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Corvid response to human settlements and campgrounds: Causes, consequences, and challenges for conservation

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ABSTRACT

Human development often favors species adapted to human conditions with subsequent negative effects on sensitive species. This is occurring throughout the urbanizing world as increases by generalist omnivores, like some crows and ravens (corvids) threaten other birds with increased rates of nest predation. The process of corvid responses and their actual effects on other species is only vaguely understood, so we quantified the population response of radio-tagged American crows (*Corvus brachyrhynchos*), common ravens (*Corvus corax*), and Steller's jays (*Cyanocitta stelleri*) to human settlements and campgrounds and examined their influence as nest predators on simulated marbled murrelet (*Brachyramphus marmoratus*) nests on Washington's Olympic Peninsula from 1995 to 2000. The behavior and demography of crows, ravens, and jays was correlated to varying degrees with proximity to human development. Crows and ravens had smaller home ranges and higher reproduction near human settlements and recreation. Annual survival of crows was positively associated with proximity to human development. Home range and reproduction of Steller's jays was independent of proximity to human settlements and campgrounds. Local density of crows increased because home ranges of neighboring breeding pairs overlapped extensively (6× more than ravens and 3× more than Steller's jays) and breeders far from anthropogenic foods traveled 10s of kilometers to access them. Corvids accounted for 32.5% of the predation events ($n = 837$) we documented on artificial murrelet nests. Small corvids (jays) were common nest predators across our study area but their contribution as predators did not vary with proximity to settlements and campgrounds. In contrast, large corvids (crows and ravens) were rare nest predators across our study area but their contribution varied greatly with proximity to settlements and campgrounds. Managers seeking to reduce the risk of nest predation need to consider the varied impacts and variable behavioral and population responses of potential nest predators. In our situation, removing large corvids may do little to reduce overall rates of nest predation because of the diverse predator assemblage, but reducing anthropogenic food in the landscape may be effective.

1. Introduction

Currently, approximately 3% of the land on Earth is covered with human dwellings and commercial structures (Meyer and Turner, 1994; Imhoff et al., 2004). Sprawl and associated recreational use of natural areas near settlements affects a much larger area (O'Meara, 1999; Bullard, 2000). This changes the quantity and quality of habitat for native wildlife (Robinson et al., 2005; Pauchard et al., 2006) which, coupled with the introduction of exotics, simplifies and homogenizes animal

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communities (Blair, 2001; McKinney, 2006). Responses of birds to such changes are illustrative: settlement reduces, perforates, and insularizes native vegetation used by birds, increases juxtaposition of native vegetation and human activity centers, and exposes birds in remaining vegetation to disturbance associated with human presence (Knight and Gutzwiller, 1995; Marzluff, 2001; Marzluff and Hamel, 2001; Drinnan, 2005). These changes favor birds adapted to life with people (Johnston, 2001), non-native species and many native, early successional and edge-associated species, while selecting against native interior forest obligates, ground nesters, and rare species with large range requirements (Gavereski, 1976; Whitcomb et al., 1981; Beissinger and Osborne, 1982; DeGraaf and Wentworth, 1986; Tilghman, 1987; Er et al., 2005; Marzluff, 2005; Clergeau et al., 2006).

Much of this change in native bird communities is in response to direct effects on vegetation, but increases in some synanthropic and non-native species may later drive reductions in other species (Bolger, 2001; Marzluff, 2001). Synanthropic, generalist predators, like some crows, ravens, and jays (corvids), for example, could reduce populations of open-nesting birds by preying on nest contents or discouraging birds from nesting where predators are most abundant. While intuitive, the connections between humans, corvids, nest predation, and populations of other birds are poorly documented and results are often contradictory. Some corvids (*Corvus brachyrhynchos, Pica pica, Corvus cornis, Corvus levaillantii, Cyanocitta cristata*) increase with settlement (Konstantinov et al., 1982; Eden, 1985; Marzluff et al., 1994; Hogrefe and Yahner, 1998; Jerzak, 2001; Haskell et al., 2001; Marzluff et al., 2001), other corvids (Steller's jay, *Cyanocitta stelleri*) do not (Marzluff et al., 1994; Luginbuhl et al., 2001; Vigallon and Marzluff, 2005a). Increases in corvids may increase nest predation on other species (Wilcove, 1985; Hogrefe and Yahner, 1998; Wong et al., 1998), but documentation of direct links between increases in corvids and increases in nest predation is rare (Angelstam, 1986; Andrén, 1992; Luginbuhl et al., 2001; Haskell et al., 2001). In fact, changes in corvid populations are not always associated with similar changes in nest predation (Chesness, 1968; Parker, 1984; Gooch et al., 1991; Parr, 1993; Broyer and Fournier, 1995; Clark et al., 1995; Haskell et al., 2001; Marzluff et al., 2001), and even where they are, determining causal connections is difficult (Neatherlin and Marzluff, 2004).

We contend that understanding behavior and ecology of nest predators can help resolve counter-intuitive results, such as those reviewed above (Marzluff and Restani, 1999). Therefore, we studied the demographic and behavioral responses of three corvids (American crow, *Corvus brachyrhynchos*; common raven, *Corvus corax*; and Steller's jay) to human settlement (e.g., towns, commercial development, rural development) and recreation (e.g., campgrounds) and their effects on artificial marbled murrelet (*Brachyramphus marmoratus*) nests in the relatively undeveloped temperate rainforests of Washington's Olympic Peninsula. These corvids are known nest predators suspected of increasing in response to settlements and campgrounds (Newton et al., 1982; Marzluff et al., 1994, 2001; Miller et al., 1997). We tested this hypothesis by comparing the relative abundance of corvids with proximity to human activity. We expected crows to respond more dramatically than ravens or Steller's jays because of the strong association between American crows and people (Marzluff et al., 2001; Marzluff and Angell, 2005); however we hypothesized that all three species would have higher reproduction and survivorship near humans because of access to supplemental foods (Richner, 1992). We expected that home range size would increase as anthropogenic foods became less available (Neatherlin and Marzluff, 2004; Boarman and Heinrich, 1999). We also expected that space use within home ranges would vary among species because corvids differ in their social and territorial response to supplemental foods (Stone and Trost, 1991).

Understanding the connection between nest predators and predation risk can increase our ability to conserve sensitive species by identifying which predators pose the greatest risk to nesting success and by determining how this risk varies with human activity. All three corvids are suspected to limit the breeding success of the federally threatened marbled murrelet (Singer et al., 1991; Nelson and Hamer, 1995; Miller et al., 1997). Previously, we demonstrated that these corvids (and other avian and mammalian nest predators) are attracted to simulated murrelet nests (Marzluff et al., 2000; Raphael et al., 2002) and used this technique to establish a general correlation between total corvid abundance and average rate of predation at the landscape scale (Luginbuhl et al., 2001). Here we refine this approach by testing the hypothesis that proximity to human settlements and campgrounds affects the correlation between corvid abundance and the risk of nest predation to marbled murrelets. We deduced such a relationship from previous studies that have shown corvid abundance to correlate with measures of nest predation in agricultural and suburban settings more often than in wildland settings (Wilcove, 1985; Marzluff and Restani, 1999).

Taken together, our approach in this paper is to first gain a demographic and behavioral understanding of how human settlements and campgrounds affect corvids. Second, we sought to determine how the abundance and foraging behavior of these predators affects the risk of nest predation. We use this understanding to suggest how best to manage human activities to conserve species sensitive to nest predation.

2. Methods

2.1. *Study area*

We worked at lower elevations (<600 m) on the western side of the Olympic Peninsula of Washington State (47°56′ N, 124°23′ W) in the Hoh, Soleduck, Quinault, and Queets River drainage's (Fig. 1). This region is characterized by steep topography, coniferous trees (*Pseudotsuga menziesii*, *Tsuga heterophylla*, *Picea sitchensis*, and *Thuja plicata*), and heavy rainfall. Large glacier-fed rivers meander from the center of the Peninsula in Olympic National Park through public and private forest to the Pacific Ocean.

European settlement of the west side of the Olympic Peninsula did not occur until around 1850 (Morgan, 1976) and timber and railroads have defined the post-settlement patterns. Settlers originally pioneered the Olympic Peninsula for agricultural purposes but now the dominant human activities are

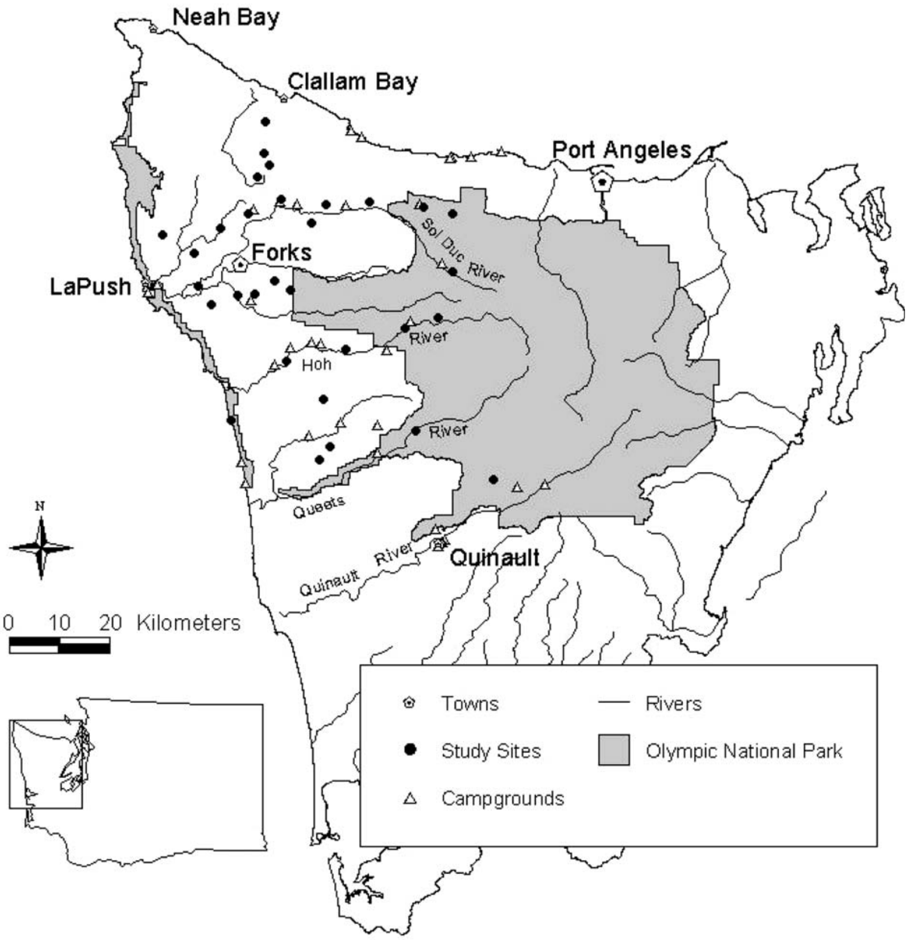

Fig. 1 – Map of the study area on the Olympic Peninsula in Washington State. Town symbol size increases with population size. Port Angeles (pop. = 18,897) was the largest town adjacent to our study area and Forks (pop. = 3,120) was the largest town within our study area.

timber harvest and recreation. Currently only one two-lane highway circumnavigates the Olympic Peninsula. Settlement is constrained to isolated towns and rural and exurban development interspersed with managed forests and recreation areas (2000 population <30,000). Primary land administrators on the Olympic Peninsula are the National Park Service (Olympic National Park, 364,800 ha), USDA Forest Service (National Forest, 254,300 ha), Washington State Department of Natural Resources (state forests, 164,000 ha), non-Federal (347, 200 ha), and Tribal (95,600 ha; Holthausen et al., 1995). Olympic National Park is western North America's second most popular park hosting >4 million visitors annually.

2.2. *Study sites*

We selected 56 sites (forest patches >50 ha in area with dominant coniferous trees 50 to >200 years old) to assess the effect of proximity to human activity on corvid abundance, demography, space use, and nest predation (Fig. 1). Sites were widely spaced across 4800 km^2 to assure independent samples of corvids. Using a geographical information system, aerial photographs, and ground reconnaissance, we stratified the entire study area according to forest structure, forest aggregation, and proximity to human development. We then selected replicate forest patches (sites) within each combination of strata at random from all available patches (Marzluff et al., 2000). Our a priori, stratified, random sampling design allows us to generalize results from the 56 sites to similar sites on the western Olympic Peninsula.

Structure of the mature forests we studied was 'simple' (a single layer of 50–80-year-old overstory trees), 'complex' (two canopy layers formed by wind disturbance events in the 1920s that toppled large, leeward sections of forest), or 'very complex' (naturally developed old growth with 2–3 canopy layers). Overstory trees were significantly taller, had greater DBH, were less dense, and had more trunk free of foliage (low crown ratio/high crown class) as we progressed from simple to complex to very complex stands (Wilks' Lambda$_{(12,80)} = 0.22$, $P < 0.001$). Overstory basal area tended to be highest in simple stands ($F_{(2,45)} = 4.86$, $P = 0.01$), and understory structure did not differ among stands classified as having different structure ($F_{(2,45)} = 0.98$, $P = 0.38$). Dominant trees within our stands were either western hemlock (*Tsuga heterophylla*), sitka spruce (*Picea sitchensis*), or silver fir (*Abies amabilis*). Western hemlocks were most common as dominants in simple stands and least common as dominants in old growth stands.

'Fragmented' stands shared a majority of their border with clearcut or young seral stage forest. 'Contiguous' stands were embedded in mature forest. The percentage of the stand boundary contacting late or mid-seral stage forest was higher for stands we classified as 'contiguous' ($\bar{x} = 83.4\%$, N = 21, SE = 3.7) than for stands classified as 'fragmented' ($\bar{x} = 21.9\%$, N = 27, SE = 4.0; $F_{(1,46)} = 119.4$, $P < 0.001$).

In this paper, we make comparisons based on proximity to human settlements and campgrounds. We sought to maximize our ability to detect human effects by randomly selecting sites that were either within 1 km of human settlements and campgrounds ($n = 22$), or >5 km from human settlements and campgrounds ($n = 34$). We chose these distance criteria based upon corvid space use (Linz et al., 1992; Sullivan and Dinsmore, 1992; Marzluff et al., 2004) and existing human settlement patterns in our study area. We defined human settlement as rural development, farms and pastures, towns (i.e., Neah Bay, Clallam Bay, Beaver, Forks, LaPush, Quinault), and Highway 101. We defined recreation as developed campgrounds with moderate to high (>500 campers per month) seasonal (May to September) camping activity (Neatherlin and Marzluff, 2004). Sites <1 km and >5 km from human settlements and campgrounds were similar in structural complexity and the amount of fragmentation immediately adjacent to the stand (structure: $\chi^2_2 = 0.85$, $P = 0.65$; fragmentation: $\chi^2_1 = 0.04$, $P = 0.84$). Elevation ranged from 60 to 530 m ($\bar{x} = 232$, SE = 15.8) for all sites and did not vary significantly between sites <1 km and >5 km from settlements and campgrounds ($F_{1,54} = 0.005$, $P = 0.95$).

2.3. Abundance

We surveyed corvids to assess relative abundance at all sites ($n = 56$) from 1995 to 2000 according to methods described in Luginbuhl et al. (2001). This survey design was loosely based on the standard point count techniques suggested by Ralph et al. (1993, 1995). We counted corvids within 50 m of each survey point and noted farther birds. To maximize our chances of detecting wide-ranging corvids we blew corvid territorial calls (Knight & Hale crow hunting call) and "predator attraction" calls (Lowman "Circe" predator call) at 2 selected points. Use of attractant calls and the similarities in forest structure and contiguity of sites that differed in proximity to human development (see above) reduces possible detection bias between sites <1 km and >5 km from human development. See Luginbuhl et al. (2001) for the effects of attractant calls and optimum corvid survey techniques using this method.

We conducted two surveys per site per season (one in late Spring and one in early Summer) and surveyed most sites in at least three separate years (2 sites surveyed 6 years; 2 sites surveyed 5 years; 7 sites surveyed 4 years; 34 sites surveyed 3 years; 11 sites surveyed 1 year). At each site we conducted 10-min counts at 7–15 points spaced evenly on a 250 m grid and recorded all vocal and visual detections. Variation in the number of sampling points reflects variation in size of sites. Counts were standardized by sampling effort (birds counted per point) and the maximum of the early and late season counts was used to represent the annual relative abundance of corvids per site. At sites counted in multiple years we averaged the annual maximum count of corvids (standardized to detections per point) and used this to represent the site's relative corvid abundance. Neither years of sampling nor sampling intensity varied systematically with treatment (<1 km from people: $\bar{x}$ years = 3.2, $\bar{x}$ points = 8.1; >5 km from people: $\bar{x}$ years = 2.7, $\bar{x}$ points = 7.9; years: $F_{(1,55)} = 2.8$, $P = 0.10$; points: $F_{(1,55)} = 0.10$, $P = 0.75$). Abundance was not normally distributed so we used non-parametric (Mann–Whitney *U*) statistics (Zar, 1999) to test for differences between sites within 1 km and those >5 km from human settlements and campgrounds.

2.4. Capture, marking, and radiotelemetry

Each season we captured adult, breeding corvids (determined by plumage, mouth lining, and breeding behavior; Good, 1952; Brown, 1963; Pyle et al., 1987; Heinrich and Marzluff, 1992) at 50 sites using a net launcher, leghold traps, mist nets, and noose carpets. We measured and color-banded all birds and fitted 58 crows, 46 ravens, and 46 jays with backpack-mounted radio transmitters (Buehler et al., 1995). Harnessed transmitters weighed 3, 14, and 27 g for Steller's jays, crows, and ravens, respectively. Steller's jay transmitter batteries lasted six months (one breeding season). Crow transmitter batteries lasted 20 months (two breeding seasons). Raven transmitter batteries lasted 40 months (three breeding seasons). We attempted to capture birds at each of the randomly selected sites ($n = 56$), but did not randomly select birds to radio-tag from among those captured because of logistical constraints. Use of radio transmitters reduced any possible detection bias in our efforts to monitor corvid use of space and demography.

We tracked birds several times per week during the breeding season (May–September) and sporadically outside the breeding season. We homed in on corvids (Mech, 1983; White and Garrot, 1990) and recorded their locations on 1:12,000 scale maps/photos of the study site and used a global positioning system to record locations in remote areas. We radio-tracked individual corvids for 1–2 h focal observation periods and plotted 2–3 locations (extreme and mid points of area used each period) for subsequent definition of the home range. We occasionally recorded single locations of animals at their roosts. We purposely recorded few locations per day on each animal to maximize the number of birds we could track and spread locations on each bird over the range of times and conditions encountered during the breeding season (Otis and White, 1999; Garton et al., 2001). We conducted aerial telemetry surveys over the western portion of the Olympic Peninsula when birds disappeared during or between breeding seasons.

2.5. Reproductive success

We monitored reproductive success for 45, 35, and 30 radio-tagged jay, crow, and raven pairs, respectively (each pair had either the male or female radio tagged). We determined reproductive success by observing nests and post-fledging family behavior. We assumed nests failed if radio-tagged adults with known nests were never seen with fledglings. Nests were considered successful when we observed radio-tagged adults feeding fledglings. During each tracking session we recorded the maximum number of fledglings observed. At the end of each breeding season, we used the maximum fledgling counts recorded for each pair to represent a pair's success. For seven crow and 17 raven pairs that we followed for $\geqslant 2$ years we used the average of the maximum fledgling counts to represent their annual success (as one would with a repeated measures design). Otherwise (38 crows and 18 ravens) we used a single year's maximum fledgling count. We compared numbers of fledglings for nesting pairs within 1 km of settlements and campgrounds to those nesting >5 km from settlements and campgrounds using a one-tailed Student's *t*-test because we expected humans would positively influence reproductive success.

2.6. *Survival analysis*

We used the Kaplan–Meier product-limit estimator (Kaplan and Meier, 1958) to estimate survivorship for 57 crows and 46 ravens (all radio-tagged). We excluded Steller's jays from this analysis because the life expectancy of their radio transmitters was only six months. We calculated survivorship based upon the number of months crows and ravens survived after attachment of the radio. We were interested in comparing breeding adult survivorship, thus, we used only crows and ravens that successfully established breeding territories (or attempted to establish breeding territories). We excluded juveniles (based on behavior, plumage, and mouth color) and individuals that were never relocated after initial radio tagging. We used the Log-rank statistic to test for differences in response to settlements and campgrounds (Winterstein et al., 2001).

2.7. *Analysis of space use*

We estimated home range size based on point locations for 42, 30, and 25 radio-tagged crows, ravens, and Steller's jays from April to September each year from 1995 to 2000. We visited radio-tagged birds on average 23 days between April and September and estimated home range with Ranges V (Kenward and Hodder, 1995) using incremental fixed kernel estimation with least squares cross validation (LSCV) smoothing techniques (Worton, 1987, 1989; Seaman et al., 1999). We used 99% fixed kernels with LSCV because they most accurately described the point locations of our birds (Seaman et al., 1999; Kernohan et al., 2001). We assumed individuals with $\geqslant 30$ point locations as 'adequately sampled' during the breeding season (Seaman et al., 1999). Within this sample, home range did not vary with sampling effort (birds with 30–49 point locations versus birds with 50–113 point locations; crows: $\bar{x}_{(30-49)} = 2888$ ha, SE = 1234; $\bar{x}_{(>50)} = 2269$ ha, SE = 1234; $n = 42$, $U = 199$, $P = 0.622$; ravens: $\bar{x}_{(30-49)} = 1402$ ha, SE = 494; $\bar{x}_{(>50)} = 257$ ha, SE = 35; $n = 30$, $U = 45$, $P = 0.355$; Steller's jays: $\bar{x}_{(30-49)} = 69$ ha, SE = 18; $\bar{x}_{(>50)} = 29$ ha, SE = 81; $n = 25$, $U = 36$, $P = 0.198$). We collected $\geqslant 2$ years breeding season home ranges for eight crows and nine ravens. For these birds we averaged annual home range sizes to produce a single range size per bird because they occupied similar areas in subsequent years (two-dimensional range overlap for crows: $\bar{x} = 66\%$, SE = 9.5%; two-dimensional range overlap for ravens: $\bar{x} = 60\%$, SE = 6.9%). We analyzed males and females together because we found no difference in home range size for male and female crows and ravens (gender assigned based on morphology and behavior; female crows: $n = 24$, $\bar{x} = 3269$ ha, SE = 1271; male crows: $n = 14$, $\bar{x} = 2028$ ha, SE = 1408; $U = 116$, $P = 0.116$; female ravens: $n = 10$, $\bar{x} = 1792$ ha, SE = 1155; male ravens: $n = 20$, $\bar{x} = 921$ ha, SE = 265; $U = 84$, $P = 0.481$). We tracked only a single member of a mated pair because mates simultaneously occupy a common range. We compared the 99% kernel home range of corvids <1 km versus >5 km from human settlements and campgrounds with Mann–Whitney *U*-tests. We consider birds, not relocation points, to be independent.

We determined the heading (degrees from nest site) of excursive forays (representative of the outer [60–99%] fixed kernel contours from their home range estimates) for six crows and nine ravens nesting >5 km from settlements and campgrounds. We assessed consistency in excursive movement directions with Rayleigh's test (Batschelet, 1981). We displayed the frequency distributions for excursive travel angles for each bird using a circular histogram. We binned the data in 45° increments for clarity.

We compared the relative differences in breeding density among heterospecific radio-tagged birds by assessing the amount of home range overlap between adjacent conspecific territories. For this analysis we used only radio-tagged breeders known to occupy adjacent territories within the same breeding season. We considered territories "adjacent" when no other pair occupied space between two territorial pairs. We assessed 20, 8, and 10 interactions from 42 crow, 30 raven, and 25 Steller's jay home range estimates, respectively. To quantify the amount of overlap we used ArcView 3.2 to calculate the volume of overlap based on 99% home range kernel estimates for adjacent pairs of radio-tagged birds. Our method calculated the volume of overlap index (Seidel, 1992; Kernohan et al., 2001) by determining what proportion of an animal's utilization distribution is shared with its neighbor. We compared the percentage of overlap between corvid species with a one-way ANOVA and used the Tukey test for pairwise comparisons (Zar, 1999). We arcsin-square root transformed percentages to increase normality.

While tracking radio-tagged birds from 1995 to 2000, we observed foraging by 46 crows ($n = 280$ foraging events), 16 ravens ($n = 27$ foraging events), and 22 Steller's jays ($n = 128$ foraging events). We identified all food items to general food item categories (e.g., invertebrate, small mammal, amphibian, refuse).

2.8. *Artificial nests*

We designed a 4-factor (forest structure, fragmentation, proximity to human development, distance to forest edge), balanced, randomized experiment to assess the potential role of corvids as nest predators on marbled murrelets. In each of our randomly selected study sites, we simulated marbled murrelet nests in mature forest canopies from 1995 to 2000. Murrelet nests are extremely difficult to locate without radio-tagged birds (Singer et al., 1991), and can be reasonably simulated because they are simple depressions in large mossy tree limbs, contain a single egg, and are often left unattended by parents (Nelson and Hamer, 1995). We randomly selected six trees of sufficient size within our 56 study sites annually to contain murrelet nest sites. We simulated both egg ($n = 585$) and chick ($n = 464$) stages of the nesting cycle using painted eggs and recently dead, preserved chicken chicks. All nest contents contained radio-transmitters, eggs were coated with paraffin, and chicks contained paraffin-coated transmitters to assure speedy and accurate identification of nest predators (see Marzluff et al., 2000 and Luginbuhl et al., 2001 for detailed methods and justification of this technique). We scattered the six nests widely in each site to avoid potential area-restricted searching by predators. At each fragmented site two nests (one with an egg, one with a chick) were created within 50 m of a forest edge, approximately 100 m from the edge, and at least 200 m from the edge (Raphael et al., 2002). At contiguous sites, all six nests were (by definition) >200 m from a forest edge. Presence of corvids during nest creation was rare and not correlated with subsequent rate of predation. Our experimental approach allowed us to identify 15 avian and mammalian nest predators (including jays, ravens, and crows) and reliably distinguished between predation by large (crows and ravens) versus small (Steller's and gray jays [*Perisoreus canadensis*]) corvids (Marzluff et al., 2000; Luginbuhl et al., 2001; Bradley and Marzluff, 2003). Inferences in this paper are confined to comparisons of nest survival at 474 nests within 1 km of settlements and campgrounds and 575 nests >5 km from settlements and campgrounds.

3. Results

3.1. *Correlations of corvid abundance with human settlements and campgrounds*

American crow abundance was strongly correlated with proximity to human settlements and campgrounds (Fig. 2). Crows were the least abundant corvid >5 km from settlements and campgrounds but their abundance increased dramatically within 1 km of settlements and campgrounds ($U = 123$, $P < 0.01$). Ravens were moderately abundant both within 1 km and >5 km from settlements and campgrounds ($U = 253$, $P < 0.05$). Steller's jays were equally abundant within 1 km and >5 km from settlements and campgrounds ($U = 345$, $P = 0.63$) and were the most abundant corvid on the Olympic Peninsula (Fig. 2; average of maximum annual detections/10 min counts: crows $\bar{x} = 0.16$, SE = 0.04; ravens $\bar{x} = 0.13$, SE = 0.02; Steller's jays $\bar{x} = 0.49$, SE = 0.04; $F_{1,57} = 37.12$, $P < 0.01$).

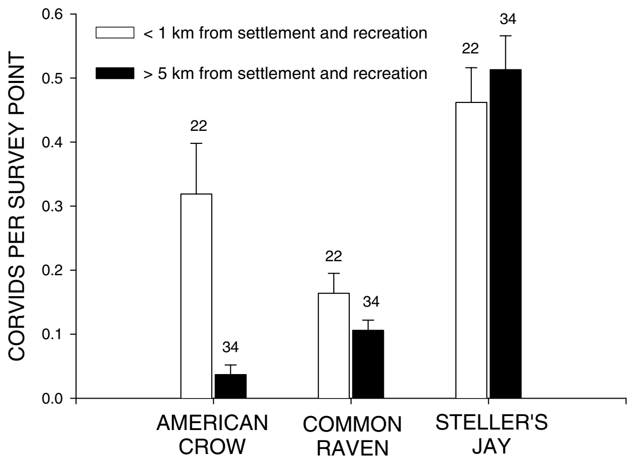

Fig. 2 – The average (±SE) count of corvids during a 10 min survey in relation to proximity to human settlements and campgrounds. We conducted 1–6 annual counts in each of 22 sites <1 km from settlements and campgrounds and 34 sites >5 km from settlements and campgrounds.

3.2. *Differences in reproduction and survivorship*

Crows and ravens fledged more young per pair within 1 km of settlements and campgrounds as predicted, but this was not the case for Steller's jays (Fig. 3; crows: $t_{43(1\text{-tailed})} = 1.68$, $P < 0.05$; ravens: $t_{33(1\text{-tailed})} = 1.99$, $P < 0.05$; Steller's jays: $t_{28(1\text{-tailed})} = 1.19$, $P = 0.123$). Steller's jays were very successful throughout our study area, fledging young 80% of the time ($n = 30$ pairs). Jays fledged up to five offspring per year ($n = 30$, $\bar{x} = 2.13$, SE = 0.27). For the three Steller's jay nests that we found over the course of the study, brood size at 7–13 days ranged from three to four nestlings ($\bar{x} = 3.33$, SE = 0.31). Across our study area, crows successfully fledged young 71% of the time (37 of 52 nests; data for all nests with radio-tagged birds). Crows fledged up to four offspring per year ($n = 45$, $\bar{x} = 1.49$, SE = 0.19). For the 10 nests where we banded young, brood size at 15–28 days ranged from one to four ($\bar{x} = 2.9$, SE = 0.28). Overall, ravens were the least productive, successfully fledging young in 60% of their nesting attempts (36 of 60 nests; data for all nests with radio-tagged birds). Brood sizes at 13–30 days for 20 nests where we banded young ranged from one to five nestlings ($\bar{x} = 2.85$, SE = 0.29). Ravens fledged up to four offspring per year ($n = 35$, $\bar{x} = 1.2$, SE = 0.21).

Crow survivorship increased significantly within 1 km of settlements and campgrounds as predicted, whereas, raven survivorship only mildly increased (Fig. 4). After 24 months, 97.7% of crows nesting within 1 km of settlements and campgrounds and 61.1% of crows nesting >5 km from settlements and campgrounds were still alive (Fig. 4A; Log-rank $\chi^2_1 = 6.84$, $P < 0.01$). Of the 57 radio-tagged crows we used in

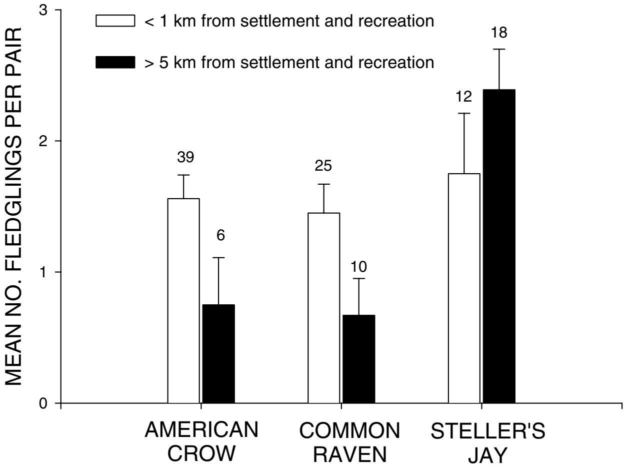

Fig. 3 – Mean number of fledglings (±SE) produced per radio-tagged pair in relation to proximity to human settlements and campgrounds. Number above error bars represents pairs of radio-tagged corvids monitored.

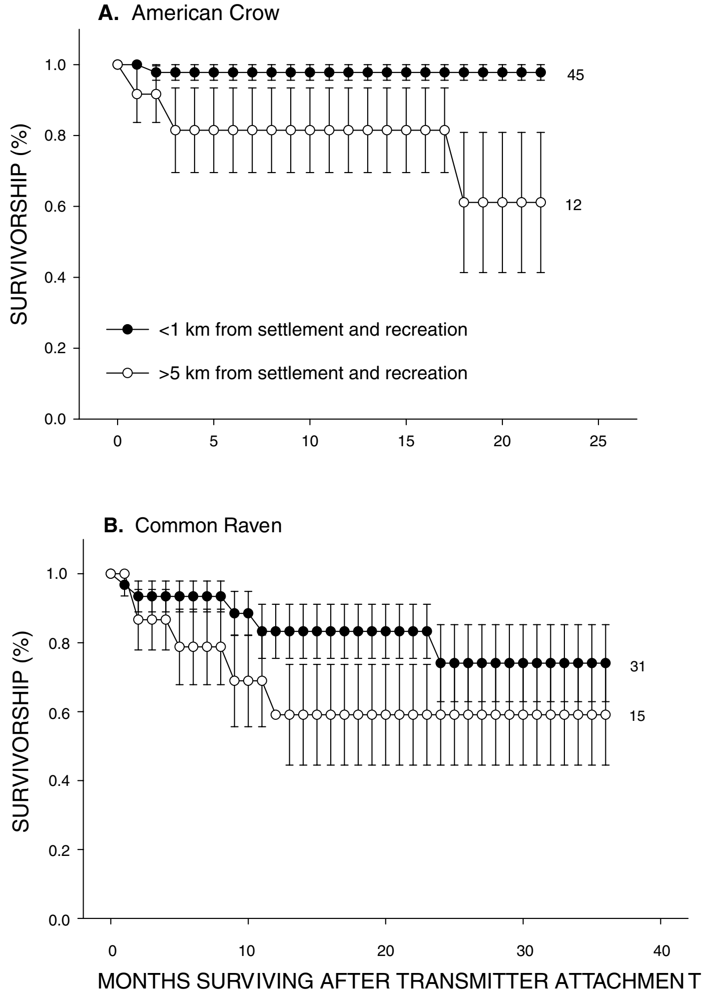

Fig. 4 – Kaplan-Meier survivorship (±SE) curves for radio-tagged crows (A) and ravens (B) in relation to proximity to human settlements and campgrounds. Number next to curve represents sample size.

our survival analysis, we confirmed only four mortalities (92.9% known-fate survivorship). Three of four mortalities were crows nesting >5 km from settlements and campgrounds. Two of these three crows were found dead within the same breeding season they were tagged. Exact cause of death was unknown but starvation or predation was suspected based on remains. One of these three crows died in Forks, Washington the winter after it was tagged. We suspect this bird was hit by a car. The only crow nesting within 1 km of settlements and campgrounds that died was shot near a residential neighborhood.

Raven survivorship was lower than crow survivorship (68.2% annual rate for all ravens versus 94.5% annual rate for all crows: Fig. 4; $\chi_1^2 = 4.7$, $P < 0.01$), and less correlated with human activity. After 36 months, only 74.1% of ravens nesting within 1 km of settlements and campgrounds and 59.1% nesting >5 km from settlements and campgrounds were still alive (Fig. 4B; Log-rank $\chi_1^2 = 2.10$, $P = 0.15$). Of the 46 radio-tagged ravens, we confirmed 10 mortalities (78.3% known-fate survivorship), five were ravens nesting >5 km from settlements and campgrounds. Three of the five raven mortalities within 1 km of settlements and campgrounds (and three of five >5 km settlements and campgrounds) occurred during the breeding season. Within 1 km of settlements and campgrounds one of the raven deaths was a confirmed shooting. Other known causes of raven mortality included predation and collisions with vehicles.

3.3. *Differences in space use*

Crows and ravens had significantly larger home ranges >5 km from settlements and campgrounds, but Steller's jays did not (Fig. 5). Crows showed the greatest difference in home range size relative to proximity to settlements and campgrounds. Crows nesting >5 km from settlements and campgrounds had ranges 5× larger than crows nesting within 1 km of settlements and campgrounds (Fig. 5A; $U = 33$, $P < 0.01$). The gap in range size increased dramatically for crows and ravens in the most extreme 60–99% of area used (Fig. 5A and B). These excursive movements (locations in the outer 60–99% contours) suggest that crows and ravens nesting >5 km from settlements and campgrounds expanded their ranges differently from one another. Crows consistently made long, uni-directional movements from core use areas (nesting area) to distant anthropogenic food resources (Table 1). Seventy-five percent (58 of 77) of excursive forays for crows nesting

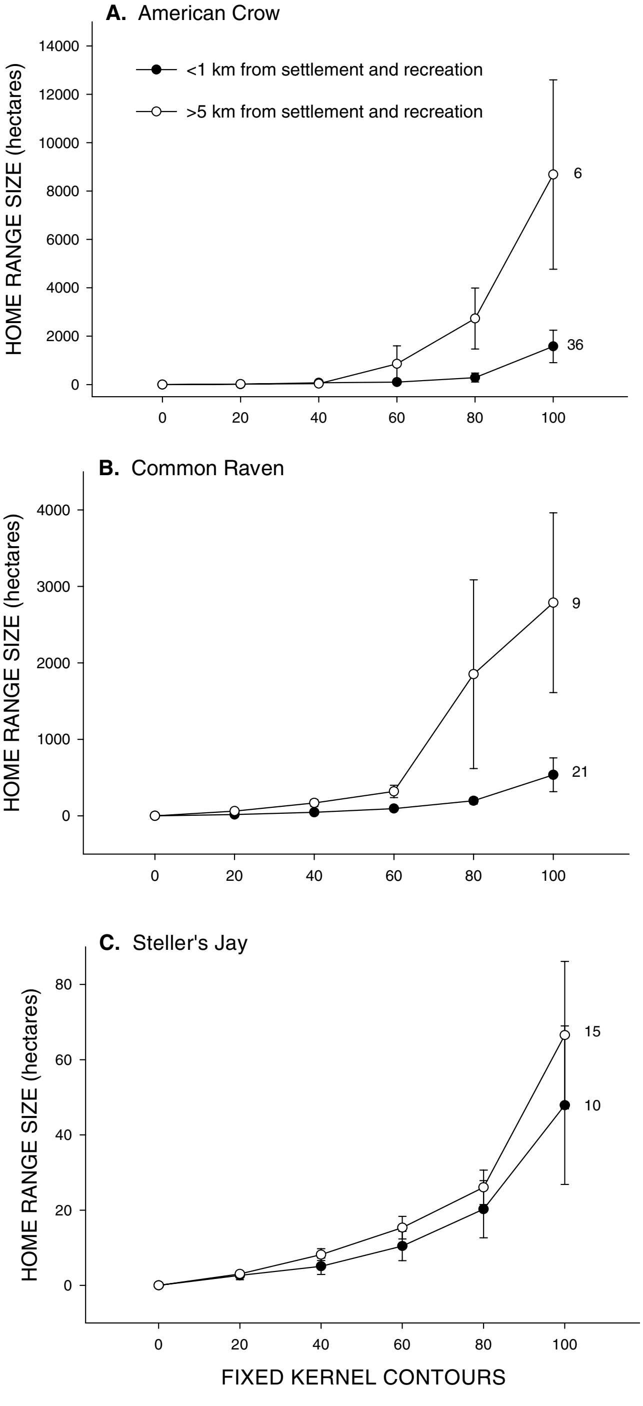

Fig. 5 – Mean (±SE) home range size for radio-tagged crows (A), ravens (B), and Steller's jays (C) as a function of the cumulative fixed kernel estimate in relation to proximity to human settlements and campgrounds. Each fixed kernel contour is displayed in 20% intervals along the X-axis. Number next to the curve represents sample size.

Table 1 – Directionality of crow and raven excursive forays (point locations in the outer 60–99% fixed kernel home range) from nests located >5 km from settlements and campgrounds

Species	*n*	$\bar{x}$ angle	R[a]	*P*-value[b]
American crow				
1	12	160	0.91	<0.01
2	14	181	0.33	>0.20
3	15	207	1.00	<0.01
4	11	75	0.98	<0.01
5	8	83	1.00	<0.01
6	17	206	0.96	<0.01
Common raven				
1	6	204	0.34	>0.20
2	13	186	0.15	>0.50
3	15	166	0.44	>0.05
4	13	178	0.25	>0.20
5	16	228	0.33	>0.10
6	13	149	0.20	>0.50
7	13	155	0.60	<0.01
8	12	175	0.31	>0.20
9	14	240	0.19	>0.50

a Rayleigh's test statistic for circular uniformity.
b Significance of Rayleigh's test indicates whether range expansion was caused by uni-directional excursions or excursions in random directions.

>5 km from settlements and campgrounds were uni-directional movements to towns, agricultural areas, waste transfer stations, or correctional facilities (Fig. 6). All but one crow showed significant consistency in the direction of these movements (Table 1). Raven home ranges were significantly larger when nesting >5 km from settlements and campgrounds than when nesting within 1 km of such landcover (Fig. 5B; $U = 20$, $P < 0.01$). However, unlike crows, most ravens nesting >5 km from settlements and campgrounds expanded their ranges with multi-directional forays from core use areas (nesting areas) to interior forests, rivers, and clearcuts. Only one of nine ravens nesting >5 km from settlements and campgrounds expanded its range with consistent movements in one direction to anthropogenic food sources (Table 1). Only 12% (14 of 115) of all excursive movements for ravens nesting >5 km from settlements and campgrounds were to anthropogenic food sources (Fig. 6). Steller's jay home ranges increased evenly as more of their range was considered and were similar in size relative to proximity to human settlements and campgrounds (Fig. 5C; $U = 48$, $P = 0.13$). Steller's jays nesting >5 km from settlements and campgrounds never visited anthropogenic sites.

We expected a positive relationship between body mass and home range size. The smallest corvid that we studied (Steller's jay) did have the smallest average home range size (99% kernel area: crows: $\bar{x} = 2593$ ha, SE = 864 ha; ravens: $\bar{x} = 1211$ ha, SE = 418 ha; Steller's jays: $\bar{x} = 59$ ha, SE = 14 ha; $H = 31.12$, $P < 0.01$). However, contrary to our expectation, overall home range size for ravens, with a body mass 3× larger than crows, was not significantly larger than crows ($U = 566$, $P = 0.47$). In fact, raven ranges averaged only half as large as crow ranges.

Increased abundance of crows <1 km from settlements and campgrounds was not simply a result of higher reproduction and survivorship and compressed home ranges. Sociality influenced the amount of space that corvids used exclusively around their nests. Breeding crows excluded neighboring crows from only the immediate nest area, which enabled them to pack into areas rich in anthropogenic and riparian food sources. Adjacent breeding crows overlapped nearly 50% of

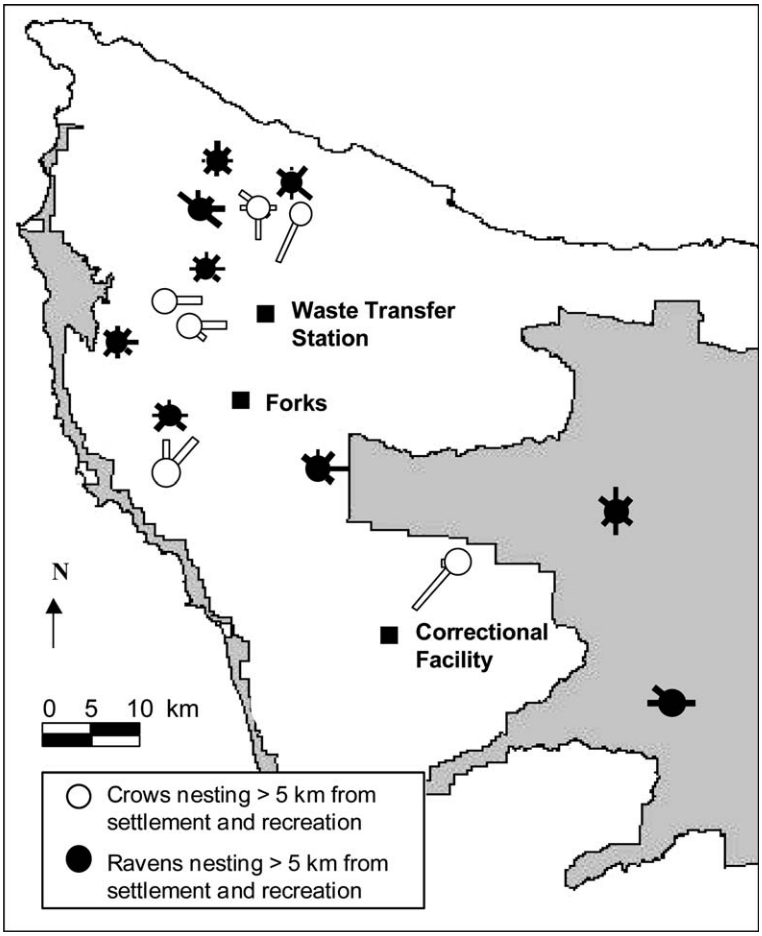

Fig. 6 – Circular histograms displaying the frequency and heading of the movements that account for the outer (60–99%) fixed kernel contours for crows and ravens nesting >5 km from human settlements and campgrounds. Each histogram represents one radio-tagged crow or raven and is centered on its respective nest location. Four of five crows expanded their ranges with uni-directional excursive movements to anthropogenic food sources (Forks, waste transfer station) and eight of nine ravens expanded their home ranges with excursive movements in multiple directions to non-anthropogenic (clearcuts, rivers, forest interior) food sources.

Table 2 – Percentage overlap in home range for adjacent conspecific radio-tagged corvids

Species	*n*	Volume[a]		Area[b]	
		$\bar{x}$ (%)	SE (%)	$\bar{x}$ (%)	SE (%)
American crow	20	48	7.4	40	5.5
Common raven	8	7.7	2.4	4.9	1.6
Steller's jay	10	17.8	5.7	12.4	8.7

a Volume is the proportion of an animal's 99% utilization distribution that is shared with its neighbor (*n* = number of adjacent pairs).
b Area is the two-dimensional overlap for the 99% contour.

each other's utilization distributions. This was 6× greater than ravens and nearly 3× greater than Steller's jays (Table 2; Volume overlap: $F_{2,17} = 6.8$, $P < 0.01$; pairwise comparisons: crows × ravens: $P = 0.01$; crows × Steller's jays: $P = 0.03$; ravens × Steller's jays: $P = 0.78$; Two-dimensional overlap: $F_{2,17} = 8.5$, $P < 0.01$; pairwise comparisons: crows × ravens: $P < 0.01$; crows × Steller's jays: $P < 0.03$; ravens × Steller's jays: $P = 0.82$).

3.4. *Diet*

Crows, ravens and Steller's jays all exploited anthropogenic food sources when nesting within 1 km of settlements and campgrounds. Crows had the most diverse diet of the three species but also relied most on anthropogenic food. We observed crows foraging on invertebrates, roadkill, nestlings, small mammals, berries/fruits/seeds, and anthropogenic food items (bread, spaghetti, fried potatoes, dog food, bagels, potato chips, sandwiches, and livestock feed). Within 1 km of settlements and campgrounds, 75% of crow foraging bouts (208 of 277) were on anthropogenic foods. Of the invertebrates eaten by crows, 24% (47 of 198) were acquired in human-converted habitats (e.g., pavement, lawns, or pastures). Ravens, foraged ($N = 27$) on anthropogenic food, invertebrates, roadkill, carrion, and were seen preying on a frog. Steller's jays within 1 km of human settlement foraged ($N = 106$) on

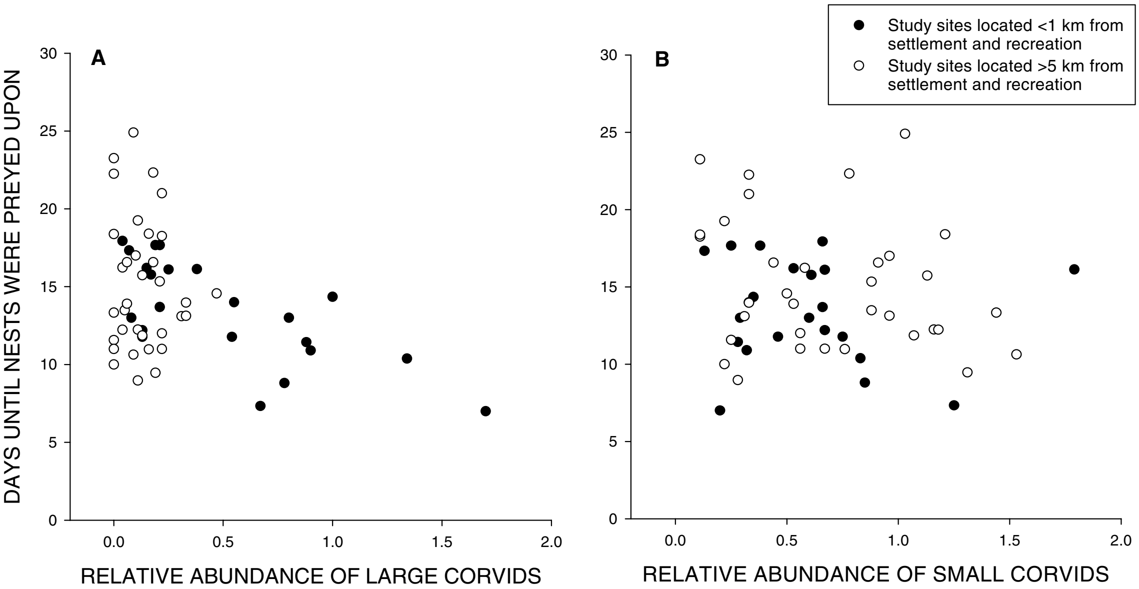

Fig. 7 – Relative abundance of large (A) and small (B) corvids in relation to artificial marbled murrelet nest survival rates. Abundance was based on multiple years of survey data from 22 sites <1 km from settlements and campgrounds and 34 sites >5 km from settlements and campgrounds. Nest survival (time to nest predation) was averaged across nests and across years for all sites.

invertebrates, berries/fruits/seeds, and anthropogenic food, but jays nesting >5 km from human settlements and campgrounds never accessed anthropogenic food sources and foraged ($N = 22$) on berries/fruits/seeds significantly more than those nesting within 1 km of settlements and campgrounds ($\chi^2_1 = 6.4$, $P < 0.01$).

3.5. *Relationship between corvid abundance and risk of nest predation*

Observations of radio-tagged corvids rarely allowed us to witness nest predation events. We observed 435 foraging events and saw only three nest predation events, all by crows residing in recreation areas. Corvids were responsible for 32.5% (272 of 837 depredated nests) of the predation events we documented on artificial marbled murrelet nests. Large corvids (crows and ravens) were rare nest predators (5.7% of all predation, 17.6% of corvid predation), but they were more important within 1 km of settlements and campgrounds than >5 km from it (8.2% of all predation within 1 km of settlements and campgrounds vs. 3.6% >5 km from settlements and campgrounds; $\chi^2_1 = 8.34$, $P < 0.01$). Jays (Steller's and gray) preyed on 26.8% of nests and were responsible for 82.4% of corvid predation.

The rate of predation on simulated nests (time in days before nests were preyed upon) correlated significantly with the relative abundance of all corvids ($r = 0.42$, $n = 56$, $P < 0.01$). However, this relationship primarily reflects a strong correlation between crow abundance and rate of nest predation at sites <1 km from settlements and campgrounds (Fig. 7A; crow: $r_{<1\text{ km}} = 0.63$, df = 21, $P < 0.01$; $r_{>5\text{ km}} = 0.04$, df = 33, $P = 0.84$; raven: $r_{<1\text{ km}} = 0.41$, df = 21, $P = 0.06$; $r_{>5\text{ km}} = 0.07$, df = 33, $P = 0.69$). In contrast, the rate of predation on simulated nests did not correlate with the variation in small corvid (jay) abundance regardless of proximity to human settlements and campgrounds (Fig. 7B; Steller's jay: $r_{<1\text{ km}} = 0.003$, df = 21, $P = 0.99$; $r_{>5\text{ km}} = 0.06$, df = 33, $P = 0.75$; gray jay: $r_{<1\text{ km}} = 0.25$, df = 21, $P = 0.27$; $r_{>5\text{ km}} = 0.28$, df = 33, $P = 0.10$).

4. Discussion

Populations of three corvids were associated to differing extent with human settlements and campgrounds in the temperate rainforests of Washington's Olympic Peninsula. Breeding crows and ravens near settlements and campgrounds reduced home range size, increased reproduction, and accordingly increased abundance. Crows also benefited from proximity to humans with increased adult survival. Steller's jay movement and demography was uncorrelated with proximity to human development.

We hypothesize that food is the most important anthropogenic resource driving the increase in corvids near settlements and campgrounds. Food is provided in both situations. We observed breeding and non-breeding jays, crows, and ravens procuring human refuse, soliciting and obtaining direct handouts of food from people, and foraging on anthropogenic surfaces like roads and lawns. Unlike desert and tundra environments where anthropogenic water, nest sites, and food fuel corvid increases (Boarman and Heinrich, personal observation), in the temperate rainforests of the Olympic Peninsula natural water and nest sites abound. Timber harvest and clearing of home sites provide additional resources. Clearing creates shrublands and edges rich in berries and insects that all corvids, especially Steller's Jays (Marzluff et al., 2004; Vigallon and Marzluff, 2005b) utilize. Young, dense trees that are planted or regenerate after timber harvest are frequently utilized for nesting by jays and crows. Larger trees in thinned plantations are frequently used for nesting by ravens. Edges, thinned forests, and smaller patches of trees created by harvest and settlement provide nest stands readily used by crows. Protection from persecution or temperature amelioration that is provided to birds in some urban settings is mostly irrelevant in the cool and rainy encampments, villages, and small cities of the Olympic Peninsula. In fact, a major source of adult mortality on ravens, and to a lesser extent on crows, in our study was shooting.

Crow ranging habits and social behavior appear to influence local abundance. Unlike ravens, crows allowed conspecific intrusion into their breeding home ranges, thereby allowing extensive range overlap and a concomitant increase in local density. This occurred despite crows having home ranges three times larger than ravens when nesting within 1 km of human settlements and campgrounds. Thus, an ability to utilize anthropogenic resources to increase reproduction and survivorship appears necessary but not sufficient to increase local corvid populations. Local density increases depend on an ability to reduce home range size and/or tolerate overlap in home ranges, both of which were done by crows.

Extensive range overlap by crows has not been previously reported (Sullivan and Dinsmore, 1992; Marzluff et al., 2001). The overlap we documented may reflect, in part, the use of our study area by the northwestern crow (*Corvus caurinus*), or hybrid American and northwestern crows that tend toward semi-colonial nesting (Verbeek and Butler, 1999). However, increased crow abundance near human settlements and campgrounds reflects more than an increase in the number of local breeders. Crows nesting >5 km from human settlements and campgrounds directed their excursive movements to anthropogenic food sources, whereas ravens did not consistently do so.

Raven populations slightly increased local density due to benefits from human activity but increases may occur at scales larger than we measured (region-wide, for example). Detecting the contribution of local breeding ravens to overall population size, however, is difficult because non-breeding ravens wander hundreds of kilometers (Bruggers, 1988; Heinrich et al., 1994; Restani et al., 2001). Previously documented increases in raven abundance in response to human activity (Singer et al., 1991; Marzluff et al., 1994; Boarman and Heinrich, 1999) likely represent such large scale changes or local changes in non-breeder abundance as young birds congregate at especially rich anthropogenic food sources. In addition, the benefit of distant anthropogenic food may be limited due to the costs of challenging defending ravens at such foods (Marzluff and Heinrich, 1991), the risks of leaving their own territories undefended, or the absence of prior knowledge (Beletsky and Orians, 1987). Crows could acquire knowledge of anthropogenic foods across the study area during winter flocking and migration away from their breeding areas, whereas, ravens remain on their breeding territories year round.

Steller's jays were the most common corvid in our study area, but despite utilizing anthropogenic foods, especially at edges between forests and settled areas (Masselink, 2001; Marzluff et al., 2004), their relative abundance did not increase near human settlements and campgrounds. This may result from a combination of territoriality, lesser mobility (jays nesting >5 km never visited anthropogenic food sources), and high reproductive success (we do not know about adult survival) across all of our sites. Juxtaposition of regenerating and mature forests may be optimum for Steller's jays (Masselink, 2001; DeSanto and Willson, 2001; Marzluff et al., 2004) and loss of secluded nesting sites and reductions in native insects and fruits as settlement increases may limit reproduction in urbanized areas (Vigallon and Marzluff, 2005a). Nonetheless, we expected access to supplemental, anthropogenic foods to increase jay abundance and reproduction in our study area because of the close proximity to regenerating and mature forest edges providing natural food. Instead, moderate levels of human settlement (as existed in our study area) had no consistent effect on reproduction or relative abundance.

The different responses of American crows and common ravens to people may have led to fundamental and unexpected differences in their basic biology. These congeneric species are typical, generalist corvids that differ grossly in body size (Marzluff and Angell, 2005). Ravens weigh 50–70% more than crows, but in our study area breeding ravens live shorter lives and occupy smaller territories than breeding crows. Based on allometric relationships, average lifespan of wild passerines scales to the 0.26 (SE = 0.02) power of mass and home range size scales to the 1.14 (SE = 0.11) power (Peters, 1983). Therefore, a 500 g crow should live 3.5 years less and occupy a home range less than half that of a 1 kg raven. We suggest crows have such large ranges and live so long because of their specialization on anthropogenic foods and use of natural foods primarily in more open settings (clearings, river corridors, and coasts). Unlike crows, ravens are forest dwellers on the Olympic Peninsula who utilize anthropogenic foods and a variety of forest fruits, insects, and vertebrates. In a forested environment crows must travel farther to access non-forest resources than ravens travel to access more uniformly distributed forest resources. Utilizing anthropogenic resources clearly is advantageous for crows. It may even be necessary for population persistence in a temperate rainforest where reproduction was poor and survival reduced greater than 5 km from settlements and campgrounds (Figs. 3 and 4). Natural selection should favor large home ranges by crows because widely ranging crows can access rich anthropogenic foods that increase important fitness components. Natural selection at present may not favor this strategy in ravens because when they specialize on anthropogenic foods they become targets of human persecution and survivorship is reduced.

4.1. *Conservation implications*

Anthropogenic food sources, even isolated ones, contribute to population increases of some corvid species in lightly settled areas (Neatherlin and Marzluff, 2004). These areas maintain extensive reaches of intact native habitat, but the quality of this habitat to nesting birds may be compromised because of increased risk of predation on nest contents by corvids. Depending on corvid social systems, their populations at local, regional, or both scales may respond, and increase predation risk. But the increase in nest predators does not simply increase predation risk.

Nest predator communities are diverse and combined effects of predators on prey can be complicated (Andrén, 1992;

Marzluff and Restani, 1999; DeSanto and Willson, 2001). On the Olympic Peninsula, we have documented 15 mammal, bird, and reptile species that prey on eggs and chicks (Marzluff et al., 2000; Bradley and Marzluff, 2003). This may be why variation in abundance of one, or even several, predator species explains, at best, 50% of the variation in risk of nest predation (Luginbuhl et al., 2001; Neatherlin and Marzluff, 2004, this paper). Detailed demographic and behavioral studies such as we present here suggest that the abundance of small corvids (jays) sets the baseline nest predation risk for other forest-nesting birds. Variation in risk may be affected by human settlements and campgrounds because crow, and to a lesser extent raven, populations increase in response to humans and elevate the risk of predation near human development. Variation in crow population size near humans explains 50% of the variation in predation risk we documented (Fig. 7) even though jays account for most nest predation by corvids. Variation in small mammals likely accounts for much of the unexplained variation in risk of predation, especially after chicks hatch (Marzluff et al., 2000; Bradley and Marzluff, 2003).

Managers interested in reducing the risk of nest predation face stiff challenges. Predators like crows may respond dramatically to human activity and influence the risk of predation, but controlling them may do little to reduce predation because other abundant predators like jays and small mammals prey on many more nests. Difficulty sorting the most important predators (jays in our case) from the most obvious ones (crows), and the high diversity of potential predators may explain why predator removal rarely succeeds in increasing nesting success (Côté and Sutherland, 1997; Dion et al., 1999). Experiments will likely be needed to determine the efficacy of predator removal on a case-by-case basis.

Control of features in the environment that affect predator populations may be more successful at reducing predation than direct predator control. In the relatively remote regions of western North America, like the Olympic Peninsula, this means control of anthropogenic resources. Controlling access to anthropogenic food on the Olympic Peninsula should reduce local predator population growth rates by reducing reproduction and survivorship and causing mobile predators like corvids to immediately disperse (e.g., Restani et al., 2001). An anecdote shows the potential of food control to reduce the risk of predation. In 1996, when flooding washed out the access road to one of the most popular visitor sites in Olympic National Park (Hoh Rainforest), visitors (and therefore food) were not allowed in the area during the breeding season. American crow and Steller's jay detections each declined by 44.6%. Raven detections remained unchanged. The probability of nest predation on simulated murrelet nests dropped from 95% ($n = 22$ nests in 1995, 1997–1999) to 50% ($n = 6$ nests in 1996). Controlling other features of the environment may have less consistent effects. For example, reducing forest fragmentation, while likely lowering Steller's jay abundance, may raise Gray jay abundance (Raphael et al., 2002; Marzluff et al., 2004).

Controlling supplemental foods provided passively by humans will require regional cooperation. Corvid populations within 1 km of concentrated food sources respond noticeably, but we also documented use of food resources by crows and ravens traveling >30 km to access these food resources. Therefore, not only do food sources in areas of management concern need to be controlled, but those at substantial distances from such areas also need to be controlled. Animal-proof garbage cans and camping regulations will not be enough to control predators. Dump closures, restrictions on agricultural activities, and increased control of garbage, animal husbandry practices, and bird feeding around residences will likely be needed.

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REFERENCES

Andrén, H., 1992. Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. Ecology 73, 794–804.

Angelstam, P., 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. Oikos 47, 365–373.

Batschelet, E., 1981. Circular Statistics in Biology. Academic Press, London, UK.

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

Beletsky, L.D., Orians, G.H., 1987. Territoriality among male red-winged blackbirds. Behavioral Ecology and Sociobiology 20, 21–34.

Blair, R., 2001. Creating a homogeneous avifauna. In: Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic, Norwell, MA, pp. 461–488.

Boarman, W.I., Heinrich, B., 1999. Common raven, *Corvus corax*. Birds of North America. Number 476, 1–32.

Bolger, D., 2001. Urban birds: population, community, and landscape approaches. In: Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic, Norwell, MA, pp. 155–177.

Bradley, J.E., Marzluff, J.M., 2003. Rodents as nest predators: influences on predatory behavior and consequences to nesting birds. Auk 120, 1180–1187.

Brown, J.L., 1963. Aggressiveness, dominance and social organization in the Steller jay. Condor 65, 460–484.

Broyer, J., Fournier, J.Y., 1995. Effect of carrion crow, *Corvus corone*, reduction on predation on artificial anatid, Anatidae, nests. Gibier Faune Sauvage 12, 95–107.

Bruggers, D.J., 1988. The behavior and ecology of the common raven in northeastern Minnesota. Dissertation, University of Minnesota, Minneapolis-St. Paul, Minnesota, USA.

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

Bullard, R.D., 2000. Anatomy of sprawl. In: Bullard, R.D., Johnson, G.S., Torres, A.O. (Eds.), Sprawl City. Island Press, Washington, DC, pp. 1–19.

Chesness, R.A., 1968. The effect of predator removal on pheasant reproductive success. Journal of Wildlife Management 32, 683–697.

Clark, R.G., Meger, D.E., Ignatiuk, J.B., 1995. Removing American crows and duck nesting success. Canadian Journal of Zoology 73, 518–522.

Clergeau, P., Croci, S., Jokimäki, J., Kaisanlahti-Jokimäki, M.L., Dinetti, M., 2006. Avifauna homogenization by urbanization: analysis at different European latitudes. Biological Conservation 127, 336–344.

Côté, I.M., Sutherland, W.J., 1997. The effectiveness of removing predators to protect bird populations. Conservation Biology 11, 395–405.

DeGraaf, R.M., Wentworth, J.M., 1986. Avian guild structure and habitat associations in suburban bird communities. Urban Ecology 9, 399–412.

DeSanto, T.L., Willson, M.F., 2001. Predator abundance and predation of artificial nests in natural and anthropogenic coniferous forest edges in southeast Alaska. Journal of Field Ornithology 72, 136–149.

Dion, N., Hobson, K.A., Larvière, S., 1999. Effects of removing duck-nest predators on nesting success of grassland songbirds. Canadian Journal of Zoology 77, 1801–1806.

Drinnan, I.N., 2005. The search for fragmentation thresholds in a southern Sydney suburb. Biological Conservation 124, 339–349.

Eden, S.F., 1985. The comparative breeding biology of magpies, *Pica pica*, in an urban and a rural habitat (Corvidae). Journal of Zoology, Series A 205, 325–334.

Er, K.B.H., Innes, J.L., Martin, K., Klinkenberg, B., 2005. Forest loss with urbanization predicts bird extirpations in Vancouver. Biological Conservation 126, 410–419.

Garton, E.O., Wisdom, M.J., Leban, F.A., Johnson, B.K., 2001. Experimental design for radiotelemetry studies. In: Millspaugh, J.J., Marzluff, J.M. (Eds.), Radiotelemetry and Animal Populations. Academic Press, Inc., San Diego, CA, pp. 16–44.

Gavereski, C.A., 1976. Relation of park size and vegetation to urban bird populations in Seattle, Washington. Condor 78, 375–382.

Gooch, S., Baillie, S.R., Birkhead, T.R., 1991. Magpie, *Pica pica*, and songbird populations. Retrospective investigation of trends in population density and breeding success. Journal of Applied Ecology 28, 1068–1086.

Good, E.E., 1952. The Life History of the American Crow *Corvus brachyrhynchos* brehm. Ohio State University, Columbus, OH, USA.

Haskell, D., Knupp, A.M., Schneider, M.C., 2001. Nest predator abundance and urbanization. In: Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic, Norwell, MA.

Heinrich, B., Marzluff, J.M., 1992. Age and mouth color in common ravens. Condor 94, 549–550.

Heinrich, B., Daye, D., Knight, T., Schaumburg, K., 1994. Dispersal and association among common ravens. Condor 96, 545–551.

Hogrefe, T.C., Yahner, R.H., 1998. Depredation of artificial ground nests in a suburban versus a rural landscape. Journal of the Pennsylvania Academy of Science 72, 3–6.

Holthausen, R.S., Raphael, M.G., McKelvey, K.S., Forsman, E.D., Starkey, E.E., Seaman, D.E., 1995. The contribution of federal and nonfederal habitat to persistence of the northern spotted owl on the Olympic Peninsula, Washington: Report of the Reanalysis Team. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, General Technical Report Number 352.

Imhoff, M.L., Bounoua, L., DeFries, R., Lawrence, W.T., Stutzer, D., Tucker, C.J., Rickets, T., 2004. The consequences of urban land transformation on net primary productivity in the United States. Remote Sensing of Environment 89, 434–443.

Jerzak, L., 2001. Synurbanization of the Magpie in the Palearctic. In: Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic, Norwell, MA, pp. 405–427.

Johnston, R.F., 2001. The synanthropic birds of North America. In: Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic, Norwell, MA, pp. 49–67.

Kaplan, E.L., Meier, P., 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistics Association 53, 457–481.

Kenward, R.E., Hodder, K.H., 1995. Ranges V: Software for Analysing Animal Location Data. Institute of Terrestrial Ecology, Wareham, UK.

Kernohan, B.J., Gitzen, R.A., Millspaugh, J.J., 2001. Analysis of animal space use and movements. In: Millspaugh, J.J., Marzluff, J.M. (Eds.), Radiotelemetry and Animal Populations. Academic Press, Inc., San Diego, CA, pp. 126–164.

Knight, R.L., Gutzwiller, K.J., 1995. Wildlife and Recreationists: Coexistence through Management and Research. Island Press, Washington, DC.

Konstantinov, V.M., Babenko, V.G., Barysheva, I.K., 1982. Numbers and some ecological features of synanthropic populations of the corvidae under the conditions of intensive urbanization. Zoologicheskii Zhurnal 61, 1837–1845.

Linz, G.M., Knittle, C.E., Johnson, R.E., 1992. Home range of breeding common ravens in coastal southern California. Southwestern Naturalist 37, 199–202.

Luginbuhl, J.M., Marzluff, J.M., Bradley, J.E., Raphael, M.G., Varland, D.E., 2001. Corvid survey techniques and the relationship between corvid relative abundance and nest predation. Journal of Field Ornithology 72, 556–572.

Marzluff, J.M., 2001. Worldwide increase in urbanization and its effects on birds. In: Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic, Norwell, MA, pp. 19–47.

Marzluff, J.M., 2005. Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. Urban Ecosystems 8, 155–175.

Marzluff, J.M., Angell, T., 2005. In the Company of Crows and Ravens. Yale University Press, New Haven, CT.

Marzluff, J.M., Hamel, N., 2001. Land Use Issues. In: Levin, S. (Ed.), Encyclopedia of Biodiversity. Academic Press, San Diego, CA, pp. 659–673.

Marzluff, J.M., Heinrich, B., 1991. Foraging by common ravens in the presence and absence of territory holders: an experimental analysis of social foraging. Animal Behaviour 42, 755–770.

Marzluff, J.M., Restani, M., 1999. The effects of forest fragmentation on avian nest predation. In: Rochelle, J.A., Lehmann, L.A., Wisniewski, J. (Eds.), Forest Fragmentation: Wildlife and Management Implications. Brill, Boston, MA, pp. 155–169.

Marzluff, J.M., Boone, R.B., Cox, G.W., 1994. Native pest bird species in the West: why have they succeeded where so many have failed? Studies in Avian Biology 15, 202–220.

Marzluff, J.M., Raphael, M.G., Sallabanks, R., 2000. Understanding the effects of forest management on avian species. Wildlife Society Bulletin 28, 1144–1155.

Marzluff, J.M., McGowan, K.J., Donnelly, R.E., Knight, R.L., 2001. Causes and consequences of expanding American Crow populations. In: Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic, Norwell, MA, pp. 331–363.

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

Masselink, M.M., 2001. Responses by Steller's jay to forest fragmentation on southwest Vancouver Island and potential impacts on marbled murrelets. Thesis, University of Victoria, Victoria, British Columbia, Canada.

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

Mech, L.D., 1983. Handbook of Animal Radio-tracking. University of Minnesota Press, Minneapolis, MN, USA.

Meyer, W.B., Turner Jr., B.L., 1994. Changes in Land Use and Land Cover: A Global Perspective. Cambridge University Press, London.

Miller, J.N., Brooks, R.P., Croonquist, M.J., 1997. Effects of landscape patterns on biotic communities. Landscape Ecology 12, 137–153.

Morgan, M.M., 1976. The Last Wilderness. University of Washington Press, Seattle, WA, USA.

Neatherlin, E.A., Marzluff, J.M., 2004. Responses of American crow populations to campgrounds in remote native forest landscapes. Journal of Wildlife Management 68, 708–718.

Nelson, S.K., Hamer, T., 1995. Nesting biology and behavior of the marbled murrelet. In: Ralph, C.J., Hunt, G.L., Jr., Raphael, M.G., Piatt, J.F., (Eds.). The ecology and conservation of the marbled murrelet in North America: an interagency scientific evaluation. United States Department of Agriculture, Forest Service, General Technical Report Number 152, pp. 57–68.

Newton, I., Davis, P.E., Davis, J.E., 1982. Ravens and buzzards in relation to sheepfarming and forestry in Wales. Journal of Applied Ecology 19, 681–706.

O'Meara, M., 1999. Reinventing cities for people and the planet. Worldwatch Paper 147. Worldwatch Institute, Washington, DC.

Otis, D.L., White, G.C., 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63, 1039–1044.

Parker, H., 1984. Effect of corvid removal on reproduction of willow ptarmigan and black grouse. Journal of Wildlife Management 48, 1197–1205.

Parr, R., 1993. Nest predation and numbers of golden plovers *Pluvialis apricaria* and other moorland waders. Bird Study 40, 223–231.

Pauchard, A., Aguayo, M., Peňa, E., Urrutia, R., 2006. Multiple effects of urbanization in the biodiversity of developing countries: the case of a fast-growing metropolitan area (Concepción, Chile). Biological Conservation 127, 272–281.

Peters, R.H., 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge.

Pyle, P., Howell, S.N.G., Yunick, R.P., DeSante, D.F., 1987. Identification Guide to North American Passerines. Slate Creek Press, Bolinas, CA.

Ralph, C.J., Guepel, G.R., Pyle, P., Martin, T.E., DeSante, D.F., 1993. Handbook of field methods for monitoring landbirds. United States Department of Agriculture, Forest Service, Pacific Southwest Research Station, General Technical Report Number 144.

Ralph, C.J., Droege, S., Sauer, J.R., 1995. Monitoring bird populations by point counts. United States Department of Agriculture, Forest Service, Pacific Southwest Research Station, General Technical Report Number 149.

Raphael, M.G., Evans, D.M., Marzluff, J.M., Luginbuhl, J.M., 2002. Effects of forest fragmentation on populations of the marbled murrelet. Studies in Avian Biology 25, 221–235.

Restani, M., Marzluff, J.M., Yates, R.E., 2001. Effects of anthropogenic food sources on movements, survivorship, and sociality of common ravens in the Arctic. Condor 103, 399–404.

Richner, H., 1992. The effect of extra food on fitness in breeding carrion crows. Ecology 73, 330–335.

Robinson, L., Newell, J.P., Marzluff, J.M., 2005. Twenty-five years of sprawl in the Seattle region: growth management responses and implications for conservation. Landscape and Urban Planning 71, 51–72.

Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., Gitzen, R.A., 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63, 739–747.

Seidel, K.S., 1992. Statistical properties and applications of a new measure of joint space use for wildlife. Thesis, University of Washington, Seattle, Washington, USA.

Singer, S.W., Naslund, N.L., Singer, S.A., Ralph, C.J., 1991. Discovery and observations of two tree nests of marbled murrelet. Condor 93, 330–339.

Stone, E., Trost, C.H., 1991. The effects of supplemental food on nest dispersion in black-billed magpies. Condor 93, 452–454.

Sullivan, B.D., Dinsmore, J.J., 1992. Home range and ranging habitat of American crows, *Corvus brachyrhychos*, in a waterfowl breeding area in Manitoba. Canadian Field Naturalist 106, 181–184.

Tilghman, N.G., 1987. Characteristics of urban woodlands affecting winter bird diversity and abundance. Forest Ecology and Management 21, 163–175.

Verbeek, N.A.M., Butler, R.W., 1999. Northwestern crow, *Corvus caurinus*. Birds of North America. Number 407, 1–24.

Vigallon, S.A., Marzluff, J.M., 2005a. Abundance, nest sites, and nesting success of Steller's jays along a gradient of urbanization in western Washington. Northwest Science 79, 22–27.

Vigallon, S.A., Marzluff, J.M., 2005b. Is nest predation by Steller's Jays incidental or the result of a specialized search strategy? The Auk 122, 36–49.

Whitcomb, R.F., Lynch, J.F., Klimkiewicz, M.K., Robbins, C.S., Whitcomb, B.L., Bystrak, D., 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Ecological Studies: Analysis and Synthesis 41, 125–205.

White, G.C., Garrot, R.A., 1990. Analysis of Wildlife Radio-tracking Data. Academic Press, San Diego, CA.

Wilcove, D.S., 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66, 1211–1214.

Winterstein, S.R., Pollock, K.H., Bunck, C.M., 2001. Analysis of survival data from radiotelemetry studies. In: Millspaugh, J.J., Marzluff, J.M. (Eds.), Radiotelemetry and Animal Populations. Academic Press, Inc., San Diego, CA, pp. 352–383.

Wong, T.C.M., Sodhi, N.S., Turner, I.M., 1998. Artificial nest and seed predation experiments in tropical lowland rainforest remnants of Singapore. Biological Conservation 85, 97–104.

Worton, B.J., 1987. A review of models of home range for animal movement. Ecological Modeling 38, 277–298.

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

Zar, J.H., 1999. Biostatistical Analysis, fourth ed. Prentice-Hall, Inc., Upper Saddle River, NJ, USA.