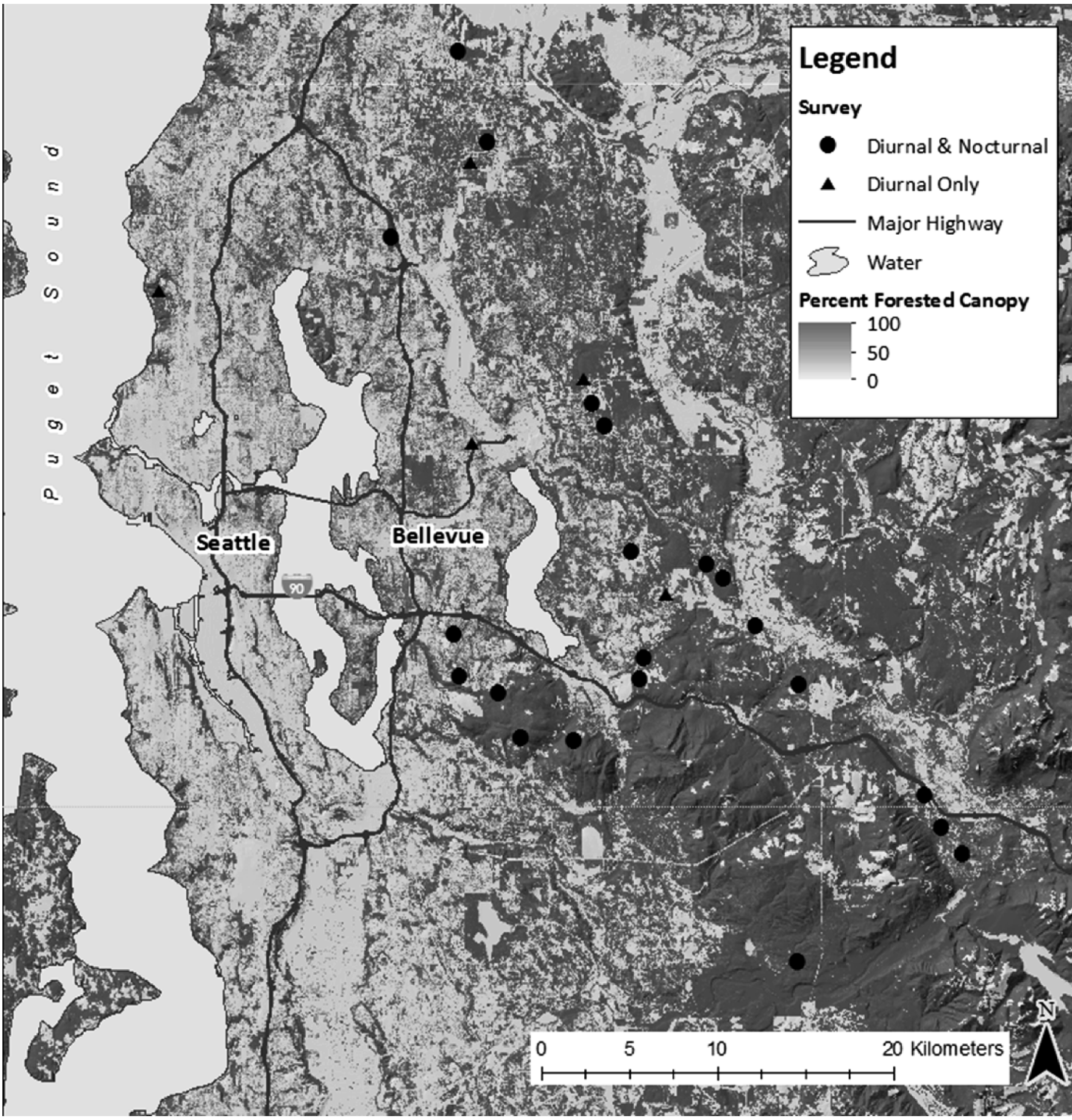

Figure 1. Study area for urban to wildland gradient in western Washington, U.S.A. Circle and triangle markers indicate survey blocks surveyed for diurnal and nocturnal raptors (circles) and diurnal raptors only (triangles).

Table 1. Logistic regression models for assessing raptor presence.

MODEL NAME	MODEL
Prey only model:	$Z = \beta_0 + \beta_1$ (Primary prey) + β_2 (Secondary prey)
Landscape only model:	$Z = \beta_0 + \beta_1$ (Primary landscape metric) + β_2 (Secondary landscape metric)
Combined model:	$Z = \beta_0 + \beta_1$ (Primary prey) + β_2 (Secondary prey) + β_3 (Primary landscape metric) + β_4 (Secondary landscape metric)

continuing to the next species in an effort to reduce the potential predation of that target species by the next target species. If the attracted raptor was still present nearby after 20 min, we moved on to the next survey point, returning after the subsequent surveys to finish. We followed a systematic approach to conducting the broadcast surveys within a site so as not to conduct surveys from adjacent survey points in consecutive surveys.

In addition to these broadcast surveys, at each study site from 2004–2008, we spot-mapped the locations of all hawk and owl species detected (Kendeigh 1944, Vickery et al. 1992), as well as potential songbird nest predators detected, including corvids, sciurids, and other small mammals. Each site was visited weekly from early April through mid-August, for an average of 60 hr of observational time per site per year throughout the field season. All eight raptor species were detected through both broadcast surveys and spot mapping.

Land-cover Metrics. We calculated land-cover metrics across all 26 sites from a 2002 land-cover/land-use dataset with 14 classes (Hepinstall-Cymerman et al. 2009) using FRAGSTATS 3.3 (McGarigal et al. 2002), reclassifying one site with significant land-cover changes between 2002 and the period of our surveys. Land-cover classes were determined at a 30-m pixel width (Hepinstall-Cymerman et al. 2009). We evaluated these metrics at two spatial scales: 1 km^2 and 7.5 km^2 to better accommodate the home range sizes of respective raptor species, based on published information (Snyder and Wiley 1976, Newton 1979, Peery 2000). The metrics reflect relative degrees of urbanization based on percent impervious surface (three categories: light-intensity urban or LIU, medium-intensity urban or MIU, and heavy-intensity urban or HIU), two categories of percent forest cover (deciduous-mixed and coniferous) and percent grass cover, which represented pasture land rather than lawn. At the 30-m pixel width, lawns typically were classified as light-intensity urban. We also created contrast-weighted edge densities in FRAGSTATS (McGarigal et al. 2002) for specific pairs of classes we deemed important for particular raptor species based on published reports (Table 2). We transformed all proportional data as necessary with the arcsine square root transformation to meet assumptions of equal variance and normality in the data (Zar 1999).

Relative Abundance of Prey Species. We calculated the relative abundances of selected raptor prey species (Table 2) from point-count data collected from 2003–2008 for each site. We conducted the surveys from eight randomly selected points within each site, with two points selected within the forest and six points in the surrounding urbanized matrix (Donnelly and Marzluff 2004b). Point counts were 10 min in duration, during which we identified all detected species within a 50-m radius. Point count sessions were conducted four times annually between 15 April and 1 August. In addition to counting birds, we also counted small diurnal mammals frequently eaten by raptors, including: Douglas squirrel *(Tamiasciurus douglasii)*, eastern gray squirrel *(Sciurus carolinensis),* and Townsend's chipmunk *(Tamias townsendii)*. We were unable to survey abundance of other important prey species including voles (*Microtus* spp.), mice, amphibians, reptiles, and large insects. As such, the assessment falls short of a complete inventory of prey, particularly for some of the small owl species.

The eight points were designed to assess species abundance at the 1-km^2 scale, but based on land-cover variability, they probably did not accurately reflect the larger 7.5 km^2 plots. To estimate the relative abundance of prey species at this larger scale, we combined the three urban land-cover classes (heavy, medium and light intensities) into one aggregate ''urban'' class, and the two forest land-cover classes (deciduous-mixed and coniferous) into one ''forest'' class and calculated the percent land cover of each type within a 7.5-km^2 circle, centered on the centroid point of each spot-mapped survey polygon. We determined the general land-cover class of each point count point using ArcMap 9.2, and we averaged and weighted the percent ''forest'' or ''urban'' counts for each prey species, across multiple years as appropriate. We then summed the urban and forest abundance values to provide a more accurate assessment of the relative abundance of prey species at a scale more appropriate for the raptor species included in our study.

Model Selection. To assess the influence of prey abundance and land cover on raptor presence, we related primary and secondary prey abundance and two landscape metrics to raptor presence using logistic regression models in SPSS Statistics, Ver. 17.0 (SPSS Inc., Chicago, Illinois, U.S.A.; see Table 1). We created a prey-only model to determine whether raptor species presence is best explained by the relative abundance of key prey. Species composition within these variables was based on the geographically relevant published reports, direct observation of raptors with prey, and an analysis of prey remains

Table 2. Prey abundance and landscape variables included in logistic regression model.

Species	Prey Abundance Variable: Primary	Prey Abundance Variable: Secondary	Landscape Variables: Primary	Landscape Variables: Secondary	References
Sharp-shinned Hawk	*Poecile atricapilla* *Poecile rufescens* *Junco hyemalis* *Carduelis pinus*	*Carpodacus mexicanus* *Melospiza melodia* *Empidonax difficilis*	% coniferous 7.5 km²	% light urban 7.5 km²	Bent 1937, Duncan 1980, Reynolds and Meslow 1984, Cringan and Horak 1989, Bildstein and Meyer 2000, Buchanan 2005e; prey remains at sites
Red-tailed Hawk	*Sciurus carolinensis* *Corvus brachyrhynchos*	*Sturnus vulgaris* *Colaptes auratus*	CWED (deciduous/ mixed forest + grass) 7.5 km²	% mixed forest 7.5 km²	Bent 1937, Austing 1964, Craighead and Craighead 1969, Stout et al. 2006, Restani 1991, Preston and Beane 1993, DeBruyn 2005
Northern Pygmy-Owl	*Junco hyemalis* *Poecile atricapilla* *Poecile rufescens* *Carduelis pinus*	*Troglodytes pacificus* *Tamias townsendii* *Melospiza melodia*	% total forest 7.5 km²	CWED (deciduous/ mixed forest + coniferous forest) 7.5 km²	Bent 1938, Holt and Leroux 1996, Holt and Petersen 2000, Buchanan 2005a, Piorecky and Prescott 2006, Sater et al. 2006
Barred Owl	*Tamiasciurus douglasii* *Corvus brachyrhynchos*	*Tamias townsendii* *Cyanocitta stelleri*	% mixed forest 7.5 km²	CWED (deciduous/ mixed forest + light intensity urban) 7.5 km²	Marks et al. 1984, Mazur and James 2000, Buchanan 2005c, Livezey 2007
Great Horned Owl	*Corvus brachyrhynchos* *Patagioenas fasciata*	*Columba livia* *Sciurus carolinensis*	% mixed forest 7.5 km²	CWED (deciduous/ mixed forest + grass) 7.5 km²	Bent 1938, Houston et al. 1998, Buchanan 2005d
Western Screech-Owl[b]	NA	NA	% mixed forest 1 km²	% non-forested wetlands 1 km²	Bent 1938, Houston et al. 1998, Buchanan 2005b
Barn Owl[c]	NA	NA	% grass 7.5 km²	CWED (deciduous/ mixed forest + grass) 7.5 km²	Bent 1938, Marti et al. 2005

[a] CWED = Contrast-weighted edge density.
[b] Western Screech-Owls prey primarily on small rodents (family Muridae), insects and occasional crayfish and rarely on any of the avian or mammalian species for which we have abundance data.
[c] Barn Owls prey primarily upon small Murid rodents.

associated with focal raptor species within the field sites (Table 2). Prey composition followed patterns suggested by optimal foraging models, with most prey falling into a narrow range of body mass, particularly for Sharp-shinned and Cooper's hawks. We tested the model that suggests land cover best explains raptor presence by relating raptor presence to a primary and secondary land-cover variable, again based on the geographically relevant literature and observations of raptor habitat use in the field (Table 2). Lastly, we tested whether a combination of prey and land-cover variables best

Red-tailed Hawk	■	■			■	■	■	■	■	■	■	■		■		■	■	■	■	■	■
Cooper's Hawk		■	■	■	■	■		■	■	■	■		■	■	■	■	■		■	■	
Barred Owl	■	■	■		■	■	■		■	■			■	■	■	■	■	■	■	■	
Sharp-shinned Hawk	■		■		■	■				■		■			■	■	■	■	■	■	■
Great Horned Owl						■	■		■				■			■	■				
Western Screech-Owl	■		■		■			■	■												
Northern Pygmy-Owl																			■	■	■
Barn Owl	■																				
Raptor species richness	5	3	4	1	5	5	3	3	5	4	2	2	3	3	3	5	5	3	5	5	3
Percent total forest cover at 7.5 km^2	9	18	27	31	33	34	37	39	41	42	42	45	48	50	53	57	62	68	79	88	96
Percent total urban cover at 7.5 km^2	91	65	64	57	45	39	24	39	43	41	50	8	33	15	31	26	29	20	7	10	0

Figure 2. Raptor species richness across 21 sites along urban to wildland gradient near Seattle, in western Washington, U.S.A., with the most urban sites on the left of the figure. Presence indicated by gray shading and species are listed in descending order of frequency across all sites.

explained raptor presence with a third model that combined the above prey and landscape metrics. We assessed relative model fit using Akaike's Information Criterion (AIC_c; Akaike 1973), using the thresholds of support based on ΔAIC_c values (Burnham and Anderson 2004), and weight of evidence derived from the AIC_c. We assessed goodness-of-fit with the Hosmer and Lemeshow chi-square test, and model explanatory power using Nagelkerke's adjusted R-squared.

Results

We detected eight species of raptors within the 21 field sites sampled with equal effort (Fig. 2). An additional six species were observed within the field sites outside the context of our sampling efforts (Osprey [*Pandion haliaetus*], Bald Eagle [*Haliaetus leucocephalus*], American Kestrel [*Falco sparverius*], Merlin [*Falco columbarius*], Peregrine [*Falco peregrinus*], and Northern Saw-Whet Owl), resulting in a total of 14 species of raptors identified along the urban to wildland gradient. Raptor presence was determined by either a visual or vocal response during broadcast surveys, by observed presence within our target survey polygons during spot-mapping and, most frequently, by both methods. Red-tailed Hawks were the most abundant raptor, detected at 81.0% of the sites, followed by Cooper's Hawks and Barred Owls, observed at 76.2% of the sites, and Sharp-shinned Hawks at 61.9% of the sites.

Raptor species richness varied from one to five species per site and was not strongly correlated with total songbird species richness ($P = 0.17$, $r^2 = 0.10$, $\beta = 0.08$), the diversity of land-cover classes using the Shannon-Weaver Diversity Index ($P = 0.49$, $r^2 = 0.03$, $\beta = -0.62$), or percent forest cover within 7.5-km^2 ($P = 0.74$, $r^2 = 0.01$, $\beta = 0.01$). Four sites with 57.4% forest cover or greater at the 7.5-km^2 scale harbored five species of raptors, whereas at the other end of the gradient, three sites with lower percent total forest (8.5–34.1%) also contained five species (Fig. 2).

Models including only land cover variables were highest ranked for three of the six species, and garnered considerable support for the remaining three species (Table 3). The weight of evidence supporting models only including land cover averaged 55% across all six species. Models including land cover and prey variables or only prey variables received consistently less support (average weight of evidence for combined models and prey models was 24% and 21%, respectively). In addition to garnering less overall support, models including prey abundance often suggested that increased prey was associated with reduced predator presence (for all except Cooper's Hawks, at least one primary or secondary prey model coefficient was negative; Table 3).

Mean abundance values for prey species and land-cover variables for each raptor species (Table 4) provided better resolution of these patterns, with the two dietary generalists, Cooper's Hawks and Barred Owls, showing similar associations with edges between mixed forest and light urban land cover and limited patterns in within prey abundance. Sharp-shinned Hawks showed an association with coniferous forests, as well as with the abundance of several prey species that are also associated with such forests. Likewise, Northern Pygmy-Owls showed a strong association with percent total forest and a contrast-weighted

Table 3. Model selection and logistic regression analysis of single-factor and combined factor models explaining raptor presence along an urban-wildland gradient in western Washington.

		SPECIES					
MODEL	MODEL AND COEFFICIENT ASSESSMENT	SHARP-SHINNED HAWK	COOPER'S HAWK	RED-TAILED HAWK	NORTHERN PYGMY-OWL	BARRED OWL	GREAT HORNED OWL
Prey abundance[a]	ΔAIC_c	0	6.59	1.75	9.58	5.01	1.28
	w_i	0.58	0.03	0.22	0.01	0.06	0.34
	Hosmer-Lemeshow test (sig.)	0.72	0.02	0.90	0.26	0.49	0.19
	r^2_{adj}	0.23	0.16	0.38	0.40	0.05	0.01
	β 1° prey	1.87	0.08	−3.44	−0.38	−0.31	−0.15
	Wald	3.37	0.004	4.00	0.10	0.05	0.01
	β 2° prey	−1.80	2.94	−0.22	4.87	−1.48	−0.57
	Wald	2.81	1.75	0.14	3.74	0.67	0.04
Land cover[b]	ΔAIC_c	0.93	0	1.52	0.40	0	0
	w_i	0.36	0.83	0.25	0.45	0.77	0.64
	Hosmer-Lemeshow test (sig.)	0.02	0.34	0.90	0.89	0.74	0.49
	r^2_{adj}	0.19	0.14	0.06	0.80	0.30	0.09
	β 1° land cover	0.10	−0.004	0.03	0.24	0.06	0.03
	Wald	3.00	0.02	0.16	1.54	1.00	0.27
	β 2° land cover	0.05	0.04	0.04	0.04	0.10	0.07
	Wald	0.66	1.59	0.54	0.31	2.24	0.83
Prey + land cover	ΔAIC_c	4.47	3.51	0	0	2.98	6.55
	w_i	0.06	0.14	0.53	0.53	0.17	0.02
	Hosmer-Lemeshow test (sig.)	0.39	0.58	0.08	1.00	0.21	0.56
	r^2_{adj}	0.29	0.27	0.42	1.00	0.42	0.09
	β 1° prey	1.49	0.82	−4.03	23.50	−0.42	0.32
	Wald	1.96	0.17	3.96	0.00	0.06	0.03
	β 2° prey	−0.79	2.78	−0.49	19.09	−3.33	−0.31
	Wald	0.31	1.36	0.51	0.00	2.37	0.01
	β 1° land cover	0.09	0.04	0.06	2.20	0.07	0.03
	Wald	1.16	0.47	0.28	0.00	0.98	0.27
	β 2° land cover	0.03	0.05	−0.08	0.53	0.14	0.06
	Wald	0.20	1.69	0.86	0.00	2.99	0.79

[a] Prey abundance is based on point count data conducted 2003–2008.

[b] Land cover for central Puget Sound, Washington, U.S.A. derived from summer and winter 2002 Landsat Thematic Mapper satellite imagery (developed by Urban Ecology Research Laboratory, University of Washington 2006–Hepinstall-Cymerman et al. 2009).

edge density assessed metric between mixed and coniferous forest, and associated interior coniferous forest-dwelling songbirds like Chestnut-backed Chickadees (*Poecile rufescens*) and Pacific Wrens (*Troglodytes pacificus*).

DISCUSSION

Western Washington's urban to wildland gradient supports a diverse population of diurnal and nocturnal raptor species, in part because of the diversity of land-cover types along this gradient. Of eight species of raptors detected on our field sites, three species of hawks (Sharp-shinned, Cooper's, and Red-tailed hawks), and three species of owls (Barn, Barred, and Great Horned owls) can all be described as habitat generalists (Preston and Beane 1993, Houston et al. 1998, Bildstein and Meyer 2000, Mazur and James 2000, Marti et al. 2005, Curtis et al. 2006). These six species occupy both deciduous and coniferous forests and woodlots throughout much of North America, and Red-tailed Hawks, Barn Owls, and Great Horned Owls also may use agricultural and other non-forested landscapes across their range. Five of these raptors also can be considered dietary generalists, feeding upon a wide range of avian and mammalian prey (Preston and Beane 1993, Houston et al. 1998, Bildstein and Meyer 2000, Mazur and James 2000, Curtis et al. 2006), with only Barn Owls demonstrating a more targeted diet of small microtone rodents (Marti et al. 2005).

Although we found a diversity of raptors across the urban to wildland gradient, our data were limited to the occurrence of the species, not viability of these predator populations. We surveyed during the breeding season, but did not assess fecundity, productivity, or survival. Our study also was focused on particular places along the gradient, rather than the full range of space utilized by a given pair of raptors. Given the large home ranges of many of these raptor species, it is possible that their foraging areas did not overlap directly with our prey survey areas or land-cover assessments. Raptor nest site locations may have been located outside our target survey area, with minimal overlap yet resulting in detections in our surveys. Males of accipiter species may also roost some distance away from their nest site (Murphy et al. 1988). In a fragmented suburban landscape, this may place them in a different forest fragment than their nest site, resulting in a different node or epicenter of hunting activity. To fully understand how a diversity of raptors responds to urbanization, we encourage demographic studies of individually tagged hawks and owls from the city center to its suburban edges.

Overall, land-cover variables explained the presence of nearly all species of raptors better than measures of the abundance of their important prey items. The unique diversity of land-cover types and the continuum of forest cover along western Washington's urban to wildland gradient accommodates both habitat generalist and specialist species of raptors. Increased edge habitat, as indicated by contrast-weighted edge density metrics, was a particularly strong predictor of presence for several species (Cooper's Hawks, Red-tailed Hawks, Barred Owls, and Great Horned Owls) that appear to thrive in fragmented landscapes associated with anthropogenic activity. High densities of potential avian and mammalian prey associated with partially developed landscapes appear to provide sufficient food resources that promote the presence of these generalist species as well.

The diverse diets of many raptors we studied may reduce the influence of the primary and secondary prey variables we considered, thereby strengthening the relative influence of the land-cover variables within the models. Given both the greater diversity and overall abundance of potential prey species associated with partially developed areas, such numbers may obfuscate any strong influence of prey on presence. In addition, the two larger owl species and Red-tailed Hawks all had negative beta estimates for both primary and secondary prey abundance, which may indicate their selection of small mammals other than the species included in our survey, a preference that may also be true for the other raptor species detected in our surveys. It is also important to note that prey abundance is not necessarily equivalent to the availability of potential prey to hunting raptors. Many factors, including foraging behavior, use of bird feeders, breeding status and courtship behaviors, nest-site selection, and overall landscape-based predation risk all may differentially influence the vulnerability of potential prey in a given area, thereby influencing the availability of prey to hunting raptors. Likewise, specific land-cover characteristics, such as those found in suburban development (edges, hedges, and fence lines) may favor the foraging strategies of some raptor species (e.g., Cooper's Hawks), thereby increasing the vulnerability of specific potential prey species that may use such landscapes. Models that included land cover provided strong support for all four species, but low adjusted r^2 values revealed the general nature of most species' habitat use. Our results suggest that these generalists should be able to find adequate prey resources within both the forest and the surrounding developed areas as long as there is appropriate land cover (including small, urban forest fragments) that provides structure for nesting.

Two species of owls, Western Screech-Owls and Northern Pygmy-Owls, can be considered habitat specialists, each using different land-cover types within the urban–wildland gradient (Holt and Petersen 2000, Cannings and Angell 2001). The highest densities of Western Screech-Owls in Washington state occur in low-elevation riparian deciduous forests (Buchanan 2005b). We detected this species at only five of 21 sites, even though stands dominated by bigleaf maple and red alder are common

Table 4. Mean primary and secondary prey abundance and land-cover variables per raptor species.

RAPTOR SPECIES	VARIABLE CATEGORY	VARIABLE	RAPTOR PRESENT $\bar{x}$	RAPTOR PRESENT n	RAPTOR PRESENT SE	RAPTOR ABSENT $\bar{x}$	RAPTOR ABSENT n	RAPTOR ABSENT SE
Sharp-shinned Hawk	1° Prey	*Poecile atricapilla*	0.27	17	0.07	0.29	9	0.08
		Poecile rufescens	0.64	17	0.07	0.53	9	0.11
		Junco hyemalis	0.46	17	0.07	0.27	9	0.09
		Carduelis pinus	0.27	17	0.05	0.21	9	0.07
	2° Prey	*Carpodacus mexicanus*	0.28	17	0.12	0.67	9	0.26
		Melospiza melodia	0.44	17	0.07	0.33	9	0.09
		Empidonax difficilis	0.29	17	0.06	0.16	9	0.05
	1° Land cover	% coniferous forest - 7.5 km^2	26.12	17	3.07	18.55	9	2.64
	2° Land cover	% light urban - 7.5 km^2	23.01	17	2.49	23.78	9	1.96
Cooper's Hawk	1° Prey	*Turdus migratorius*	0.80	21	0.07	0.80	5	0.13
		Colaptes auratus	0.11	21	0.02	0.10	5	0.04
		Cyanocitta stelleri	0.23	21	0.06	0.18	5	0.05
		Columba livia	0.13	21	0.04	0.002	5	0.00
	2° Prey	*Corvus brachyrhynchos*	0.56	21	0.08	0.40	5	0.22
		Picoides villosus	0.03	21	0.01	0.04	5	0.02
		Tamiasciurus douglasii	0.18	21	0.05	0.09	5	0.02
		Tamias townsendii	0.02	21	0.00	0.02	5	0.01
	1° Land cover	% deciduous-mixed forest - 7.5 km^2	41.42	21	2.64	45.89	5	10.09
	2° Land cover	CWED (% deciduous-mixed forest-light urban - 7.5 km^2)	53.15	21	4.30	38.47	5	10.27
Red-tailed Hawk	1° Prey	*Sciurus carolinensis*	0.03	20	0.01	0.04	6	0.03
		Corvus brachyrhynchos	0.43	20	0.08	0.89	6	0.11
	2° Prey	*Sturnus vulgaris*	0.44	20	0.12	1.11	6	0.57
		Colaptes auratus	0.09	20	0.02	0.14	6	0.06
	1° Land cover	CWED (% deciduous-mixed forest-grass - 7.5 km^2)	11.32	20	1.65	9.41	6	2.12
	2° Land cover	% deciduous-mixed forest -7.5 km^2	31.75	20	2.33	27.81	6	3.07
Northern Pygmy-Owl	1° Prey	*Junco hyemalis*	0.41	4	0.17	0.39	22	0.07
		Poecile atricapilla	0.13	4	0.04	0.31	22	0.06
		Poecile rufescens	1.00	4	0.17	0.53	22	0.05
		Carduelis pinus	0.20	4	0.12	0.26	22	0.04
	2° Prey	*Troglodytes pacificus*	0.78	4	0.11	0.21	22	0.04
		Tamias townsendii	0.01	4	0.01	0.02	22	0.00
		Melospiza melodia	0.35	4	0.15	0.41	22	0.06
	1° Land cover	% total forest - 7.5 km^2	65.16	4	5.82	38.12	22	2.16
	2° Land cover	CWED (% deciduous-mixed forest-coniferous - 7.5 km^2)	74.81	4	9.15	37.77	22	4.11
Barred Owl	1° Prey	*Tamiasciurus douglasii*	0.18	19	0.05	0.16	7	0.07
		Corvus brachyrhynchos	0.50	19	0.08	0.46	7	0.20

Table 4. Continued.

Raptor Species	Variable Category	Variable	Raptor Present $\bar{x}$	Raptor Present n	Raptor Present SE	Raptor Absent $\bar{x}$	Raptor Absent n	Raptor Absent SE
	2° Prey	*Tamias townsendii*	0.02	19	0.01	0.02	7	0.01
		Cyanocitta stelleri	0.19	19	0.04	0.38	7	0.20
	1° Land cover	% deciduous-mixed forest - 7.5 km^2	32.46	19	2.41	28.79	7	1.75
	2° Land cover	CWED (% deciduous-mixed forest-light urban - 7.5 km^2)	33.69	19	2.38	22.73	7	6.41
Great Horned Owl	1° Prey	*Corvus brachyrhynchos*	0.43	6	0.07	0.46	15	0.10
		Patagioenas fasciata	0.05	6	0.02	0.05	15	0.01
	2° Prey	*Columba livia*	0.09	6	0.05	0.10	15	0.06
		Sciurus carolinensis	0.02	6	0.01	0.02	15	0.01
	1° Land cover	% deciduous-mixed forest - 7.5 km^2	34.90	6	3.75	31.66	15	2.63
	2° Land cover	CWED (% deciduous-mixed forest-grass -7.5 km^2)	13.52	6	4.18	9.94	15	1.45
Western Screech-Owl	1° Land cover	% deciduous-mixed forest - 1 km^2	29.22	5	4.78	35.12	16	3.42
	2° Land cover	% non-forested wetlands - 1 km^2	0.74	5	0.72	0.68	16	0.45

throughout the low-elevation forest fragments in the western Washington region. Anecdotal evidence indicates that the recent range expansion of the larger Barred Owl into the Pacific Northwest (Mazur and James 2000, Livezey 2009) has either directly reduced Western Screech-Owl populations (Cannings and Angell 2001, Elliott 2006, Acker 2012), or reduced their detectability in response to Barred Owl presence. Northern Pygmy-Owls were detected at two of the three forest reserve sites, and a third developed site with 79% total forest cover. They were not present at any site with less than 59% forest cover. This species was associated with forest edges in Canada (Piorecky and Prescott 2006), but our observations of these owls were primarily from interior forest habitat at our more forested reserve sites, with no detections within 300 m of a forest edge.

Management. In contrast to many other parts of the country in which urban/suburban raptors have been studied (Tucson, Arizona: Boal and Mannan 1998, 1999; Southern California: Bloom and McCrary 1996; Waco, Texas: Gehlbach 1996; Milwaukee, Wisconsin: Rosenfield et al. 1996; southwestern Ohio: Dykstra et al. 2012), western Washington provides woodland raptors with an abundance of natural structure and native forest habitat. King and Snohomish counties, the counties within which our research took place, are composed of 57% and 68% mixed deciduous and coniferous forest cover, respectively (King County 2007, Snohomish County 2009). King County also maintains 17% forest cover within designated urban areas (King County 2007), much of which is mandated for protection under King County's Critical Areas Ordinance (King County 2008). This protected status includes streams and associated riparian forest buffers, forested wetlands, and steep slopes. Continued protection may ensure the long-term presence of these raptor species (and other forest species) within the urban landscapes of western Washington.

Large tracts of native, second-growth forest make up the eastern parts of both King and Snohomish counties, and much of this is private and state-owned land managed for timber production. Higher elevations include National Forest and designated wilderness areas. The close proximity of these large forested regions to the more developed landscape in the lowlands may function as a population source landscape for raptors. This may result from a rather spatially compressed urban to wildland gradient, with large tracts of protected forest beginning within 16 km of downtown Seattle, many of which are contiguous with the larger forested areas in the Cascade Mountains. Because additional development of more lowland forests is projected for the western Washington region (Hepinstall et al. 2008), the creation of nondeveloped forest reserves should be a priority for regional planners. This increased conversion to urban land-cover within the western Washington lowlands would most likely negatively affect populations of Northern Pygmy-Owls, and to a lesser degree, Sharp-shinned Hawks (assuming some plasticity in their nest-site preferences). Both species would benefit from preservation of large forested tracts and maintenance of managed timber production lands in the lowlands, which would provide both the forest edge (as suggested by Piorecky and Prescott [2006]) and early seral coniferous stands for nesting Sharp-shinned Hawks.

Even at the smaller 1-km^2 scale, all our study sites have some degree of riparian forest habitat, much of which has been set aside under King County's Critical Areas Ordinance (King County 2008). This may allow for sufficient nesting habitat for Western Screech-Owls as they adapt to the increasing populations of Barred Owls in the western Washington lowlands. Gehlbach (1996) notes increased nesting success in Eastern Screech-Owls nesting in suburban landscapes, but more information on their relationship with Barred Owls is strongly warranted before making similar claims for the Western Screech-Owl in the Northwest.

Many forested riparian areas are too steep to be easily developed, thereby preserving those areas *de facto*. Developers also may maintain nondeveloped forested areas intentionally within planned developments for both aesthetic and financial reasons. Parcels nearer preserved forested open space frequently have higher property values associated with them based on the hedonic pricing model (Tyrväinen 1997, Oleyar et al. 2008). Many of these parcels may be too small in size for habitat sensitive species like Northern Pygmy-Owls, but these urban forest fragments may provide sufficient nesting habitat for several of the other more adaptive raptor species that inhabit the western Washington lowlands.

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