Corvid Distribution, Human Recreation, and Park Management in
Mount Rainier National Park, Washington

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Abstract

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As our urban areas grow in population and physical prominence on the landscape, the use of nearby natural areas for outdoor recreation also increases. Although some local effects of human recreation in wilderness areas have been documented, landscape level responses of wildlife species to patterns of human recreation have not been previously evaluated.

I studied the avian Family Corvidae (crows, ravens, jays, and magpies) in Mount Rainier National Park. Using data collected from over 1400 point counts across areas varying in type and level of visitor use, I calculated predicted density and occupancy values using the programs DISTANCE and PRESENCE, while allowing for variation in detection probability. I then investigated aspects of the human and natural landscapes that best explained patterns of corvid density and occupancy and evaluated the influence of food availability on the use of these features by corvids.

Although level of visitor use and the availability of food subsidy was important in explaining the distribution patterns of three corvid species—Steller's jay, Clark's nutcracker,

and common raven—a species-specific suite of vegetative and landscape variables were also consistently important in describing occupancy and density patterns. Steller's jays tended to occupy edgy landscapes and other patchy, forested areas while gray jays occupied high elevation contiguous forests. Clark's nutcracker occupied areas with open forest edges near stands of whitebark pine and common ravens used forests and roads.

Corvids are intelligent generalist-omnivores that serve important ecosystem functions such as songbird nest predation, nutrient cycling, and seed dispersal. Wildland landscapes that support human recreation provide anthropogenic food subsidies and may benefit these synanthropic species while potentially reducing ecosystem function. In Mount Rainier National Park, Steller's jays (*Cyanocitta stelleri*), Clark's nutcrackers (*Nucifraga columbiana*), and common raven (*Corvus corax*) all changed their use of landscape features in areas where anthropogenic food subsidies were available. Gray jays (*Perisoreus canadensis*), although frequently observed in areas of food subsidy, did not appear to shift their use of the landscape in response to human subsidized foods.

Corvids respond to both human presence and patterns of anthropogenic development on the landscape. Corvids are also gregarious, easily recognized, and relatively easy to monitor and thus may be ideal bioindicators of anthropogenic ecosystem change. Changes in Steller's jay distribution or abundance may indicate increases in landscape fragmentation and nest predation while increases in raven presence along roads or at point subsidies may indicate a reduction in nutrient cycling in other natural areas. Increases in Clark's nutcracker abundance at an area of anthropogenic food subsidy may indicate a decrease in the seed dispersal of large wingless seeded pines, such as whitebark pine (*Pinus albicaulis*), with which nutcrackers are highly coevolved. American crows, although not observed during surveys in Mount Rainier, are strongly associated with urban and suburban development. Should crows appear in great abundance within wildland natural areas such as Mount Rainier, it would likely indicate increased development or the presence of a significant and reliable point subsidy.

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Chapter 1

Recreation Changes the Use of a Wild Landscape by Corvids:
Local Effects and Possible Landscape Repercussions

Recreation, ecotourism, and other relatively low levels of human disturbance, affect native wildlife communities and wildland ecosystems and landscapes (Edington and Edington 1986, Knight and Gutzwiller 1995, Czech and Krausman 1997, Liddle 1997). The presence of outdoor photographers, rock climbers, hikers, and horseback riders in natural areas exposes wildlife to direct human disturbance while the creation of access roads, bike paths, campgrounds, and picnic areas affects the composition and pattern of native landscapes. While most native species of wildlife are negatively affected by human recreation in natural areas (Knight and Gutzwiller 1995, Czech and Krausman 1997), the magnitude and direction of impacts of human disturbance on wild landscapes may vary by species, animal condition, season, amount of visitation, type of recreation, and visitor behavior (Kuss *et al.* 1990, Liddle 1997, Steidl and Powell 2006). Although localized responses, both positive and negative, to recreation are well documented (Burger and Gochfeld 1998, Gutzwiller *et al.* 1998, Gutzwiller *et al.* 2002, Neatherlin and Marzluff 2004, Marzluff and Neatherlin 2006), landscape level responses of wildlife species to patterns of human recreation have not been evaluated. However, through varying levels of human disturbance and the direct and indirect provisioning of anthropogenic food, human recreation favors some species over others, which may result in changes in the use of landscape features by species, immediately affecting landscape integrity and ecosystem function and ultimately causing evolutionary change. Managers of natural areas are thus challenged to achieve a balance between the provision of recreational opportunities and the resulting positive and negative influences on the native species, landscapes, and the performance of ecosystem functions.

Songbird communities may be especially sensitive to nonconsumptive wildland recreation (Boyle and Samson 1985, Knight and Gutzwiller 1995, Miller *et al.* 1998). Recreation may decrease bird species diversity and skew density in favor of a few species (Beissinger and Osborne 1982, Hansen *et al.* 2005, Devictor *et al.* 2008) by affecting avian

fecundity and survivorship (Miller *et al.* 2001, Sandrik and Barrett 2001, Bolduc and Guillemette 2003). Nesting birds in recreational areas may suffer increased nest desertion, decreased hatching success, reduced parental attendance at the nest, increased foraging effort, or increased nest parasitism (Hickman 1990, Burger and Gochfeld 1998, Miller *et al.* 1998, Chace and Walsh 2006). Additionally, egg and chick predation, the primary cause of nest failure in songbirds (Martin 1993), may increase due to the attraction of mammalian (Bradley and Marzluff 2003, Martin and Joron 2003, Gutzwiller and Riffell 2008,) and avian predators (Wilcove 1985, Gutzwiller *et al.* 2002, Marzluff and Neatherlin 2006, Piper and Catterall 2006, Marzluff *et al.* 2007).

The vulnerability of particular species to the above impacts is likely to depend on various life history traits as well as their resource requirements (Knight and Gutzwiller 1995, Hill *et al.* 1997). Bird species that are likely to be negatively affected by an increase in nonconsumptive recreation include those requiring specialized resources, ground nesters, rare species, and species that require large contiguous home ranges (Knight and Gutzwiller 1995, Neatherlin and Marzluff 2004, Marzluff and Neatherlin 2006). In contrast, human recreational use of natural areas may benefit generalist species, such as corvids (birds of the Family Corvidae, including jays, crows, ravens, magpies, and nutcrackers), which are able to adapt to living with humans and are associated with diverse landscapes. Corvids and other avian predators may benefit from increased visibility and juxtaposition of diverse resources (i.e. edge habitats; Martin and Joron 2003).

Corvids are intelligent generalist-omnivores that are well-adapted to associating with humans, often flourishing in urban areas and in areas of more moderate human presence such as recreation areas (Marzluff and Angell 2005, Marzluff and Neatherlin 2006). In recreation areas with anthropogenic food, corvids may maintain smaller home ranges and populations may increase in both number and density (Gutzwiller *et al.* 2002, Storch and Leidenberger 2003, Neatherlin and Marzluff 2004, Marzluff and Neatherlin 2006, Bui *et al.* 2010). The response of corvids to recreation may reduce the ability of wildland reserves to conserve rare species such as greater sage grouse (*Centrocercus urophasianus*; Bui *et al.* 2010) and marbled murrelet (*Brachyramphus marmoratus*; Luginbuhl *et al.* 2001). Changing corvid communities may also affect important ecosystem functions including carrion decomposition (Knight and Kawashima 1993, Mason and MacDonald 1995) and seed dispersal (Vander

Wall and Balda 1977, Ligon 1978, Hutchins and Lanner 1982, Tomback 1982, Tomback and Taylor 1987, Johnson *et al.* 1997).

The response of corvids to recreation potentially influences local and large scale processes. Corvids are wide ranging birds that serve ecosystem functions across broad spatial scales. For example, nutcrackers are known to cache pine seeds up to tens of kilometers from the parent tree (Vander Wall and Balda 1977) and blue jays may transport nuts and acorns between widely separated fragments of native vegetation (Johnson *et al.* 1997). For songbird nest predators including Steller's jays, habitat fragmentation may result in an increase in nest predation along forest edges and in small forest fragments (Andrén 1992, Marzluff and Restani 1999, Ibarzabal and Desrochers 2004). A landscape perspective on the response of corvids to human recreation may increase our understanding of recreation's effect on ecosystem processes.

In this study, I evaluated the impact of anthropogenic food subsidy and varying levels of human recreation on the distribution patterns and landscape-level habitat use of five corvid species in Mount Rainier National Park: American crow (*Corvus brachyrhynchos*), Clark's nutcracker (*Nucifraga columbiana*), common raven (*Corvus corax*), gray jay (*Perisoreus canadensis*), and Steller's jay (*Cyanocitta stelleri*). I predicted corvid populations in general to concentrate around areas of high visitor use and with food subsidy, including visitor centers, picnic areas, and drive-up campgrounds. In areas of low visitor use, I predicted corvid presence to coincide with the locations of hike-in campgrounds, the areas most likely to provide consistent anthropogenic food resources. Clark's nutcrackers are highly coevolved with whitebark pine (*Pinus albicaulis*) in the northwestern United States (Hutchins and Lanner 1982, Tomback 1982) and I predicted nutcrackers to concentrate primarily in areas near stands of whitebark pine.

Although corvids are already known to be highly associated with humans and man-made habitat features on the landscape (Knight and Gutzwiller 1995, Neatherlin and Marzluff 2004, Marzluff and Angell 2005, Marzluff and Neatherlin 2006), no research has shown the direct effects of food subsidy on the distribution patterns of corvids and their use of landscape habitat features in wildland ecosystems. In this study, I expected to see evidence for changes in use of landscape-level habitat features in response to the provision of food subsidy for all species. However, I expected the effect of food subsidy to be weakest

for American crows in the park as these birds are already highly associated with areas of high human development that already have food subsidy; areas with human food subsidy are the niche for American crows in the Pacific Northwest (Marzluff *et al.* 2001, Marzluff and Neatherlin 2006). Likewise, Steller's jays may also show a weak response to food subsidy because their habitat preferences naturally coincide with areas also likely to have food subsidy, i.e. low elevation forests with many edges (Vigallon and Marzluff 2005a). Gray jays tend to use higher elevation contiguous forests and I expected that, in areas where food subsidy is provided, they may use patchier or lower elevation landscapes. Ravens are wide ranging birds that are likely to appear in low densities across much of Mount Rainier National Park. However, I predicted that they are most likely to be associated with roads, foraging for road kill (Knight *et al.* 1995). Additional direct sources of food provisioning such as backcountry campgrounds may also subsidize ravens and affect their use of landscape features away from roads. Although I predicted nutcrackers to be found near whitebark pine, in high elevation open patchy forests, food subsidy may draw this species farther from pine stands to forage, perhaps to lower elevations or to areas of more contiguous vegetation (Tomback and Taylor 1987).

METHODS

Study Area

I surveyed corvids throughout Mount Rainier National Park (Figure 1.1). Mount Rainier is a 4392 meter volcanic peak located on the west side of the Cascade Range, approximately 100 km southeast of Seattle in southwestern Washington. The national park encompasses 235,625 acres and, as established by the Washington Park Wilderness Act of 1988 (Public Law 100-668), is 97 percent designated wilderness.

Mount Rainier National Park is characterized by long, cool, wet winters and relatively warm, dry summers, typical of the Pacific Northwest. Due to the combined effects of the steep elevation gradient and precipitation levels that change both with elevation and with the east-west rain-shadow effect, vegetation and habitat features vary widely throughout the park. Lower elevations, below 1000 m, are characterized by mature forests dominated by Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*). Mixed forests of western white pine (*Pinus monticola*), western hemlock, and Pacific silver fir (*Abies amabilis*) can be found at mid-level elevations between 1000 and 1500 m. Relatively open mixed forests and subalpine meadows characterize elevations from 1500 to 2000 m and dominant tree species include subalpine fir (*Abies lasiocarpa*), mountain hemlock (*Tsuga mertensiana*), Alaska yellow cedar (*Callitropsis nootkatensis*), and whitebark pine. Subalpine meadow vegetation may include heather species (*Cassiope* sp. or *Phyllodoce* sp.), huckleberry (*Vaccinium* sp.), subalpine lupine (*Lupinus arcticus* spp. *subalpinus*), false hellebore (*Veratrum viride*), sedges, alpine aster (*Aster alpinus*), paintbrush (*Castilleja* sp.), western anemone (*Anemone occidentalis*), or fescues (*Festuca* sp.). Above 2000 m is an alpine zone covered mostly by heather communities, snow, glaciers, rock outcrops, and talus fields. In total, approximately 58 percent of the park is forested, 23 percent is subalpine, and the remainder is alpine.

The wide variety of plant communities found within Mount Rainier National Park provides numerous recreational opportunities, from picnicking to alpine climbing, and the park welcomes over two million visitors every year. The park maintains four visitor centers, three wilderness information centers, four drive-up campgrounds, 41 hike-in campgrounds,
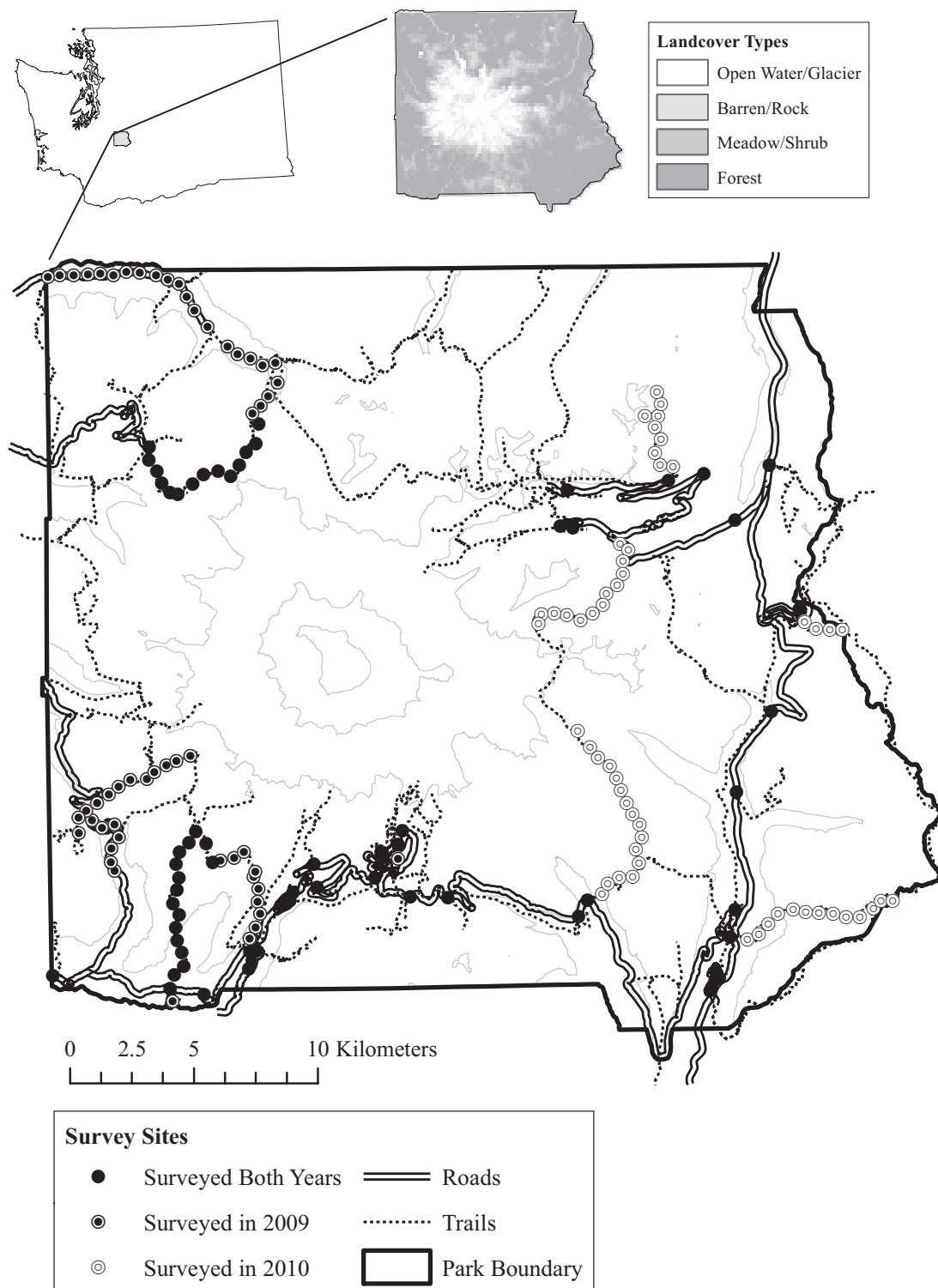
Figure 1.1. Mount Rainier National Park, with corvid survey point locations. Contours lines mark elevation differences of 1000 m.

and over 400 km of trail, including the 150 km Wonderland Trail which encircles the peak of Mount Rainier.

Survey Design

Incorporating areas with a variety of vegetation types, recreational impacts, and park management uses, I surveyed 168 points for corvid presence throughout Mount Rainier National Park during the summer, post-breeding seasons (mid-June through late-September) of 2009 and 2010. I surveyed 113 points in 2009 and 114 points in 2010, including 59 points in both survey seasons (Figure 1.1). During each field season, I visited each point between two and ten times, totaling 639 visits in 2009 and 774 visits in 2010. Although there is wide variability in the number of visits to each point, ranging from two to 18 visits across both seasons, I used analysis methods that take this into account, minimizing the bias of varying survey effort. Most points received at least six visits (n=141). Of those points with less than six visits (n=27), both low and high visitors use areas and points both with and without food subsidy were represented, although most were located in low visitor use areas without food subsidy (n=23). Both analysis programs DISTANCE v.5.0 (density; Thomas *et al.* 2006) and PRESENCE (occupancy; http://www.mbr-pwrc.usgs.gov/software/ presence.html) allow unequal survey effort. DISTANCE averages observations across visits to compute an average predicted density estimate for each site. Occupancy and detectability modeling in PRESENCE is robust to missing observations and an equal sampling effort across all sites is not required (MacKenzie *et al.* 2005). Visits to each point were spaced out across the survey season to minimize within season differences.

I chose survey points to reflect a variety of visitor uses and sorted points into four site types based on differences in level of human use and the availability of anthropogenic food subsidy. Points with high visitor use (n=35), including visitor centers, drive-up campgrounds, road pullouts and trailheads, are defined as areas that can be reached by vehicle and are commonly used by day visitors. Approximately half of high visitor use points had food subsidy available (drive-in sites with picnic tables and/or trash cans; n=17). Low visitor use points (n=133) can only be reached by foot and include wilderness campsites and

trails. Most of these points did not have food (hike-in trail sites; n=119), but food subsidy was available at hike-in campgrounds (n=14).

At campgrounds, administrative areas and visitor centers, survey points were located at the approximate center of the human use area. Along roads, I surveyed points in pull-outs or parking areas. To remove the influence of the trail corridor on visual corvid detections, I surveyed forested trail points at a random distance (between 10 and 50 m) and right-angle direction off trail. I separated all survey points by a minimum distance of approximately 500 m.

Survey Methodology

I conducted distance sampling at all point count locations (Buckland *et al.* 2001), recording the horizontal distance to each corvid detected visually or audibly during a twenty minute period. In addition to following standard point count techniques described by Ralph *et al.* (1993, 1995), I also considered specific variables influential to corvids, such as weather and time of day (Luginbuhl *et al.* 2001). I conducted surveys on days with only light wind (less than 19 kph), no more than light precipitation (U. S. National Weather Service 1995), and between sunrise and early afternoon, the time of day when birds are most active.

Across two field seasons, three observers conducted all corvid surveys and each observer surveyed the majority of the sites at least once. At each survey point and during each point count, we additionally noted characteristics of weather, vegetation, and visitor use which we expected to be important in explaining patterns of corvid detection, distribution, or abundance (for variable descriptions, see Table 1.1). For each survey point, we noted the elevation, general vegetation type within 50 m, forest structure, and canopy cover. Based on designations outlined in Mount Rainier National Park's 2001 General Management Plan, we also classified each point by zone type, a classification of the type of visitor use. We also recorded start time (used to calculate the time after sunrise), precipitation, cloud cover, noise, wind, and number of observed visitors (used to calculate average number of visitors for each site).

Table 1.1. Description of count, point, and landscape level variables used in occupancy, density, and detection analyses. *Count level features were only used only to model detection. [‡]Canopy cover, habitat, and structure were used to model detection in addition to occupancy and density. [◦]Distance to whitebark pine was used only in Clark's nutcracker analyses.

Count Features*	Definition
Cloud Cover	percentage of cloud cover in visible sky, 0-100%; only used to model detectability
Noise	measure of noise level at beginning of count: 1 (no noise), 2 (gentle babbling brook noise), 3 (babbling creek noise), 4 (rushing creek noise), 5 (roaring creek/river noise); noise levels 4 and 5 aggregated for analyses; only used to model detectability
Precipitation	presence of precipitation during ≥ 5 minutes (25%) of count: no rain or rain; only used to model detectability
Time After Sunrise	time elapsed between sunrise and the start of count, number of minutes converted to decimal fraction of a day; only used to model detectability
Wind	measure of wind level at beginning of count, Beaufort scale (0-6); wind levels 0 and 1 and levels 3 and greater aggregated for analyses; only used to model detectability
Point Features	
Average Visitors	average number of visitors observed across all counts
Canopy Cover[‡]	estimation of canopy cover directly above survey point: none (< 11%), little, 11-40%), partial (41-70%), full cover (71-100%); also used to model detectability
Elevation	elevation at survey site, in meters
Habitat[‡]	description of dominant habitat type within 50 m of site: forest or non-forest (non-forest can be either open forest or meadow); also used to model detectability
Site Type	sites are classified as either high visitor use (able to reach by vehicle) or low visitor use (hike-in only) and as either with food subsidy (with picnic tables, trashcans, and/or campsites) or without food subsidy
Forest Structure[‡]	description of general forest structure within 50 m: very complex (2 or more canopy layers and multiple openings), complex (1 or 2 canopy layers with few openings), simple (simple forest structure with 1 canopy layer and no openings or meadow habitat with few/no trees; also used to model detectability
Zone Type	as defined by 2001 General Management Plan: backcountry camp, trail zone, or day use
Landscape Metrics	
Contrast-weighted Edge Density within 2 km	density of important edges within 2 km radius of survey point, meters/hectare: forest-developed edge weight = 1, forest-meadow edge weight = .5, other = 0
Contrast-weighted Edge Density within 5 km	density of important edges within 5 km radius of survey point, meters/hectare; weights described above
Distance to Campground	distance to nearest campground, meters
Distance to Road	distance to nearest road, meters
Distance to Whitebark Pine[◦]	distance to nearest stand of whitebark pine, meters; location of stands based on shapefile provided by National Park Service; used only in analyses for Clark's Nutcracker

Table 1.1 continued

Length of Road Edge within 2 km	2 x length of road within 2 km of survey point, meters
Length of Road Edge within 5 km	2 x length of road within 5 km of survey point, meters
Patch Richness within 2 km	number of different types of landcover patches within 2 km
Patch Richness within 5 km	number of different types of landcover patches within 5 km
Percent Forest within 2 km	percentage of forest landcover within 2 km radius of survey point
Percent Forest within 5 km	percentage of forest landcover within 5 km radius of survey point

Landscape Metrics

To assess the relationship between corvid distributions and broad scale landscape characteristics, I used ArcGIS v.9.3.0 (ESRI 2008) to measure the distance from each survey point to the nearest road, the nearest campground, and the nearest stand of whitebark pine (Table 1.1). The distance to whitebark pine was used only in the analyses of Clark's nutcracker observations. I also used the NPScape 2001 landcover dataset for Mount Rainier National Park (Homer *et al.* 2004, National Park Service 2010) to represent the landcover patterns surrounding each survey point within buffer areas of 2 and 5 km radii. I chose these buffer areas because they approximate the average home range sizes of the targeted corvid species. Using FRAGSTATS v.3.3 (McGarigal 2002), I calculated landscape metrics within each buffer area for each survey point, including percent forest, Shannon's diversity index, contagion, patch richness, length of road edge, and contrast-weighted edge density. These metrics were chosen because they reflect the amount of edge and degree of fragmentation on the landscape, both known to be important characteristics in predicting corvid presence and abundance. For contrast-weighted edge density, edges between forest and developed land received a weight of 1, edges between forest and meadow/shrub received a weight of 0.5, and all other land cover edges received a zero weight. Because Shannon's diversity index, contagion, and percent forest were highly correlated when considering both radii (2 km: $r^2>0.91$, $p<0.001$; 5 km: $r^2>0.93$, $p<0.001$), I included only percent forest, contrast-weighted edge density, patch richness, and length of road edge, in my final analyses (Table 1.1).

Detectability

To make accurate estimates of the density and occupancy of wildlife species based on observation in varying field conditions, it is necessary to correct for potential differences in detection. Detectability, defined as the probability of observing an organism during a survey given the organism is present, may vary by distance from the observer, observer ability, numerous environmental and temporal factors, and species-specific characteristics (Rosenstock *et al.* 2002 and references therein). Bird, and specifically corvid, detection may vary by wind, noise, precipitation, time after sunrise, and light intensity (Anderson and

Ohmart 1977, Luginbuhl *et al.* 2000, Restani *et al.* 2001, Donnelly and Marzluff 2006, Marzluff and Neatherlin 2006). Thus, in modeling density and occupancy patterns of corvid populations, I considered the potential effects of differing detectability to avoid biases. In all occupancy and density analyses described below, I compare models considering the effects of eight variables on detectability, including habitat, forest structure, canopy cover, precipitation, time after sunrise, noise, cloud cover, and wind (Table 1.1). Each point was surveyed multiple times by at least two of three observers to help minimize the effects of differences between observers and I did not consider the effect of observer on detectability.

Occupancy

I used the program PRESENCE (http://www.mbr-pwrc.usgs.gov/software/ presence.html) to provide occupancy estimates and site-specific predictions while allowing for varying detectability and to provide predicted occupancy values for each corvid species. I considered 18 variables as potential explanatory variables for occupancy of each corvid species (Table 1.1). In addition, I considered the distance to the nearest stand of whitebark pine to explain occupancy for Clark's nutcracker (Table 1.1).

For some variables, values were scaled to avoid numerical convergence issues with the logit link function in PRESENCE. I converted percent forest and cloud cover to proportions and elevation and distance measurements were expressed in kilometers with the exception that length of road edge was scaled to hundreds of kilometers. I divided values for average number of visitors and patch richness by ten.

A large variable set inhibited the comparison of a predetermined set of models. Thus, for all analyses, I used forward model selection and Akaike's Information Criterion, corrected for small sample size (AIC_c; Akaike 1974), to identify the most parsimonious model to best explain the data in each analysis for each species. I first compared all single variable models of occupancy and selected the model with the lowest AIC_c. I then tested all models considering that single occupancy variable with a single detection variable. Again considering the model with the lowest AIC_c, I considered another set of models with a secondary occupancy variable. I continued this process, adding detection and occupancy variables one at a time until no additional variable improved (lessened) the AIC_c.

Before calculating predicted occupancy values for the entire data set, I tested for the significance of survey year in explaining observed corvid patterns at 59 points surveyed in both seasons. I found the best detection model using forward model selection and eight detection variables and considered both a null model with no explanatory occupancy variables and a model considering only year. Year was not included in the best model for any species (ΔAIC_c reported is difference between best null model and model including year; Steller's jay ΔAIC_c: 2.48; gray jay ΔAIC_c: 2.79; common raven ΔAIC_c: 2.79; Clark's nutcracker ΔAIC_c: 2.68). Because the models including year were less competitive than the best null model, I used the single season analysis engine in PRESENCE to calculate predicted occupancy estimates for each species in all subsequent occupancy analyses.

To evaluate how corvid occupancy varies in areas with different levels of visitor use and with the provision of food subsidy, I used PRESENCE to model detectability using eight detection variables and calculate predicted occupancy estimates for each species at each individual survey point. I then divided the points into four site types defined by level of visitor use and the availability of food subsidy and calculated an average occupancy for each site type for each species.

To best explain overall corvid occupancy patterns in Mount Rainier National Park, I used the single season analysis engine in PRESENCE to evaluate the influence of count, point, and landscape level variables (Table 1.1) on occupancy and detectability to fit the best occupancy model to the observations of each species. I calculated the effect size of anthropogenic food availability on each species occupancy patterns.

Finally, to assess how corvids change their use of the landscape due to the availability of food subsidy, I evaluated the importance of interactions between food availability and other variables included in the competitive models ($\Delta AIC_c < 2$) describing each species overall occupancy.

Density

I used the program DISTANCE v.5.0 (Thomas *et al.* 2006) to estimate site-specific density for each corvid species while allowing for variation in detection probability. I truncated observations for each species to exclude the greatest 10% of distances and binned

the remaining observations into distance categories. Bins were generally 10 m wide, although bin width varied between species and analyses. Bin sizes were also uneven within each species because of awkward truncation distances and because bins were offset from multiples of five due to an observer tendency to round distances to these values. I evaluated half-normal and hazard-rate key functions with cosine, polynomial, and hermite series expansions, allowing for the inclusion of up to five adjustment terms. As with occupancy analyses (described above), I considered potential effects of eight vegetation and weather variables on detectability (see Table 1.1). In detection analyses in DISTANCE, I used forward model selection and AIC_c to identify the most parsimonious model to describe the data for each corvid species. Top detection models of corvid density may be found in Appendix 1.A.

While DISTANCE identifies variables that influence detection and supplies predicted density estimates, the program cannot investigate variables that may influence density alone. With the program R v. 2.10.0 (R Development Core Team 2009) and the R Commander package (Fox *et al.* 2009), I evaluated the importance of point and landscape-level habitat variables on predicted corvid densities using linear regression models. However, because the density estimates use a common estimated detection function, they are not independent as assumed in the linear regression models I examined. For all analyses, I used forward model selection and chose the most parsimonious model using AIC_c.

Before analyzing the entire data set, I tested for the significance of survey year in explaining observed corvid patterns at 59 points surveyed in both seasons. I compared predicted densities at each point for each survey year and found no significant difference between years for any species (n=59; Steller's jay: t=0.31, p=0.76, common raven: t=0.55, p=0.59, gray jay: t=1.69, p=0.10, Clark's nutcracker: t=0.97, p=0.34). Thus, in further analyses I treated all observations as if they were from a single survey season and did not consider year as a design variable.

To evaluate how corvid density varies in areas with different levels of visitor use and with the provision of food subsidy, I calculated predicted density estimates for each species at each survey point using DISTANCE and calculated an average density for each species in each of the four recreation site types defined by visitor use and the availability of food subsidy. I then evaluated the influence of other point and landscape level variables (see

Table 1.1) to best describe overall corvid density patterns across all sites. Finally, I evaluated the influence of food availability on the use of landscape features by corvids by testing for the significance of interactions between food and other explanatory variables from competitive density models ($\Delta AIC_c < 2$) for each species.

Comparison of Occupancy and Density

As occupancy and density patterns may tell us different things about a species' distribution (Bui *et al.* 2010), I compared average occupancy and density predictions across site types defined by level of visitor use and the availability of anthropogenic food (Figure 1.2a-d). Although the comparison is limited because occupancy ranges only from zero to one and density is a continuous variable, the degree of linear correlation between the two measures can give us an idea of whether both are needed to identify interesting distribution patterns for each species. For Steller's jays and nutcrackers, occupancy and density changed proportionally across the four site types (n=4; jay: r^2_a=0.97, p=0.01; nutcracker: r^2_a=0.94, p=0.02). Gray jay occupancy and density were somewhat proportional (n=4; r^2_a=0.75, p=0.09) across the four site types while raven occupancy and density were inconsistent (n=4; r^2_a=0.63, p=0.13). This suggests that both occupancy and density are important for accurately interpreting raven distribution patterns. In subsequent analyses for each species, I report primarily occupancy results for the four species, except when density analyses produced exceptionally different results. Complete density analyses for all species can be found in Appendices 1.A-C.
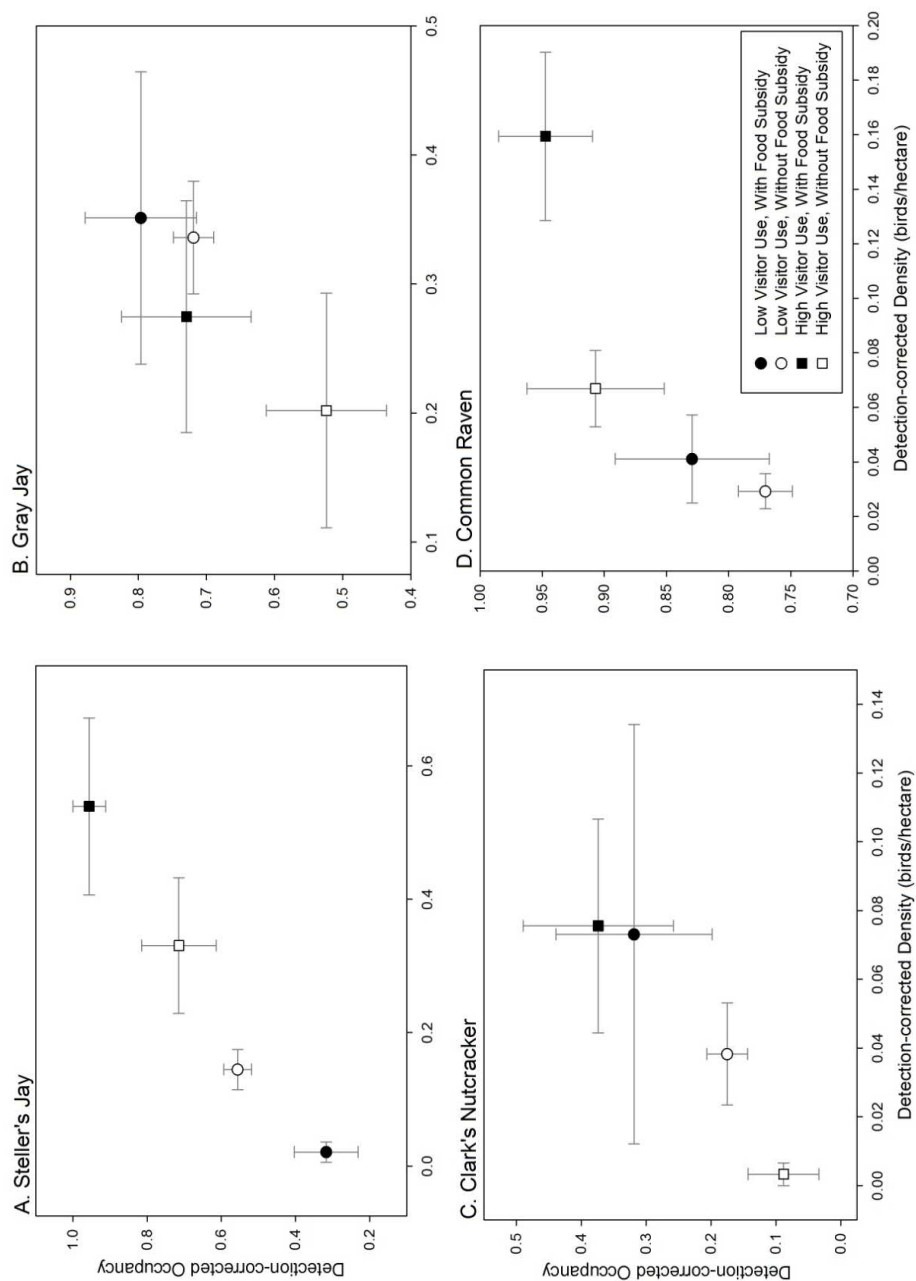
Figure 1.2. Average predicted occupancy and density values of four observed species in four site types defined by level of visitor use and the availability of anthropogenic food subsidy. Circles mark low visitor use points; squares are points in high visitor use areas. Open symbols are points with no food subsidy and closed symbols are points with food. Error bars are standard errors.

RESULTS

I detected four of the five possible corvid species during surveys conducted during the summers of 2009 and 2010. I did not observe American crows either during my surveys or, anecdotally, in additional time spent within park boundaries, although they were observed just outside the park, in the town of Ashford, WA. I observed Steller's jays 415 times at nearly half (48.2%) of 168 points, including 80% of high visitor use points (94.1% of 17 points with food subsidy, and 6.7% of 18 without) and 39.8% of low visitor use points (14.3% of 14 points with food subsidy, 42.9% of 119 without). I observed common ravens 273 times at 53% of points. I detected ravens at 85.7% of 35 high visitor use points, including 88.2% of points with and 83.3% of points without food subsidy. At sites with low visitor use, I observed ravens at 57.1% of points with food subsidy and 42.9% of points without. I made 395 observations of gray jays at 53% of points, including 17 high visitor use sites (64.7% of 17 points with food subsidy, 33.3% of 18 points without), 64.3% of low visitor use points with food subsidy, and 52.9% points of low visitor use, without food subsidy. Of the four species observed, I saw Clark's nutcrackers least frequently. I made only 176 observations of nutcrackers at 16.7% of points including 7 high visitor use points (35.3% of points sites with food subsidy, 5.6% of points without) and 21 sites with low visitor use (28.6% of points with food subsidy, 14.3% of points without).

Corvid Detection

Combinations of weather, vegetation, and temporal variables explain patterns of detection of occupancy for all corvid species (Table 1.2) and were consistent across competitive models (Appendix 1.D). In general, corvid detection was affected by noise level, while canopy cover, forest structure, habitat, and the time after sunrise were also important (Table 1.2). Steller's jays were best detected in complex forests with moderate to high canopy cover and moderate noise levels. Gray jays, on the other hand, were best detected in quiet landscapes of simply-structured forests. For Clark's nutcrackers, detection was best in quiet meadows with little canopy cover. Nutcracker detection also increased with

naturalistnatTable 1.2. Landscape attributes associated with corvid occupancy across all survey points. Table values are coefficients and standard error values of variables in top models describing occupancy for all species. Variables in occupancy models have been scaled (see text) and coefficients are untransformed logit values. [‡] Variables in bold are included in all competitive models ($\Delta AIC_c < 2$). * The ΔAIC_c listed is for the second-best model, not shown.

Steller's Jay	Coefficient	SE	Model Selection	
Occupancy				
Intercept	-10.90	3.13	AIC_c	1146.84
Visitor Use (High)[‡]	30.75	5.45	ΔAIC_c*	0.49
Food (With)	27.99	5.44	w_i	0.05
Food (With):Visitor Use (High)	-29.28	5.41		
Contrast-weighted Edge Density within 5 km	14.69	6.11		
Patch Richness within 5 km	21.02	5.03		
Elevation	-3.02	0.96		
Canopy Cover (71-100%)	22.49	2.64		
Canopy Cover (41-70%)	-21.78	2.64		
Canopy Cover (11-40%)	-20.31	2.73		
Forest Structure (Very Complex)	21.15	2.63		
Forest Structure (Complex)	19.95	2.68		
Detection				
Intercept	-1.95	0.32		
Canopy Cover (71-100%)	0.43	1.11		
Canopy Cover (41-70%)	0.74	1.11		
Canopy Cover (11-40%)	-0.15	1.13		
Forest Structure (Very Complex)	0.26	1.14		
Forest Structure (Complex)	0.82	1.16		
Noise (Level 2)	0.41	0.19		
Noise (Level 3)	-0.02	0.22		
Noise (Level 4)	0.42	0.33		

Gray Jay				
Occupancy				
Intercept	-7.42	4.65	AIC_c	1073.79
Elevation	10.33	2.04	ΔAIC_c	0.72
Percent Forest within 2 km	8.19	2.90	w_i	0.08
Forest Structure (Very Complex)	23.47	4.01		
Forest Structure (Complex)	25.07	4.07		
Patch Richness within 5 km	-22.53	7.40		
Habitat (Forest)	-21.64	4.03		
Habitat (Open Forest)	1.72	1.56		
Distance to Campground	0.58	0.27		
Detection				
Intercept	-1.28	0.24		
Noise (Level 2)	-0.002	0.19		
Noise (Level 3)	-0.61	0.24		
Noise (Level 4)	-1.47	0.49		
Forest Structure (Very Complex)	-0.35	0.33		
Forest Structure (Complex)	-1.23	0.38		
Habitat (Forest)	1.00	0.42		
Habitat (Open Forest)	0.32	0.36		

Table 1.2 continued

Clark's Nutcracker

Occupancy				
Intercept	-3.49	3.28	AIC$_c$	331.08
Distance to Whitebark Pine	-3.47	1.28	ΔAIC$_c$	0.78
Average Visitors	2.46	1.09	w$_i$	0.13
Contrast-weighted Edge Density within 2 km	43.46	18.21		
Forest Structure (Very Complex)	-12.23	6.28		
Forest Structure (Complex)	-4.40	4.77		
Food (With)	7.25	3.63		
Habitat (Forest)	6.45	4.97		
Habitat (Open Forest)	8.36	3.55		

Detection		
Intercept	-0.80	0.36
Noise (Level 2)	-0.74	0.42
Noise (Level 3)	-1.12	0.45
Noise (Level 4)	-0.62	0.96
Forest Structure (Very Complex)	22.01	3.58
Forest Structure (Complex)	17.98	3.88
Canopy Cover (71-100%)	-18.25	3.80
Canopy Cover (41-70%)	-20.82	3.57
Canopy Cover (11-40%)	-20.96	3.63
Habitat (Forest)	-0.19	0.86
Habitat (Open Forest)	-1.13	0.54
Time After Sunrise	3.08	1.95

Common Raven

Occupancy				
Intercept	-84.88	3.97	AIC$_c$	982.87
Contrast-weighted Edge Density within 2 km	192.92	17.87	ΔAIC$_c$	0.86
Percent Forest within 5 km	81.33	4.19	w$_i$	0.09
Average Visitors	38.52	8.05		
Forest Structure (Very Complex)	-4.15	4.07		
Forest Structure (Complex)	-14.30	5.39		

Detection		
Intercept	-1.59	0.25
Noise (Level 2)	0.03	0.19
Noise (Level 3)	-0.89	0.25
Noise (Level 4)	-1.64	0.54
Time After Sunrise	-3.30	1.12
Canopy Cover (71-100%)	0.41	0.24
Canopy Cover (41-70%)	0.78	0.25
Canopy Cover (11-40%)	0.03	0.34
Wind (Level 2)	0.39	0.19
Wind (Level 3)	0.37	0.33

time after sunrise. Common ravens were best detected in quiet mornings on landscapes with moderate canopy cover and little wind.

In explaining patterns of corvid density, different variables were identified as important for detecting the four corvid species (Appendix 1.A). Steller's jays were best detected in areas with moderate noise and low wind while gray jay detection was affected by precipitation. Clark's nutcracker detection was best in forests of complex and simple structure. Ravens were best detected on landscapes of low noise and wind, as well as low canopy cover.

Correlates of Species Occurrence

Both human-influenced and natural aspects of the landscape help describe patterns in overall occupancy for all species (Table 1.2; all competitive models shown in Appendix1.D). Although both food and visitor use were important in describing Steller's jay occupancy and food was important for Clark's nutcracker occupancy, in general, vegetation (forest or meadow), degree of fragmentation, and the availability of edges, particularly roads, were most important in characterizing corvid distribution. There was rarely a single model that clearly represented the data however. The full complement of competitive models (models with a $\Delta AICc < 2$) had a substantial combined weight of evidence in their favor, ranging from 22 to 44%.

Each species was consistently related to a few aspects of the landscape. Steller's jays tended to occupy edgy landscapes and other patchy, forested areas with high visitor use and food subsidy, a pattern supported by 12 competitive models with a combined weight of evidence of 0.34 (Table 1.2). Gray jays occupied high elevation contiguous forests; ten competitive models had a combined weight of 0.44 (Table 1.2). Clark's nutcracker occupied areas with open forest edges near stands of whitebark pine and with anthropogenic food subsidy. This association was based on three competitive models with a total weight of 0.28 (Table 1.2). Common ravens used forests and roads, a pattern supported by three competitive occupancy models with a combined weight of 0.22 (Table 1.2). For each corvid species, variables explaining density patterns were similar to those important for explaining

occupancy (Appendices 1.B and 1.C). Raven density, however, also responded positively to areas of high visitor use and food subsidy.

Influence of Food Subsidies on Corvid Use of Landscapes

Across all survey points, corvid occurrence was dependent on elevation, forest cover, and amount of edge (see above). At survey points with anthropogenic food subsidy, however, species used landscape features differently than at points without food subsidy (Table 1.3). With food subsidy, all corvids used points with more visitors that were closer to roads and campgrounds and in open forests with less overall forest cover on the landscape. Food subsidy tended to draw species closer to areas with more visitor use and with more human development on the landscape, although this effect varied between species and specific landscape measures. For example, common ravens and gray jays occupied areas over 760 m closer to campgrounds when food subsidy was available, a significant difference for gray jays. Steller's jays moved only 380 m closer to campgrounds. In contrast, Steller's jays were over 860 m closer to roads in areas with food, a significant shift, while ravens were only 50 m closer. The effect of food subsidy on raven use of roads and edges was weak relative to the observed effect on the jays. Ravens occupied landscapes with an additional 4 km of nearby road edge when food subsidy was available. Gray jays and Steller's jays, however, occupied areas with 9 and 13 km of additional road edge respectively. The difference in nearby road edge was significant for Steller's jays. Clark's nutcrackers used areas 150 m closer to whitebark pine stands when food subsidy was available, although this shift was not significant. All species used sites with a significantly higher number of average observed visitors at sites with food.

In evaluating the impact of food subsidy on corvid distribution patterns, Steller's jays, ravens, and Clark's nutcrackers significantly changed aspects of their use of landscape features when food subsidy was available (Table 1.4). Neither gray jay occupancy nor density patterns were significantly changed by food subsidy. Steller's jays were less common in simple and very complex forest structures when food subsidies were not available. On the other hand, Clark's nutcrackers used areas of complex and very complex forest structure less when food subsidy was available. Nutcrackers were in greater abundance at lower elevations

Table 1.3. Effect of food subsidy on use of landscape features by corvids. For continuous variables, effect size is equal to the difference between the average variable value at occupied sites in areas with and without food subsidy. For categorical variables, effect size is the difference between the percentage of occupied sites in areas with and without food subsidy. Negative values indicate that the use of the landscape feature decreased in areas of food subsidy. *95% confidence interval does not include zero.

	Effect Size of Food Subsidy (occ. sites with food – occ. sites without food)			
Variable	**Steller's Jay**	**Gray Jay**	**Clark's Nutcracker**	**Common Raven**
Average Visitors	9.95*	8.52*	11.82*	6.49*
Contrast-weighted Edge Density within 2 km (m/ha)	4.59	3.91	-3.04	0.58
Contrast-weighted Edge Density within 5 km (m/ha)	2.13	1.34	-1.07	0.33
Distance to Campground (m)	-382.71	-760.58*	-736.69	-763.45
Distance to Road (m)	-863.41*	-347.75	-381.67	-48.22
Distance to Whitebark Pine (m)	----	----	-152.48	----
Elevation (m)	-31.58	-12.83	0.24	-62.15
Length of Road Edge within 2 km (m)	13259.73*	9039.44	6579.18	3801.59
Length of Road Edge within 5 km (m)	21527.67	8487.52	3632.16	4023.76
Patch Richness within 2 km	0.33	0.47*	0.18	0.15
Patch Richness within 5 km	-0.06	-0.04	-0.04	-0.06
Percent Forest within 2 km	-3.60	-9.80	-12.64	-2.21
Percent Forest within 5 km	-4.34	-6.52	-11.66	-2.05
Percentage of Occupied Sites with:				
Canopy Cover (<11%)	-15.08*	-8.99	-26.67	-20.29
Canopy Cover (11-40%)	-7.14	-1.59	20.00	-4.74
Canopy Cover (41-70%)	17.46	11.01	-2.22	28.13
Canopy Cover (71-100%)	4.76	-0.44	8.89	-3.10
Forest Structure (Simple)	-13.49	-8.99	-21.11	-18.78
Forest Structure (Complex)	15.08	11.16	-6.67	15.09
Forest Structure (Very Complex)	-1.59	-2.17	27.78	3.69
Habitat (Forest)	-7.14*	-15.07	-7.78	3.49
Habitat (Meadow)	-5.56	-7.39	-24.44	-15.35
Habitat (Open Forest)	12.70	22.46	32.22	11.86
Visitor Use (High)	69.84	46.30	54.44	42.49
Visitor Use (Low)	-69.84	-46.30	-54.44	-42.49
Zone Type (Backcountry Campground)	11.11	45.00	40.00	33.27
Zone Type (Day Use)	48.41	34.06	54.44	27.54
Zone Type (Trail Zone)	-59.52*	-79.06	-94.44	-60.80

Table 1.4. Significant changes in landscape feature use by corvids due to the availability of anthropogenic food subsidy. Table values are coefficients and standard error values of variables in top models considering food interactions for both occupancy and density for all species. Only models which were significantly better than analyses which did not consider food interactions are shown. Variables in occupancy models have been scaled (see text) and occupancy coefficients are untransformed logit values. * The ΔAIC_c listed is for the best overall model without food interactions, shown in Appendix 1.B for density and Table 1.2 for occupancy.

Steller's Jay	Coefficient	SE	Model Selection	
Density				
Intercept	0.16	0.16	AIC_c	370.98
Zone Type (Day Use)	0.60	0.11	ΔAIC_c*	0.37
Zone Type (Trail Zone)	0.49	0.12		
Food (Without)	-0.20	0.12		
Elevation	<-0.001	<0.001		
Forest Structure (Simple)	0.34	0.19		
Forest Structure (Very Complex)	0.51	0.13		
Contrast-weighted Edge Density within 2 km	0.01	0.003		
Food (Without):Forest Structure (Simple)	-0.20	0.20		
Food (Without):Forest Structure (Very Complex)	-0.37	0.14		
Clark's Nutcracker				
Occupancy				
Intercept	-2.76	4.12	AIC_c	330.74
Distance to Whitebark Pine	-6.60	2.25	ΔAIC_c	0.34
Average Visitors	-7.05	5.03		
Contrast-weighted Edge Density within 2 km	75.15	28.98		
Forest Structure (Very Complex)	-21.29	27.39		
Forest Structure (Complex)	-4.50	27.89		
Food (With)	89.34	7.24		
Habitat (Forest)	9.38	27.71		
Habitat (Open Forest)	14.98	5.57		
Food (With):Forest Structure (Very Complex)	-73.91	6.05		
Food (With):Forest Structure (Complex)	-90.60	9.68		
Detection				
Intercept	-0.87	0.37		
Noise (Level 2)	-0.74	0.41		
Noise (Level 3)	-1.09	0.43		
Noise (Level 4)	-0.58	0.97		
Forest Structure (Very Complex)	55.30	1.19		
Forest Structure (Complex)	51.73	1.69		
Canopy Cover (71-100%)	-51.79	1.51		
Canopy Cover (41-70%)	-53.99	1.18		
Canopy Cover (11-40%)	-54.25	1.32		
Habitat (Forest)	-0.24	0.83		
Habitat (Open Forest)	-1.11	0.52		
Time After Sunrise	3.12	1.95		
Clark's Nutcracker				
Density				
Intercept	-0.08	0.15	AIC_c	-659.74

Table 1.4 continued

Distance to Whitebark Pine	<-0.001	<0.001	ΔAICc	24.88
Percent Forest within 5 km	0.01	0.001		
Percent Forest within 2 km	-0.005	0.001		
Food (Without)	-0.02	0.15		
Forest Structure (Simple)	-0.93	0.13		
Forest Structure (Very Complex)	0.04	0.03		
Canopy Cover (11-40%)	-0.46	0.11		
Canopy Cover (<11%)	0.45	0.16		
Canopy Cover (41-70%)	-0.23	0.05		
Elevation	<0.001	<0.001		
Food (Without):Distance to Whitebark Pine	<0.001	<0.001		
Food (Without):Canopy Cover (11-40%)	0.43	0.12		
Food (Without):Canopy Cover (<11%)	0.49	0.1		
Food (Without):Canopy Cover (41-70%)	0.24	0.06		
Food (Without):Elevation	<0.001	0.001		

Common Raven

Density

Intercept	0.13	0.04	AICc	-862.79
Food (Without)	-0.11	0.04	ΔAICc	1.23
Visitor Use (Low)	-0.12	0.04		
Length of Road Edge within 5 km	<0.001	<0.001		
Average Number of Visitors	-0.004	0.001		
Food (Without):Visitor Use (Low)	0.11	0.04		
Food (Without):Length of Road Edge within 5 km	<-0.001	<0.001		

and used areas of greater canopy cover when food subsidy was available. Their association with stands of whitebark pine was also stronger when food subsidy was available. Ravens were less abundant in heavily roaded areas without the additional subsidy of direct food provisions.

Comparison of Occupancy and Density

Although species responses to recreation varied, corvid presence in general was correlated with high visitor use and anthropogenic food subsidy (Figure 1.2a-d). Common raven occupancy was significantly greater at points with high visitor use then areas of low visitor use (ΔAIC_c = 7.12, the difference between model including visitor use and the null model). The response of raven density to food subsidy depended on the level of visitor use ($F_{1,164}$=11.65, p=0.001). Gray jay occupancy was greater at sites with low visitor use (ΔAIC_c = 0.06, the difference between model including visitor use and the null model). Clark's nutcracker occupancy and density was greatest in areas with food subsidy (occupancy: ΔAIC_c = 3.60, the difference between model including food availability and the null model; density: $F_{1,166}$=5.04, p=0.026). The response of both Steller's jay occupancy and density to food subsidy depended on level of visitor use (occupancy: ΔAIC_c = 17.81, the difference between model including food availability, visitor use, and their interaction, and the null model; density: $F_{1,164}$=9.58, p=0.002). In areas of high visitor use, Steller's jays were most common at points with food but, at low visitor use points, they were most common when no food subsidy was available.

DISCUSSION

Recreation in wildlands can affect native species by increasing levels of predation, decreasing productivity, and changing species distribution patterns. As a result, recreation is one of the leading causes of species endangerment (Czech and Krausman 1997). These extreme effects of recreation are increasingly well recognized yet more subtle effects of nonconsumptive recreation on wilderness ecosystems are less appreciated. Landscape level responses of wildlife species to human recreation and food subsidy have not been evaluated although such responses may affect species' ecological niche and subsequently broad-scale ecosystem function. My study demonstrates how recreation changes the association of birds with aspects of the landscapes in which they live. Corvids adjusted their use of wild landscapes to human recreation in ways that may affect important ecosystem functions. Corvids were in greater abundance and density in areas with high visitor use relative to remote areas of low visitor use. Corvids also responded to the provision of anthropogenic food subsidy and three species changed their use of native vegetation and landscape features. These broad scale responses to recreation by corvids could affect aspects of ecosystem function such as predation, nutrient cycling (i.e. carrion removal), and seed dispersal.

Corvid Distribution Patterns

<u>Occupancy and Density</u>

The observed relationship between occupancy and density for each of the four corvids was not consistent. Variation likely stems from species specific behaviors. Common ravens, which display the weakest correlation between occupancy and density when comparing averages at the four site types, are large, wide-ranging birds known to use roads for foraging (Knight and Kawashima 1993, Knight *et al.* 1995). In Mount Rainier National Park, they are found in low numbers throughout the backcountry (remote areas away from human development) and occupy most areas near roads even when direct anthropogenic food subsidy is not available. In areas of low visitor use, points of food subsidy are used consistently by few ravens (Restani *et al.* 2001, Bui *et al.* 2010). In areas of high visitor use however, where ravens already likely occur, food subsidy supports higher densities of

foraging ravens (Marzluff and Neatherlin 2006). Bui *et al.* (2010) found similar significant differences between raven occupancy and density on a human-modified landscape in Wyoming. Ravens used oil fields (i.e. low human use areas) consistently but were observed at low densities. Large flocks of ravens, however, made infrequent visits to landfills (i.e. points with food subsidy), resulting in patterns of high density but low occupancy.

For Clark's nutcrackers, stands of whitebark pine may influence occupancy and density patterns much like the effect of roads and anthropogenic food subsidy on raven distribution. Although in this study I found that nutcracker occupancy was correlated with density, there was high variability in the observations. In addition, I made relatively few observations of nutcrackers overall in comparison with other species. More observations may have elucidated a clearer relationship. Additionally, nutcrackers collect and cache pine seeds mostly in the late summer and fall (Vander Wall and Balda 1977), and thus season may play a strong role in the observed patterns in Clark's nutcracker distribution. In future nutcracker survey efforts, surveys conducted in the fall may see stronger differences between patterns of occupancy and density then observed here.

Territorial species, such as Steller's jay and gray jay, may forage in pairs or small family groups but are unlikely to be observed in large foraging flocks, even at points of food subsidy. The patterns of occupancy and density were, as expected, closely correlated for each of these species, especially Steller's jay. Gray jay density was variable and may have been affected by their habit of partial dispersal in the post-breeding season (Strickland 1991). Even after young have become independent, gray jays may forage in groups of three or four, including two adults and one or, less commonly, two juveniles. This is in contrast with Steller's jays, which were most often observed as individuals or pairs.

Future research should consider the specific behavior traits of targeted species when designing surveys to measure either occupancy or density, or both. The distribution and abundance of territorial species is likely to be fairly consistent and either occupancy or density alone may adequately describe the species' use of landscape features. For, flocking or wide-ranging species, occupancy and density may reveal different patterns in landscape use.

Effects of Recreation on Ecosystem Function and Landscape Integrity

Human presence and the availability of anthropogenic food subsidy in otherwise wildland landscapes may result in broad scale changes in the use of landscape features by corvids. Because corvids also serve a variety of important ecosystem functions, changes in corvids use of landscape features may affect landscape integrity. I found evidence that food subsidy affected the distribution and abundance patterns of Steller's jays, Clark's nutcrackers, and common ravens in Mount Rainier National Park.

On natural landscapes, corvids prey on a variety of birds and small mammals and can thereby affect songbird community structure. Changes in the use of landscape features by corvids due to recreation may result in new patterns of predation on the landscape. To provide access for recreation, humans create novel edges through otherwise contiguous wild landscapes by building roads, clearing hiking trails, and developing campgrounds and parking areas. In addition to the benefit of increased visibility (Martin and Joron 2003), human-made edges may also attract corvids because of their proximity to anthropogenic food subsidy, artificially inflating local rates of predation and potentially reducing predation rates away from human-created edges. In Mount Rainier National Park, both Steller's jay and common raven are closely associated with fragmented forest landscapes and tend to occupy areas with edges, particularly along roads and around developed areas. In general, Steller's jays and ravens use areas of high visitor use and with the availability of food subsidy. This is consistent with previous studies, where Steller's jays and ravens used forest edges, especially along campgrounds and other areas of human development (Marzluff *et al.* 2004, Marzluff and Neatherlin 2006). Common ravens also used smaller home ranges and foraged at greater densities at campgrounds (Marzluff and Neatherlin 2006). In contrast, gray jays, another nest predator, use mostly contiguous forest landscapes in low visitor use areas on Mount Rainier and do not appear to change their habitat use when anthropogenic food subsidy is available. Edges along developed areas in Mount Rainier National Park, in particular areas with high visitor use and food subsidy, may suffer high nest predation rates by Steller's jay and common raven. Both Steller's jay and ravens use areas of low visitor use and contiguous landscapes less frequently. While the shift away from contiguous forests by Steller's jays and ravens may indicate that these habitats might suffer lower rates of songbird predation, gray jays are highly associated with these landscapes. Songbird and songbird nest predation

by gray jays in areas of high elevation contiguous forest may help maintain landscape integrity and avian community richness. Human recreation may simply shift corvid predation niches or disrupt the natural patterns and ecosystem functionality of corvid predation on songbirds and future research should focus on this distinction.

Nutrient cycling is an important ecosystem process necessary to the integrity of all landscapes. Through carrion removal, corvids such as the common raven perform a vital ecosystem function. In a wild landscape, carrion is produced through a variety of means but is frequently the result of predation events (Stahler *et al.* 2002). In human-influenced landscapes, carrion may be produced through encounters with vehicles and common ravens are drawn to roads because of easy foraging opportunities (Knight and Kawashima 1993, Knight *et al.* 1995). Thus, roads provide a sort of indirect anthropogenic food subsidy to ravens and other carrion eaters (i.e. vultures). In Mount Rainier National Park, common ravens use roaded areas and roads were more important in explaining raven distribution than any other landscape feature, even considering other aspects of human recreation such as visitor use or direct human food subsidy. Ravens concentrating on roads for an easy meal may be missing harder-to-find carcasses on the forested landscape away from roads, impacting the effectiveness of carrion removal and nutrient cycling in wildlands. Gray jays also feed on carrion, although they tend to avoid roads in preference of contiguous forest habitat. Because the use of landscape features by gray jays was not affected by food subsidy in this study, nutrient cycling by gray jays in areas away from intense human development is likely to be functional.

The caching and dispersal of large wingless pine seeds by some corvids is an ecosystem service that supplements the diets of other seed-eating birds and rodents and is necessary to maintain both genetic diversity of specific pine species (Bruederie *et al.* 1998) and biodiversity on the landscape (Tomback and Kendall 2001). Clark's nutcrackers are highly coevolved with whitebark pines in the Pacific Northwest and a single bird might cache tens of thousands of seeds each year (Vander Wall and Balda 1977, Tomback 1982). In Mount Rainier National Park, Clark's nutcrackers were present in areas near whitebark pine stands, regardless of level of visitor use or anthropogenic food subsidy. However, some features of nutcracker landscape use did respond to aspects of human recreation, particularly the provision of anthropogenic food subsidy. When food subsidies were available,

nutcrackers use landscapes of complex and very complex forest structure less and were more abundant at lower elevations and in areas of moderate canopy cover. Their association with stands of whitebark pine was also stronger when food subsidy was available; in areas near whitebark pine, nutcrackers may also utilize food subsidies provided by visitors. Anecdotally, nutcrackers were observed foraging on anthropogenic food refuse at Sunrise Ranger Station and Paradise Inn, both high visitor use sites with large numbers of visitors observed during point counts. Although there is no evidence that food subsidies are negatively impacting the use of whitebark pine by nutcrackers in Mount Rainier National Park, food subsidy may still be an important energy source for nutcrackers in years with low seed crops, potentially upsetting the link between nutcracker and whitebark pine populations. If food subsidy allows nutcracker populations to remain relatively high even through periods of low seed crop, a greater proportion of seed caches may be retrieved, reducing whitebark recruitment (Siepielski and Benkman 2007). Alternatively, nutcrackers may become less dependent on seed caches in general, potentially reducing whitebark seed dispersal (Tomback and Taylor 1987). Thus, human recreation, and the provision of food subsidy in particular, may impact the important ecosystem service of pine seed dispersal and recruitment and, in Mount Rainier National Park, threaten the already vulnerable whitebark pine (Campbell and Antos 2000, Tomback and Achuff 2010).

In wildland recreation areas, corvids are attracted to areas of human use and may benefit from man-made edges and the direct provision of anthropogenic food subsidy at campgrounds, picnic areas, and refuse facilities. Food provisioning in recreation areas may also result in changes in corvid use of landscape features, indicating a possible shift in landscape integrity due to decreases in the performance of ecosystem functions including predation, seed dispersal, and nutrient cycling. I found that corvid species responded to patterns of human recreation in different ways that may reflect a species' particular life history traits. For generalist species, like Steller's jays and common ravens, that eat a wide variety of food types, it is likely easier to adapt to anthropogenic food sources than for specialist species. Flexible foraging strategies may have enabled these species to utilize areas of high visitor use and change their use of other landscape features in areas of food subsidy. Species which specialize on specific foods, for example Clark's nutcracker which mainly forage on the large wingless seeds of pines such as the whitebark pine, may be less

likely to respond to anthropogenic food subsidy. On Mount Rainier, nutcrackers seem to use food subsidies, but only in areas which are near stands of whitebark pine. Species which naturally use vegetative features similar to those created by human development, for example Steller's jays use of edges, are more likely to use developed areas with high visitor use in wildland preserves such as Mount Rainier. Gray jays, however, use contiguous habitat in natural settings which may account for their low use of visitor areas in Mount Rainier and lack of change in landscape use in the presence of anthropogenic food subsidy. Because of their differential responses to human activity, ecosystem functions performed by both generalists and specialists, edge lovers as well as inhabitants of contiguous vegetation, may be affected by human recreation and food subsidy as generalists may be drawn away from natural landscape features and specialists find less landscape area suitable for their needs.

Chapter 2

Corvids as Bioindicators of Anthropogenic Ecosystem Change

Over the past century the global human population has more than tripled (Klein Goldewijk and van Drecht 2006), leading to increased impact on the environment (Vitousek *et al.* 1997). Humans affect native ecosystems and landscapes by fragmenting and converting native vegetation, overutilizing natural resources, releasing carbon stores, increasing nitrogen fixation, and modifying genomes of plant and animal species for domestication and food production. Some direct measurements can be made of the human impact on the environment (i.e. land cover change and carbon dioxide emissions), but the cumulative and interactive effects of these changes on ecosystem function are harder to quantify. Bioassays are ideal for understanding the summed effects of humans on native ecosystems because they measure the response of affected species to environmental change and are commonly used to describe the impact of large scale human activity. For example, bioindicators of phenology and range shifts are indicative of the global biological effects of climate change (Walther *et al.* 2002). Likewise, changes in the composition of aquatic invertebrate communities can give us insight into the integrity of freshwater ecosystems (Bonada *et al.* 2006). Bioassays may be additionally useful in monitoring the effects of land conversion such as urbanization and even more subtle human impacts, such as nonconsumptive human recreation.

Urbanization is one of the most direct and visible effects of human population growth. As human populations have grown, cities have become larger, both in population and physical space on the landscape (Marzluff *et al.* 2008). Cities couple human and natural systems in unique ways, often intricately affecting ecological functions and evolutionary trajectories of plants and animals (Clucas and Marzluff 2011). However, the use of bioassays to assess the myriad impacts of urbanization has been relatively limited. Bioassays have been frequently used to monitor the effects of urban runoff on rivers, estuaries, and watersheds (Fulton *et al.* 1993, Cooper *et al.* 2009, Corsi *et al.* 2010) but relatively few bioindicators measure the terrestrial impacts of urbanization. Of those terrestrial studies,

wildlife bioindicators are uncommon and most studies use plant or lichen indicators of human impact. For example,vegetation composition and forest structure is indicative of anthropogenic stressors in Nova Scotian urban parks (LaPaix and Freedman 2010). In western Georgia, concentrations of airborne contaminants in tree cores and lichens indicated pollution levels along an urban-wildland gradient (Styers and Chappelka 2009).

As cities grow, people seek recreational opportunities in nearby wildlands (Cole 1996). Preserved public natural areas are thus increasingly stressed to both provide the public with recreational opportunities and preserve native landscapes for ecosystem function and service.   For wilderness areas in the United States, the Wilderness Act of 1964 (Public Law 88-577) legally mandates managers to maintain this balance between conflicting needs of humans and wildlife communities. In U. S. National Parks and Forests, bioassays are used to establish visitor use thresholds or "visitor carrying capacities" and visitor impact management frameworks are used to assess resource integrity and recreational experience by monitoring changes in wildlife, vegetation, soil, water, and air, as well as campsite and trail quality, litter quantity, and noise pollution (Merigliano 1990a and 1990b, Leung and Marion 2000). Wildlife bioindicator species may be monitored for significant changes in population abundance or distribution that can then be correlated with changes in human use patterns and indicate potential thresholds of visitor impact (Kuss *et al.* 1990). The presence of American black bears (*Ursus americanus*) at campgrounds in Yosemite National Park, California, for example, indicates an increase in the provision of anthropogenic food subsidy (Greenleaf *et al.* 2009). Species may also be monitored for specific behavioral responses indicative of disturbance stress. Behaviors in response to recreation can be very complicated and may vary between species and within species, between sexes, age groups, or individuals. For example, boat traffic may disturb many marine wildlife species, including Florida manatees (*Trichechus manatus latirostris*; Nowacek *et al.* 2004), orcas (*Orcinus orca*; Williams *et al.* 2002), dugongs (*Dugong dugon*; Hodgson and Marsh 2007), and crocodilians (caiman, *Caiman crocodilus fuscus*; Grant and Lewis 2010). But in the case of orca, males and females respond to approaching boats in subtly different ways, perhaps due to differing energy needs and "costs of transport" (Williams and Noren 2009). While males maintained their speed and took a smooth but indirect path away from the boats, females swam faster and took a more direct path while increasing the angle between dives (Williams *et al.* 2002).

In this case, monitoring the amount of boat traffic alone would not provide insight into either how orcas in general respond to boats or how orca sexes differ in their responses.

In both urban and wildland areas, wildlife species indicate cumulative ecosystem responses to humans. Such responses, however, may be difficult to interpret and link directly to specific human activity. Additionally, the magnitude and direction of the effect of human presence may vary by species, condition of the animal, season, number of people, or human behaviors (Kuss *et al.* 1990, Steidl and Powell 2006). Useful wildlife bioindicators must therefore cover a variety of human impacts, both direct, such as vehicle-caused mortality, the provision of food subsidy, and consumptive recreation such as hunting or fishing, and indirect, including changes in the pattern and composition of vegetation or the invasion of non-native species (Kuss *et al.* 1990, Knight and Gutzwiller 1995, Liddle 1997, Steidl and Powell 2006). Although wildlife indicators can, in general, be difficult to monitor because species may be hard to detect and behaviors difficult to interpret, avian populations and communities are relatively easy to study compared with other vertebrates and thus provide researchers with a unique opportunity to investigate the wide-reaching, cumulative, and interactive effects of an increasing human presence in urban and natural areas (Furness *et al.* 1993, Hutto and Young 2002).

Avian species that are particularly responsive to human action are likely to be useful indicators of the effects of both urbanization and human recreation in natural areas (Merigliano 1990b, Furness *et al.* 1993). Habitat specialists, ground nesters, rare species, and birds that require large contiguous home ranges may be negatively affected by an increase in human presence on the landscape (Knight and Gutzwiller 1995, Neatherlin and Marzluff 2004, Marzluff and Neatherlin 2006). In contrast, human presence may benefit species that are habitat generalists, able to adapt to living with humans, and associated with habitat edges. Avian predators may benefit from increased visibility and juxtaposition of diverse resources (i.e. edge habitats; Martin and Joron 2003) and thus habitat fragmentation may result in an increase in nest predation along vegetation edges (Andrén 1992, Marzluff and Restani 1999, Ibarzabal and Desrochers 2004; Figure 2.1). In particular, changes in the abundance and distribution of synanthropic avian species, which are able to adapt to human development and may benefit from the provision of food subsidies (Knight and Gutzwiller 1995, Marzluff and Neatherlin 2006), may provide evidence for cumulative ecosystem
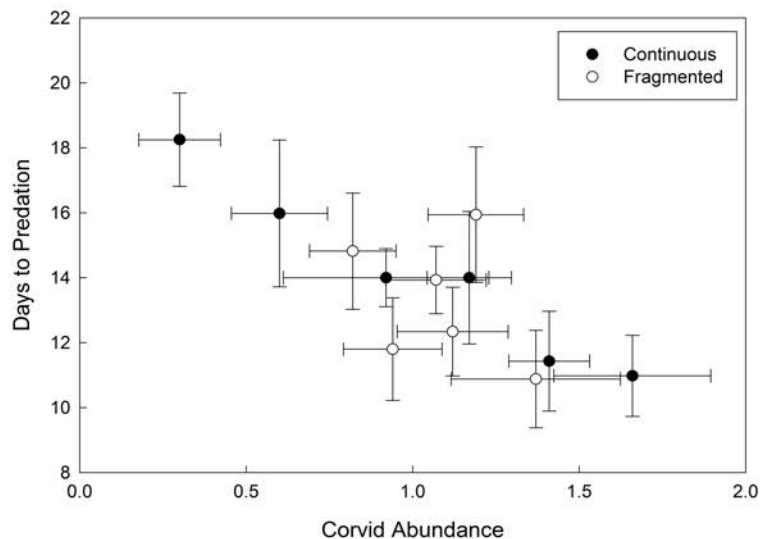
Figure 2.1. Landscape level relationship between corvid abundance and risk of nest predation. Each point represents the maximum per point average of all corvids detected versus average days to predation for nests containing eggs for plots grouped by apriori landscape category. Open symbols indicate that survey point was located in fragmented forest; closed symbols indicate contiguous forests. For details on methods, see Luginbuhl *et al.* (2001).

responses to humans and provide useful thresholds of human impact.

Here I present and discuss a synanthropic avian family that may be ideally suited to indicate anthropogenic effects on the landscape. I also present a case study in Mount Rainier National Park which demonstrates how synanthropic species may change their use of landscape features in the presence of visitors and anthropogenic food subsidies. As birds are drawn from natural patterns of landscape use, changes in species' distribution or abundance may indicate anthropogenic ecosystem effects and loss of ecosystem function.

CORVIDAE

Corvids (birds of the Family Corvidae, including jays, crows, ravens, magpies, and nutcrackers; Figure 2.2) are large, conspicuous, and often gregarious birds found in terrestrial habitats worldwide outside of Antarctica. Although some species are specialists, such as many neotropical jays and the nutcrackers that are highly coevolved with large wingless-seeded pines (Vander Wall and Balda 1977, Tomback 1982), most tend to be generalist omnivores, eating everything from insects, spiders and earthworms to flower nectar, seeds, and nuts, as well as eggs, carrion, and small rodents, herptiles, and birds. In part due to their diverse diet, corvids perform numerous important ecosystem functions including nutrient cycling (achieved through carrion removal; Mason and MacDonald 1995, Devault *et al.* 2003), seed dispersal (by leaving unclaimed seed caches to germinate; Vander Wall and Balda 1977, Tomback 1982), and predation (Sieving and Willson 1998, Terborg *et al.* 2001, Marzluff *et al.* 2007). Among the most intelligent of birds, corvids have relatively large brains (Cnotka *et al.* 2008) which, in combination with their omnivorous, non-specialized way of life, allow them to explore a variety of foraging opportunities (Lefebvre *et al.* 2001). Corvids are known to indirectly exploit other animal species for food acquisition, including wild ungulates (hogs: Baber and Morris 1980; deer: Fitzpatrick and Woolfenden 1996, Genov *et al.* 1998; horses: Ashley 1998), wolves (*Canis lupus*; Stahler *et al.* 2002, Wilmers *et al.* 2003, Vucetich *et al.* 2004), and humans (Marzluff and Angell 2005).

Corvids are coevolved with humans throughout most of their range. Outside of South America, corvids flourish in urban areas (Marzluff and Angell 2005); in North America, populations of the American crow (*Corvus brachyrhynchos*; Marzluff *et al.* 2001) are growing in size and density in cites and urbanizing landscapes. Corvid populations also respond to more moderate human presence such as in rural, agricultural, or wildland recreation areas (Andrén 1992, Storch and Leidenberger 2003, Marzluff and Neatherlin 2006). Corvids often increase in abundance and density in fragmented landscapes (Marzluff and Restani 1999, Luginbuhl *et al.* 2001) and forage along roads (Knight and Kawashima 1993, Knight *et al.* 1995) and other anthropogenic edges including trails (Hickman 1990), agricultural fields (Andrén 1992, Bayne and Hobson 1997), and clear cuts (Luginbuhl *et al.* 2001). In South America and on tropical islands, where corvids remain mostly associated

A.

B.

C.

D.

Figure 2.2. Four North American corvids: (A) gray jay (*Perisoreus canadensis*), (B) American crow (*Corvus brachyrhynchos*), (C) Steller's jay (*Cyanocitta stelleri*), and (D) common raven (*Corvus corax*). Throughout their worldwide range, corvids are associated with humans and human-impacted landscapes. They also perform important ecosystem services that may be affected by their relationship with people. Photo Credit for gray jay, American crow, and Steller's jay: Jorge A. Tomasevic. Photo Credit for common raven: Dalene Edgar.

with contiguous native vegetation, corvids may indicate loss of native vegetation or increases in invasive species, for example the Mariana crow (*Corvus kubaryi*) and the brown tree snake (*Boiga irregularis*) on the island of Guam (Fritts and Rodda 1998, Wiles *et al.* 2003).

Corvids and Wildland Nonconsumptive Recreation

Acting as both human commensals and important participants in natural ecological processes, corvids may serve as useful bioindicators of the human effect on native ecosystems. They may be particularly useful for quantifying the subtle effects of nonconsumptive recreation and could be used by managers of public natural areas to identify imbalances between the dual mandates of providing human recreational opportunities and protecting native wildland ecosystems. In wildland recreation areas, corvids are attracted to areas of human use and may benefit from man-made edges and the direct provision of anthropogenic food subsidy at campgrounds, picnic areas, or from refuse. In the German Alps, a variety of corvids, including carrion crows (*Corvus corone*), common magpies (*Pica pica*), Eurasian jays (*Garrulus glandarius*), alpine choughs (*Pyrrhocorax graculus*), spotted nutcrackers (*Nucifraga caryocatactes*), and common ravens (*Corvus corax*), were associated with areas around tourist mountain huts when compared with control areas (Storch and Leidenberger 2003). Alpine chough attendance to tourist areas in the French Alps was related to the amount of human activity on a seasonal scale (Delestrade 1995). In the mountains of Scotland, carrion crows and rooks (*Corvus frugilegus*) were more abundant in disturbed areas after the development of ski areas, especially around parking areas (Watson 1979). In Yellowstone National Park, Wyoming, common ravens may indicate the success of management efforts to restore previously lost ecosystem function. Grey wolves were reintroduced to the Yellowstone ecosystem in 1995 (Bangs and Fritts 1996, Phillips and Smith 1997) and today common ravens follow wolves to scavenge from wolf-killed carcasses, indicating that wolves in Yellowstone may now represent a functionally intact predator population along with its attendant cadre of scavengers (Stahler *et al.* 2002, Wilmers *et al.* 2003).

Corvids are conspicuous and familiar, making them relatively easy to recognize and enumerate compared with other birds. Corvid presence and abundance on the landscape can

be determined through the use of standard point counts (Ralph *et al.* 1993), although corvid-specific methodologies have been developed that require few repeat surveys (Luginbuhl *et al.* 2001). Because corvids are fixtures on the landscape, i.e. they do not migrate and they have limited altitudinal migration, and they are generally territorial and responsive to calls and playbacks, corvids can be reliably surveyed year round. Also, although they respond to calls, corvids do not defend their territories with song and therefore may be surveyed during most hours of the day (Luginbuhl *et al.* 2001). Therefore, reliable and consistent data on corvid abundance and distribution may be relatively easy to collect by those with little specialized training.

A CASE STUDY: CORVIDS AS BIOINDICATORS IN A WILDLAND SETTING

Mount Rainier National Park is a large reserve (235,625 acres) centered on a 4392 meter volcanic peak in the Cascade Range, approximately 100 km southeast of Seattle, Washington (Figure 2.3). The national park, as established by the Washington Park Wilderness Act of 1988 (Public Law 100-668), is 97 percent designated wilderness and receives over two million visitors every year who use the park for a variety of recreational activities, including hiking, backcountry camping, car camping, picnicking, alpine climbing, snow-shoeing, horse-back riding, and scenic photography. Five corvid species can be found within the park, including American crow (*Corvus brachyrhynchos*), Clark's nutcracker (*Nucifraga columbiana*), common raven, gray jay (*Perisoreus canadensis*), and Steller's jay (*Cyanocitta stelleri*) (Wilkerson *et al.* 2005).

In 2001, a General Management Plan for Mount Rainier National Park was finalized, instituting a visitor use management framework to measure and monitor resource conditions, visitor experiences, and protect the quality of both through the development of visitor use thresholds. Several indicators were suggested for measuring visitor impact including measures of soil, vegetation, air quality, aquatic resources, noise, trails, and wildlife. Among the proposed wildlife measures of visitor impact was the degree of food habituation, a measure listed with corvids in mind.

Mount Rainier Corvids

In the summers of 2009 and 2010, I surveyed corvids in Mount Rainier National Park to determine their distribution in relation to level of visitor use, availability of anthropogenic food subsidy, and numerous weather, vegetation, and landscape variables (Seckel 2011). I also evaluated the effect of food subsidy on the use of landscape features by corvids. Using data collected during more than 1400 visits to 168 survey points, I found, in agreement with previous research, that corvids were most common in areas with high visitor use, especially where visitors provided food subsidies. Additionally, some corvid species—Steller's jay, Clark's nutcracker, and common raven—significantly changed their use of the landscape when food subsidies were provided. Steller's jays were more common in simple

A.

B.

Figure 2.3. View of (A) the eastern face of Mount Rainier from Wonderland Trail, overlooking Indian Bar and the valley draining the Ohanapecoch Glacier and (B) the southwestern face of the peak, rounding Mount Ararat on the Kautz Creek Trail, approaching Indian Henry's Hunting Grounds.

and very complex forest structures when food subsidies were available. Food availability also affected the use of different forest structures by Clark's nutcrackers. Nutcrackers were less present in landscapes of complex and very complex forest structure when food subsidies were provided. Nutcrackers were also in greater abundance at lower elevations and used areas of greater canopy cover when food subsidy was available. Their association with stands of whitebark pine was also stronger when food subsidy was available. Ravens used roads to forage for roadkill regardless of direct food subsidy but were less abundant in heavily roaded areas without the additional subsidy of food provisions.

To effectively use corvids as bioindicators of human impact, baselines of corvid presence from which to measure responses must be established. In Mount Rainier, baseline corvid presence for natural landscapes can be estimated using corvid densities in areas with low visitor use and without food subsidy (Figures 2.4 and 2.5; Corvid densities are predicted density values from distance sampling analyses of point count observations. See Seckel 2011 for detailed methods.) Corvid densities in areas of high visitor use and with anthropogenic food subsidy may then be indicative of changes in density due to human recreation in the park. Species-specific patterns may provide insight into particular effects of anthropogenic landscape change.

In Mount Rainier National Park, the level of landscape fragmentation as well as the risk of songbird nest predation may be indicated by distribution patterns of Steller's and gray jays (Figures 2.4 and 2.5). Steller's jays were found on patchy forested landscapes with abundant anthropogenic edge, a pattern consistent with previous research conducted in western Washington State (Vigallon and Marzluff 2005a, Marzluff and Neatherlin 2006). Thus, increases in Steller's jay abundance or movement of Steller's jays into previously unoccupied areas, may indicate increased levels of fragmentation and landscape patchiness, as well as songbird nest predation (Vigallon and Marzluff 2005b). Gray jays, in contrast, were observed in high elevation contiguous landscapes with large amounts of forest and few edges or patches. Increased gray jay presence may be indicative of higher rates of nest predation but it also indicates a functionally connected landscape on Mount Rainier. This may be a regional finding as gray jays in Quebec were found to be highly associated with forest edges, particularly when home ranges were more heavily forested (Ibarzabal and Desrochers 2004).
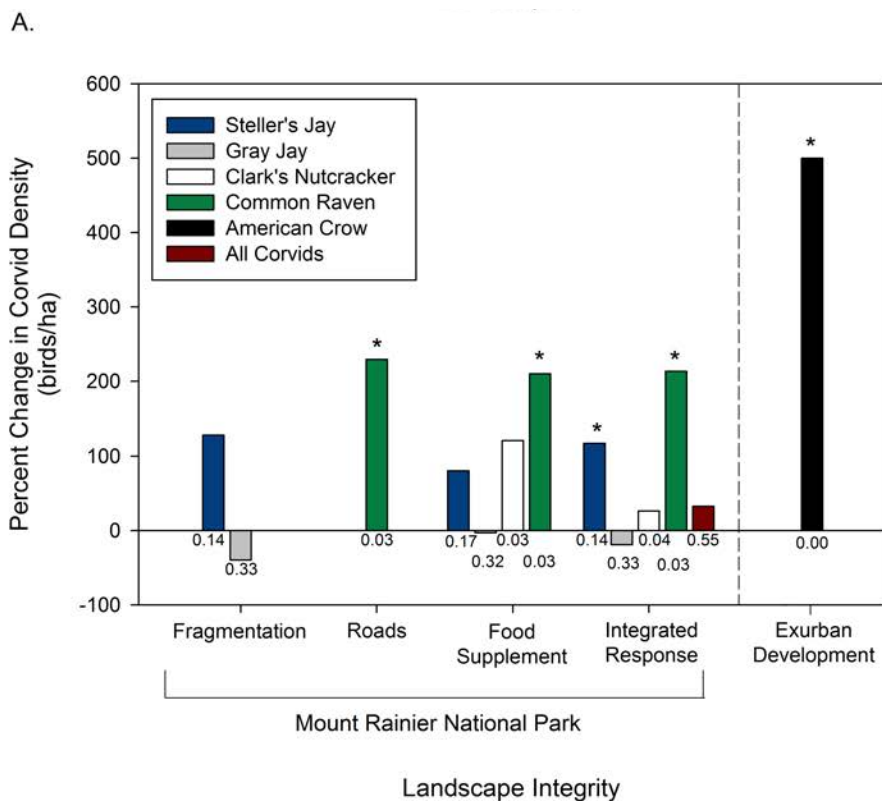
Figure 2.4. Assessment of the effects of human recreation on landscape integrity. Reported numbers are baseline corvid densities. Fragmentation is represented by average differences between areas with low and high visitor use. Food supplementation compares corvid densities at sites with or without food subsidy, regardless of visitor use. The response to roads measures the difference between average raven density within and farther than 0.5 km of roads. The integrated response shows the combined effect of high visitor use and food subsidy on corvid densities. The change in crow density is from wildlands to areas of exurban development (Marzluff *et al.* 2001). * Significant changes in corvid density from baseline (using unpaired t-test).
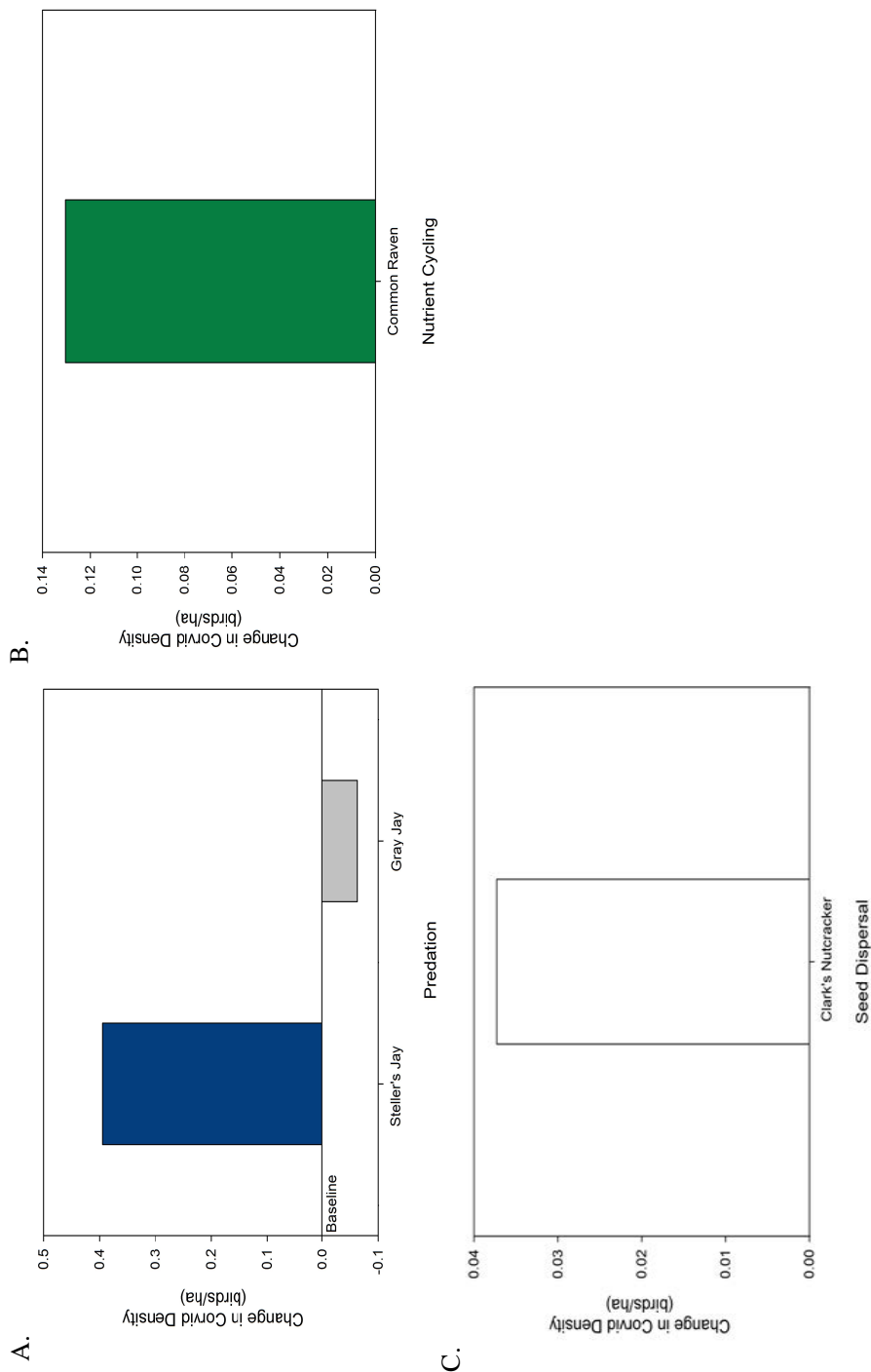
Figure 2.5. Assessment of the effects of human recreation on the performance of ecosystem function by corvids. In (A) and (C), effects on levels of predation and seed dispersal are represented by changes in Steller's jay, gray jay, and Clark's nutcracker densities from areas of low visitor use, without food subsidy to areas with high visitor use and anthropogenic food. For Steller's jay, the change was from 0.14 to 0.54 birds/ha. Gray jay densities changed from 0.34 to 0.27 birds/ha. For Clark's nutcrackers, the baseline was 0.04 birds/ha and, in areas of high visitor use and food subsidy, 0.08. For (D) nutrient cycling, the effect of roads is represented by the change in common raven density from 0.03 birds/ha, in areas farther than 2 km from the nearest road, to 0.16 birds /ha, in areas within 0.5 km of roads.

The broader ecosystem effects of roads on the landscape, including nutrient cycling, may be indicated by common raven abundance and distribution (Figures 2.4 and 2.5). In Mount Rainier, common ravens were commonly present, and most abundant, in forested areas fragmented by roads. Previous studies give insight into the ways in which ravens use roads to forage for vehicle-produced road-kill (Knight and Kawashima 1993, Knight *et al.* 1995). Ravens concentrating on roads for an easy meal may be missing harder-to-find carcasses on the forested landscape away from roads, impacting the effectiveness of carrion removal and nutrient cycling in wildlands. Increases in raven presence may thus indicate both increased landscape effects of roads as well as a reduction in the ecosystem function of nutrient cycling.

The ecosystem function of seed dispersal may be indicated by changes in patterns of Clark's nutcracker distribution (Figure 2.5). Sufficient dispersal of seeds is vital for both overall landscape integrity and the survival of some specialized plant species. In particular, seed dispersal by Clark's nutcrackers is vital for the propagation of whitebark pine, a species already threatened by destructive outbreaks of insects and fungi (Campbell and Antos 2000, Tomback and Achuff 2010). In Mount Rainier National Park, nutcrackers were found in areas of open forest near whitebark pine. They were also associated with areas with many visitors as well as anthropogenic food subsidy. In the Rocky Mountains, where nutcrackers are also known to utilize food subsidies, Tomback and Taylor (1987) speculated that the provision of food subsidies may result in decreased whitebark pine seed dispersal. However, on Mount Rainier, nutcrackers only used anthropogenic food sources when they were also near stands of whitebark pine. In the future, increased presence of Clark's nutcrackers in areas far from whitebark pine but with high visitor use and food subsidy may indicate a reduction in seed dispersal.

Even low levels of human development may be indicated by the presence or increased abundance of American crows (Figure 2.4). Crows were not observed during my surveys of Mount Rainier National Park and previous extensive surveys recorded only one crow observation (Wilkerson *et al.* 2005). However, from other areas and previous research, crows are known to indicate human development across the urban to wildland gradient.   In suburban and urban areas throughout North America, crow populations are expanding and are highly correlated with areas of human food subsidy (Marzluff *et al.* 2001, Marzluff and

Angell 2005). In wildland areas on the Olympic Peninsula, higher densities of American crows around campgrounds were caused by decreases in home ranges and increases in reproduction and survival, likely resulting from food subsidy and decreased harassment (Neatherlin and Marzluff 2004, Marzluff and Neatherlin 2006). Thus, an increase in crow presence in Mount Rainier National Park may indicate increased human development or the increased availability of permanent and reliable anthropogenic food sources.

Visitor use and the provision of food subsidy in Mount Rainier National Park is responded to strongly by corvid populations, indicating that landscape integrity may be impacted in approximately 18% of the park's land (areas within 0.5 km of roads or campgrounds). Although much of the preserve likely retains an intact and functional ecosystem, significant changes in landscape use by corvids have already been observed in developed areas. These results do not define a threshold for visitor use and only highlight the known ecosystem response to recreation in Mount Rainier, as indicated by corvids. Park managers interested in the ecosystem effects of roads or food supplementation could monitor common raven populations, while managers interested in the impacts of fragmentation could rely on patterns in Steller's jay abundance and distribution (Figure 2.4). Both Steller's jay and common raven respond significantly to summed visitor effects, suggesting that either species could be used as an indicator of the overall impacts of human presence in a wildland preserve.

These results demonstrate the utility of corvids as bioindicators of human impact in wildland recreation areas. Continued surveys for corvids in areas of high and low visitor use, and areas with and without food subsidy, could document the relative effects of recreational use in the park on corvids and thus ecosystem function. Additionally, continued surveys may reveal additional trends; for example, corvids may be impacted differently by visitor use in different seasons, following particularly harsh winters, dry summers, or, for nutcrackers, low pine seed crop. The methods used in this case study are applicable to other wildland preserves as well as urban areas and corvids may be useful bioindicators of the effects of human development on ecosystem function across the wildland to urban gradient. For example, Steller's jays are also common in suburban settings in the western United States and jay abundance along trails and parking areas in suburban parks may indicate increased nest predation along these edges. In more developed settings, even small patches of native

vegetation are important for songbird foraging and reproduction (Marzluff and Rodewald 2008) and minimizing the number of trails and other fragmenting features may help keep Steller's jay predation levels low. American crow abundance may be particularly useful for indicating relative level of human development. As cities grow in population and physical expanse, surrounding suburban and rural areas subsequently become increasingly developed, a shift that may be indicated by increasing crow populations.

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APPENDIX 1.A. TOP DETECTION MODELS IN DENSITY ANALYSES

Vegetation and weather attributes associated with corvid detection when modeling density. Table values are coefficients and standard error values of variables in top models describing detection for all species. Detection variables used to correct density estimates were modeled using half normal or hazard rate key functions and considered cosine, simple polynomial, and hermite adjustments. There was rarely a single model that clearly represented the data. The full complement of competitive models (models with a $\Delta AICc < 2$) had a substantial weight of evidence in their favor.

Steller's Jay detection is hindered by high levels of noise and wind. This is summarized by 11 competitive models with a combined weight of 0.43. Gray Jay detection is affected by precipitation, a pattern supported by a single competitive model with a likelihood of 0.99. Clark's Nutcrackers detection, as described by six competitive models with a total combine weight of 0.40, is lowest during counts with high winds in areas of complex forests. Common Raven detection was hindered by loud noise, increased canopy cover, and wind, a pattern supported by seven competitive models with a combined weight of 0.39. [‡]Variables in bold are included in all competitive models ($\Delta AIC_c < 2$). * The ΔAIC_c listed is for the second-best model, not shown.

Steller's Jay Detection	Coefficient	SE	Model Selection	
Best Model: Half Normal Key				
Intercept	43.59	2.73	AIC_c	1520.64
Noise: Level 1[‡]	0.82	0.21	ΔAIC_c*	0.80
Noise: Level 2	0.66	0.16	w_i	0.07
Noise: Level 3	0.39	0.16		
Wind: Level 1	-0.41	0.25		
Wind: Level 2	-0.57	0.25		
Gray Jay Detection				
Best Model: Half Normal Key, Simple Polynomial				
Intercept	35.13	3.46	AIC_c	1138.50
Precipitation: None	-0.08	0.12	ΔAIC_c	11.94
Adjustment of Order 4	2.00	5.80	w_i	0.99
Clark's Nutcracker Detection				
Best Model: Hazard Rate Key				
Intercept	78.56	1.19	AIC_c	413.11
Power Parameter	6.37	12.35	ΔAIC_c	0.65
Forest Structure: Complex	-0.25	0.17	w_i	0.11
Forest Structure: Simple	0.42	0.10		
Common Raven Detection				
Best Model: Half Normal Key, Cosine				
Intercept	65.73	5.84	AIC_c	1065.37
Noise: Level 1	-0.02	0.31	ΔAIC_c	0.48
Noise: Level 2	0.08	0.31	w_i	0.10
Noise: Level 3	-0.32	0.33		
Canopy Cover: 71-100%	0.13	0.09		
Canopy Cover: 11-40%	-0.14	0.11		
Canopy Cover: <11%	0.41	0.18		
Wind: Level 1	0.26	0.20		
Wind: Level 2	0.06	0.20		
Adjustment of Order 2	0.23	0.10		

APPENDIX 1.B. TOP DENSITY MODELS

        Landscape attributes associated with corvid density across all survey points. Table values are coefficients and standard error values of variables in top models describing density for all species. [‡] Variables in bold are included in all competitive models ($\Delta AIC_c < 2$). * The ΔAIC_c listed is for the second-best model, not shown.

Steller's Jay	Coefficient	SE	Model Selection	
Density				
Intercept	0.35	0.14	AIC_c	-370.61
Zone Type (Day Use)[‡]	0.56	0.11	ΔAIC_c*	1.53
Zone Type (Trail Zone)	0.44	0.12	w_i	0.15
Food (Without)	-0.41	0.09		
Elevation	<-0.001	<0.001		
Forest Structure (Simple)	0.18	0.09		
Forest Structure (Very Complex)	0.22	0.06		
Contrast-weighted Edge Density within 2 km	0.01	0.003		
Gray Jay				
Density				
Intercept	-0.64	0.29	AIC_c	-317.13
Elevation	<0.001	<0.001	ΔAIC_c	0.24
Percent Forest within 2 km	0.005	0.002	w_i	0.12
Contrast-weighted Edge Density within 2 km	-0.01	0.004		
Clark's Nutcracker				
Density				
Intercept	-0.08	0.10	AIC_c	-634.86
Distance to Whitebark Pine	<-0.001	<0.001	ΔAIC_c	0.91
Percent Forest within 5 km	0.008	0.001	w_i	0.13
Percent Forest within 2 km	-0.005	0.001		
Food (Without)	-0.08	0.03		
Forest Structure (Simple)	-0.91	0.15		
Forest Structure (Very Complex)	0.04	0.03		
Canopy Cover (11-40%)	-0.07	0.04		
Canopy Cover (<11%)	0.84	0.15		
Canopy Cover (41-70%)	-0.03	0.03		
Elevation	<0.001	<0.001		
Common Raven				
Density				
Intercept	0.18	0.03	AIC_c	-861.56
Food (Without)	-0.18	0.03	ΔAIC_c	0.50
Visitor Use (Low)	-0.15	0.03	w_i	0.17
Length of Road Edge within 5 km	<0.001	<0.001		
Average Number of Visitors	-0.004	0.001		
Food (Without):Visitor Use (Low)	0.15	0.03		

APPENDIX 1.C. COMPETITIVE DENSITY MODELS

Landscape attributes associated with corvid density across all survey points. Table values are coefficients and standard error values of variables in all competitive models (ΔAIC$_c$ < 2) describing density for each species. Using DISTANCE (Thomas *et al.* 2005), I produced predicted density values based on varying corvid detection due to weather and temporal variables (Table 1.1). Then, in the program R (R Development Core Team 2009, Fox *et al.* 2009), I evaluated the importance of numerous variables describing vegetation, visitor use, and landscape metrics (Table 1.1) on corvid density using forward selection of linear regression models.

Steller's Jay Competitive Density Models

AIC$_c$	ΔAIC$_c$	w$_i$		
-370.61	0.00	0.15	Density	0.35 + 0.56*Zone Type (Day Use) + 0.44*Zone Type (Trail Zone) + -0.41*Food (Without) + -0.0004*Elevation + 0.18*Structure (Simple) + 0.22*Structure(Very Complex) + 0.01*Contrast-weighted Edge Density within 2 km
-369.08	1.53	0.07	Density	0.31 + 0.52*Zone Type (Day Use) + 0.42*Zone Type (Trail Zone) + -0.42*Food (Without) + -0.0004*Elevation + 0.16*Structure (Simple) + 0.21*Structure(Very Complex) + 0.01*Contrast-weighted Edge Density within 2 km + 0.00003*Distance to Campground
-369.01	1.6	0.07	Density	0.39 + 0.62*Zone Type (Day Use) + 0.43*Zone Type (Trail Zone) + -0.40*Food (Without) + -0.0004*Elevation + 0.19*Structure (Simple) + 0.20*Structure(Very Complex)
-368.88	1.73	0.06	Density	0.58 + 0.56*Zone Type (Day Use) + 0.45*Zone Type (Trail Zone) + -0.41*Food (Without) + -0.0005*Elevation + 0.18*Structure (Simple) + 0.22*Structure(Very Complex) + 0.01*Contrast-weighted Edge Density within 2 km + -0.002*Percent Forest within 5 km
-368.62	1.99	0.06	Density	0.31 + 0.62*Zone Type (Day Use) + 0.47*Zone Type (Trail Zone) + -0.42*Food (Without) + -0.0005*Elevation + 0.17*Structure (Simple) + 0.23*Structure(Very Complex) + 0.01*Contrast-weighted Edge Density within 2 km + 0.00003*Distance to Road

Gray Jay Competitive Density Models

AIC$_c$	ΔAIC$_c$	w$_i$		
-317.13	0.00	0.12	Density	0.64 + 0.0006*Elevation + 0.01*Percent Forest within 2 km + -0.01*Contrast-weighted Edge Density within 2 km
-316.89	0.24	0.11	Density	-0.91 + 0.0006*Elevation + 0.005*Percent Forest within 2 km + -0.01*Contrast-weighted edge Density within 5 km within 2 km + 0.02*Contrast-weighted edge Density within 2 km
-316.54	0.59	0.09	Density	-0.64 + 0.0006*Elevation + 0.004*Percent Forest within 2 km + -0.01*Contrast-weighted Edge Density within 5 km within 2 km + 0.000001*Length of Road Edge within 2 km
-315.98	1.15	0.07	Density	-0.66 + 0.0006*Elevation + 0.005*Percent Forest within 2 km + -0.01*Contrast-weighted Edge Density within 2 km within 2 km + 0.000004*Length of Road Edge within 2 km

Appendix 1.C. continued

-315.83	1.30	0.06	Density	-0.85 + 0.0006*Elevation + 0.01*Percent Forest within 2 km + -0.01*Contrast-weighted Edge Density within 2 km + 0.04*Patch Richness within 2 km
-315.62	1.51	0.06	Density	-0.59 + 0.0006*Elevation + 0.005*Percent Forest within 2 km + -0.01*Contrast-weighted Edge Density within 2 km + -0.00003*Distance to Nearest Road
-315.48	1.64	0.05	Density	0.64 + 0.0006*Elevation + 0.01*Percent Forest within 2 km
-315.27	1.86	0.05	Density	-0.58 + 0.0006*Elevation + 0.01*Percent Forest within 2 km + -0.01*Contrast-weighted Edge Density within 2 km + -0.09*Visitor Use (Low)

Clark's Nutcracker Competitive Density Models

-634.86	0.00	0.13	Density	-0.08 + -0.00002*Distance to Nearest Whitebark Pine Stand + 0.01*Percent Forest within 5 km + 0.01*Percent Forest within 2 km + -0.08*Food (Without) + -0.91*Forest Structure (Simple) + 0.04*Forest Structure (Very Complex) + -0.07*Canopy Cover (11-40%) + 0.84*Canopy Cover (<11%) + -0.03*Canopy Cover (41-70%) + 0.0001*Elevation
-633.95	0.91	0.09	Density	0.71 + -0.00002*Distance to Nearest Whitebark Pine Stand + 0.01*Percent Forest within 5 km + 0.01*Percent Forest within 2 km + -0.08*Food (Without) + -0.90*Forest Structure (Simple) + 0.05*Forest Structure (Very Complex) + -0.05*Canopy Cover (11-40%) + 0.87*Canopy Cover (<11%) + 0.02*Canopy Cover (41-70%)
-633.80	1.06	0.08	Density	-0.22 + -0.00002*Distance to Nearest Whitebark Pine Stand + 0.01*Percent Forest within 5 km + 0.01*Percent Forest within 2 km + -0.08*Food (Without) + -0.91*Forest Structure (Simple) + 0.03*Forest Structure (Very Complex) + -0.08*Canopy Cover (11-40%) + 0.84*Canopy Cover (<11%) + 0.03*Canopy Cover (41-70%) + 0.0001*Elevation + 0.02*Patch Richness within 2 km
-633.63	1.23	0.07	Density	-0.21 + -0.00002*Distance to Nearest Whitebark Pine Stand + 0.01*Percent Forest within 5 km + 0.01*Percent Forest within 2 km + -0.08*Food (Without) + -0.91*Forest Structure (Simple) + 0.03*Forest Structure (Very Complex) + -0.07*Canopy Cover (11-40%) + 0.84*Canopy Cover (<11%) + 0.02*Canopy Cover (41-70%) + 0.0001*Elevation + 0.004*Contrast-weighted Edge Density within 5 km
-633.37	1.49	0.06	Density	-0.10 + -0.00002*Distance to Nearest Whitebark Pine Stand + 0.01*Percent Forest within 5 km + 0.01*Percent Forest within 2 km + -0.08*Food (Without) + -0.92*Forest Structure (Simple) + 0.03*Forest Structure (Very Complex) + -0.07*Canopy Cover (11-40%) + 0.85*Canopy Cover (<11%) + 0.02*Canopy Cover (41-70%) + 0.0001*Elevation + -0.00001*Distance to Nearest Road
-633.11	1.75	0.06	Density	-0.11 + -0.00002*Distance to Nearest Whitebark Pine Stand + 0.01*Percent Forest within 5 km + 0.01*Percent Forest within 2 km + -0.09*Food (Without) + -0.92*Forest Structure (Simple) + 0.03*Forest Structure (Very Complex) + -0.07*Canopy Cover (11-40%) + 0.85*Canopy Cover (<11%) + 0.03*Canopy Cover (41-70%) + 0.0001*Elevation + 0.00001*Distance to Nearest Campground

Appendix 1.C. continued

-632.94	1.92	0.05	Density	-0.12 + -0.00002*Distance to Nearest Whitebark Pine Stand + 0.01*Percent Forest within 5 km + -0.01*Percent Forest within 2 km + -0.07*Food (Without) + -0.91*Forest Structure (Simple) + 0.03*Forest Structure (Very Complex) + -0.07*Canopy Cover (11-40%) + 0.84*Canopy Cover (<11%) + -0.03*Canopy Cover (41-70%) + 0.0001*Elevation + 0.0000001*Length of Road Edge within 2 km

Common Raven Competitive Density Models

-861.56	0.00	0.17	Density	0.18 + -0.18*Food (Without) + -0.15*Visitor Use (Low) + 0.0000005*Length of Road Edge within 5 km + -.004*Average Number of Visitors + 0.15*Food (Without):Visitor Use (Low)
-861.06	0.50	0.13	Density	0.13 + -0.18*Food (Without) + -0.14*Visitor Use (Low) + 0.0000004*Length of Road Edge within 5 km + -.004*Average Number of Visitors + 0.003*Contrast-weighted edge Density within 5 km + 0.15*Food (Without):Visitor Use (Low)
-861.00	0.56	0.13	Density	0.13 + -0.18*Food (Without) + -0.15*Visitor Use (Low) + 0.0000005*Length of Road Edge within 5 km + -.004*Average Number of Visitors + 0.01*Patch Richness within 2 km + 0.15*Food (Without):Visitor Use (Low)
-860.91	0.65	0.12	Density	0.16 + -0.19*Food (Without) + -0.15*Visitor Use (Low) + 0.0000005*Length of Road Edge within 5 km + -.004*Average Number of Visitors + 0.001*Contrast-weighted edge Density within 2 km + 0.16*Food (Without):Visitor Use (Low)

APPENDIX 1.D. COMPETITIVE OCCUPANCY MODELS

Landscape attributes associated with corvid occupancy and detection across all survey points. Table values are coefficients and standard error values of variables in competitive models ($\Delta AIC_c < 2$) describing occupancy for all species. Variables in occupancy models have been scaled (see text) and coefficients are untransformed logit values. Using PRESENCE (http://www.mbr-pwrc.usgs.gov/software/ presence.html), I produced predicted occupancy values based on varying corvid detection due to weather and temporal variables (Table 1.1). I evaluated the importance of numerous variables describing vegetation, visitor use, and landscape metrics (Table 1.1) on corvid occupancy using forward selection of logit link models.

AIC_c	ΔAIC_c	w_i		Steller's Jay Competitive Occupancy Models
1146.84	0.00	0.05	logit Occupancy	-10.90 + 30.75*Visitor Use (High) + 27.99*Food (With) + -29.28*Visitor Use (High):Food (With) + 14.69*Contrast-weighted Edge Density within 5 km + 21.02*Patch Richness within 5 km + -3.02*Elevation + -22.49*Canopy Cover (71-100%) + -21.78*Canopy Cover (41-70%) + -20.31*Canopy Cover (11-40%) + 21.25*Forest Structure (Very Complex) + 19.95*Forest Structure (Complex)
			logit Detection	-1.95 + 0.43*Canopy Cover (71-100%) + 0.74*Canopy Cover (41-70%) + -0.15*Canopy Cover (11-40%) + 0.26*Forest Structure (Very Complex) + 0.82*Forest Structure (Complex) + 0.41*Noise (Level 2) + -0.02*Noise (Level 3) + 0.42*Noise (Level 4)
1147.33	0.49	0.04	logit Occupancy	-10.72 + 30.50*Visitor Use (High) + 28.10*Food (With) + -29.43*Visitor Use (High):Food (With) + 14.63*Contrast-weighted Edge Density within 5 km + 19.96*Patch Richness within 5 km + -2.58*Elevation + -1.82*Canopy Cover (71-100%) + -0.80*Canopy Cover (41-70%) + 0.08*Canopy Cover (11-40%)
			logit Detection	-2.00 + 0.50*Canopy Cover (71-100%) + 0.75*Canopy Cover (41-70%) + -0.14*Canopy Cover (11-40%) + 0.32*Forest Structure (Very Complex) + 0.80*Forest Structure (Complex) + 0.41*Noise (Level 2) + -0.002*Noise (Level 3) + 0.39*Noise (Level 4)
1147.52	0.68	0.04	logit Occupancy	-10.78 + 4.91*Visitor Use (High) + 2.85*Food (With) + -4.35*Visitor Use (High):Food (With) + 13.56*Contrast-weighted Edge Density within 5 km + 17.14*Patch Richness within 5 km + -1.73*Elevation
			logit Detection	-1.82 + 0.43*Canopy Cover (71-100%) + 0.75*Canopy Cover (41-70%) + -0.10*Canopy Cover (11-40%) + 0.13*Forest Structure (Very Complex) + 0.66*Forest Structure (Complex) + 0.41*Noise (Level 2) + -0.03*Noise (Level 3) + 0.42*Noise (Level 4)

Appendix 1.D. continued

1147.96	1.12	0.03	logit Occupancy	-10.67 + 21.49*Visitor Use (High) + 18.76*Food (With) + -20.03*Visitor Use (High):Food (With) + 19.23*Contrast-weighted Edge Density within 5 km + 22.15*Patch Richness within 5 km + -3.18*Elevation + -27.67*Canopy Cover (71-100%) + -26.95*Canopy Cover (41-70%) + -25.37*Canopy Cover (11-40%) + 26.32*Forest Structure (Very Complex) + 25.02*Forest Structure (Complex) + -3.27*Patch Richness within 2 km
			logit Detection	-1.96 + 0.44*Canopy Cover (71-100%) + 0.74*Canopy Cover (41-70%) + -0.15*Canopy Cover (11-40%) + 0.28*Forest Structure (Very Complex) + 0.83*Forest Structure (Complex) + 0.41*Noise (Level 2) + -0.01*Noise (Level 3) + 0.42*Noise (Level 4)
1148.04	1.20	0.03	logit Occupancy	-11.93 + 36.41*Visitor Use (High) + 33.85*Food (With) + -34.67*Visitor Use (High):Food (With) + 12.46*Contrast-weighted Edge Density within 5 km + 21.87*Patch Richness within 5 km + 2.74*Elevation + -61.89*Canopy Cover (71-100%) + -61.24*Canopy Cover (41-70%) + -59.53*Canopy Cover (11-40%) + 60.65*Forest Structure (Very Complex) + 59.36*Forest Structure (Complex) + 0.29*Distance to Nearest Campground
			logit Detection	-1.98 + 0.44*Canopy Cover (71-100%) + 0.75*Canopy Cover (41-70%) + -0.15*Canopy Cover (11-40%) + 0.30*Forest Structure (Very Complex) + 0.85*Forest Structure (Complex) + 0.40*Noise (Level 2) + -0.02*Noise (Level 3) + 0.43*Noise (Level 4)
1148.14	1.30	0.03	logit Occupancy	-10.89 + 30.74*Visitor Use (High) + 27.99*Food (With) + -29.29*Visitor Use (High):Food (With) + 14.63*Contrast-weighted Edge Density within 5 km + 21.02*Patch Richness within 5 km + 3.02*Elevation + -25.07*Canopy Cover (71-100%) + -24.37*Canopy Cover (41-70%) + -22.90*Canopy Cover (11-40%) + 23.75*Forest Structure (Very Complex) + 22.55*Forest Structure (Complex)
			logit Detection	-1.80 + 0.44*Canopy Cover (71-100%) + 0.75*Canopy Cover (41-70%) + -0.14*Canopy Cover (11-40%) + 0.24*Forest Structure (Very Complex) + 0.80*Forest Structure (Complex) + 0.43*Noise (Level 4) + 0.01*Noise (Level 3) + 0.46*Noise (Level 4) + -1.19*Time After Sunrise
1148.30	1.46	0.02	logit Occupancy	-9.65 + 26.68*Visitor Use (High) + 24.23*Food (With) + -25.70*Visitor Use (High):Food (With) + 13.71*Contrast-weighted Edge Density within 5 km + 17.08*Patch Richness within 5 km + 2.17*Elevation + -0.35*Forest Structure (Very Complex) + -1.42*Forest Structure (Complex)
			logit Detection	-1.96 + 0.37*Canopy Cover (71-100%) + 0.73*Canopy Cover (41-70%) + -0.12*Canopy Cover (11-40%) + 0.27*Forest Structure (Very Complex) + 0.87*Forest Structure (Complex) + 0.43*Noise (Level 2) + -0.02*Noise (Level 3) + 0.46*Noise (Level 4)

Appendix 1.D. continued

1148.53	1.69	0.02	logit Occupancy	-14.16 + 23.73*Visitor Use (High) + 21.03*Food (With) + -22.24*Visitor Use (High):Food (With) + 15.73*Contrast-weighted Edge Density within 5 km + 23.04*Patch Richness within 5 km + -2.71*Elevation + -41.08*Canopy Cover (71-100%) + -40.34*Canopy Cover (41-70%) + -38.86*Canopy Cover (11-40%) + 39.73*Forest Structure (Very Complex) + 38.54*Forest Structure (Complex) + 1.92*Percent Forest within 5 km
			logit Detection	-1.94 + 0.43*Canopy Cover (71-100%) + 0.74*Canopy Cover (41-70%) + -0.15*Canopy Cover (11-40%) + 0.25*Forest Structure (Very Complex) + 0.81*Forest Structure (Complex) + 0.42*Noise (Level 2) + -0.01*Noise (Level 3) + 0.45*Noise (Level 4)
1148.54	1.71	0.02	logit Occupancy	-10.71 + 25.00*Visitor Use (High) + 22.62*Food (With) + -23.94*Visitor Use (High):Food (With) + 14.56*Contrast-weighted Edge Density within 5 km + 19.94*Patch Richness within 5 km + -2.58*Elevation + -1.80*Canopy Cover (71-100%) + -0.79*Canopy Cover (41-70%) + -0.09*Canopy Cover (11-40%)
			logit Detection	-1.85 + 0.51*Canopy Cover (71-100%) + 0.76*Canopy Cover (41-40%) + -0.12*Canopy Cover (11-40%) + 0.29*Forest Structure (Very Complex) + 0.78*Forest Structure (Complex) + 0.43*Noise (Level 2) + 0.02*Noise (Level 3) + 0.42*Noise (Level 4) + -1.20*Time After Sunrise
1148.57	1.74	0.02	logit Occupancy	-14.44 + 28.20*Visitor Use (High) + 25.84*Food (With) + -27.08*Visitor Use (High):Food (With) + 15.98*Contrast-weighted Edge Density within 5 km + 22.15*Patch Richness within 5 km + -2.21*Elevation + -1.80*Canopy Cover (71-100%) + -0.78*Canopy Cover (41-70%) + 0.08*Canopy Cover (11-40%) + 2.20*Percent Forest within 5 km
			logit Detection	-1.99 + 0.49*Canopy Cover (71-100%) + 0.74*Canopy Cover (41-40%) + -0.13*Canopy Cover (11-40%) + 0.31*Forest Structure (Very Complex) + 0.79*Forest Structure (Complex) + 0.42*Noise (Level 2) + 0.01*Noise (Level 3) + 0.42*Noise (Level 4)
1148.60	1.76	0.02	logit Occupancy	-10.77 + 4.99*Visitor Use (High) + 2.94*Food (With) + 4.44*Visitor Use (High):Food (With) + 13.50*Contrast-weighted Edge Density within 5 km + 17.13*Patch Richness within 5 km + 1.73*Elevation
			logit Detection	-1.67 + 0.44*Canopy Cover (71-100%) + 0.77*Canopy Cover (41-70%) + -0.09*Canopy Cover (11-40%) + 0.11*Forest Structure (Very Complex) + 0.66*Forest Structure (Complex) + 0.43*Noise (Level 2) + 0.0005*Noise (Level 3) + 0.45*Noise (Level 4) + -1.22*Time After Sunrise
1148.77	1.93	0.02	logit Occupancy	-14.30 + 5.21*Visitor Use (High) + 3.08*Food (With) + -4.53*Visitor Use (High):Food (With) + 14.85*Contrast-weighted Edge Density within 5 km + 19.36*Patch Richness within 5 km + 1.36*Elevation + 1.95*Percent Forest within 5 km

Appendix 1.D. continued

			logit Detection	-1.84 + 0.42*Canopy Cover (71-100%) + 0.75*Canopy Cover (41-70%) + -0.10*Canopy Cover (11-40%) + 0.15*Forest Structure (Very Complex) + 0.69*Forest Structure (Complex) + 0.42*Noise (Level 2) + -0.01*Noise (Level 3) + 0.45*Noise (Level 4)

Gray Jay Competitive Occupancy Models

1073.79	0.00	0.08	logit Occupancy	-7.42 + 10.33*Elevation + 8.19*Percent Forest within 2 km + 23.47*Forest Structure (Very Complex) + 25.07*Forest Structure (Complex) + -22.53*Patch Richness within 5 km + -21.64*Habitat (Forest) + 1.72*Habitat (Open Forest) + 0.58*Distance to Nearest Campground
			logit Detection	1.72 + -0.002*Noise (Level 2) + -0.61*Noise (Level 3) + -1.47*Noise (Level 4) + -0.35*Forest Structure (Very Complex) + -1.23*Forest Structure (Complex) + 1.00*Habitat (Forest) + 0.32*Habitat (Open Forest)
1074.51	0.72	0.06	logit Occupancy	-9.37 + 10.58*Elevation + 9.19*Percent Forest within 2 km + 23.49*Forest Structure (Very Complex) + 24.67*Forest Structure (Complex) + -21.23*Patch Richness within 5 km + -22.01*Habitat (Forest) + 1.80*Habitat (Open Forest) + 0.69*Distance to Nearest Campground + 1.11*Food (With)
			logit Detection	-1.28 + 0.001*Noise (Level 2) + -0.60*Noise (Level 3) + -1.41*Noise (Level 4) + -0.35*Forest Structure (Very Complex) + -1.21*Forest Structure (Complex) + 1.00*Habitat (Forest) + 0.32*Habitat (Open Forest)
1074.66	0.87	0.05	logit Occupancy	-7.56 + 10.25*Elevation + 8.18*Percent Forest within 2 km + 23.38*Forest Structure (Very Complex) + 24.94*Forest Structure (Complex) + -22.09*Patch Richness within 5 km + -21.57*Habitat (Forest) + 1.74*Habitat (Open Forest) + 0.57*Distance to Nearest Campground
			logit Detection	-1.11 + 0.01*Noise (Level 2) + -0.61*Noise (Level 3) + -1.45*Noise (Level 4) + -0.35*Forest Structure (Very Complex) + -1.21*Forest Structure (Complex) + 0.99*Habitat (Forest) + 0.31*Habitat (Open Forest) + -1.38*Time After Sunrise
1075.10	1.31	0.04	logit Occupancy	-7.34 + 10.40*Elevation + 8.24*Percent Forest within 2 km + 23.47*Forest Structure (Very Complex) + 25.07*Forest Structure (Complex) + -22.92*Patch Richness within 5 km + -21.62*Habitat (Forest) + 1.72*Habitat (Open Forest) + 0.58*Distance to Nearest Campground
			logit Detection	-1.22 + -0.004*Noise (Level 2) + -0.61*Noise (Level 3) + -1.43*Noise (Level 4) + -0.34*Forest Structure (Very Complex) + -1.22*Forest Structure (Complex) + 1.01*Habitat (Forest) + 0.33*Habitat (Open Forest) + -0.20*Cloud Cover
1075.18	1.39	0.04	logit Occupancy	-4.38 + 9.99*Elevation + 7.06*Percent Forest within 2 km + 23.26*Forest Structure (Very Complex) + 25.04*Forest Structure (Complex) + -22.81*Patch Richness within 5 km + -21.87*Habitat (Forest) + 1.14*Habitat (Open Forest) + 0.54*Distance to Nearest Campground + -5.72*Contrast-weighted Edge Density within 2 km

Appendix 1.D. continued

			logit Detection	-1.30 + -0.02*Noise (Level 2) + -0.63*Noise (Level 3) + -1.45*Noise (Level 4) + -0.35*Forest Structure (Very Complex) + -1.24*Forest Structure (Complex) + 1.03*Habitat (Forest) + 0.36*Habitat (Open Forest)
1075.39	1.60	0.04	logit Occupancy	-7.81 + 10.61*Elevation + 8.65*Percent Forest within 2 km + 23.38*Forest Structure (Very Complex) + 24.93*Forest Structure (Complex) + -23.01*Patch Richness within 5 km + -21.52*Habitat (Forest) + 1.76*Habitat (Open Forest) + 0.61*Distance to Nearest Campground
			logit Detection	-1.27 + -0.04*Noise (Level 2) + -0.68*Noise (Level 3) + -1.52*Noise (Level 4) + -31.96*Forest Structure (Very Complex) + -32.69*Forest Structure (Complex) + 0.83*Habitat (Open Forest) + 31.55*Canopy Cover (71-100%) + 31.90*Canopy Cover (41-70%) + 31.47*Canopy Cover (11-40%)
1075.42	1.63	0.04	logit Occupancy	-8.35 + 10.39*Elevation + 9.39*Percent Forest within 2 km + 23.37*Forest Structure (Very Complex) + 25.18*Forest Structure (Complex) + -23.22*Patch Richness within 5 km + -21.62*Habitat (Forest) + 1.52*Habitat (Open Forest) + 0.62*Distance to Nearest Campground + 0.29*Distance to Nearest Road
			logit Detection	-1.29 + -0.005*Noise (Level 2) + -0.62*Noise (Level 3) + -1.48*Noise (Level 4) + -0.35*Forest Structure (Very Complex) + -1.24*Forest Structure (Complex) + 1.00*Habitat (Forest) + 0.33*Habitat (Open Forest)
1075.56	1.77	0.03	logit Occupancy	-8.61 + 10.53*Elevation + 8.04*Percent Forest within 2 km + 23.47*Forest Structure (Very Complex) + 25.03*Forest Structure (Complex) + -22.86*Patch Richness within 5 km + -21.67*Habitat (Forest) + 1.69*Habitat (Open Forest) + 0.57*Distance to Nearest Campground + 2.67*Patch Richness within 2 km
			logit Detection	-1.29 + -0.003*Noise (Level 2) + -0.61*Noise (Level 3) + -1.47*Noise (Level 4) + -0.35*Forest Structure (Very Complex) + -1.22*Forest Structure (Complex) + 1.01*Habitat (Forest) + 0.33*Habitat (Open Forest)
1075.59	1.80	0.03	logit Occupancy	-8.72 + 10.03*Elevation + 8.24*Percent Forest within 2 km + 23.56*Forest Structure (Very Complex) + 24.95*Forest Structure (Complex) + -20.00*Patch Richness within 5 km + -21.67*Habitat (Forest) + 1.94*Habitat (Open Forest) + 0.53*Distance to Nearest Campground + 0.48*Average Number of Visitors
			logit Detection	-1.27 + 0.00009*Noise (Level 2) + -0.61*Noise (Level 3) + -1.47*Noise (Level 4) + -0.34*Forest Structure (Very Complex) + -1.21*Forest Structure (Complex) + 0.99*Habitat (Forest) + 0.31*Habitat (Open Forest)

Appendix 1.D. continued

1075.65	1.86	0.03	logit Occupancy	-5.24 + 10.35*Elevation + 8.64*Percent Forest within 2 km + 23.37*Forest Structure (Very Complex) + 25.07*Forest Structure (Complex) + -25.95*Patch Richness within 5 km + -21.73*Habitat (Forest) + 1.44*Habitat (Open Forest) + 0.62*Distance to Nearest Campground + -2.55*Length of Road Edge within 2 km
			logit Detection	-1.29 + -0.01*Noise (Level 2) + -0.62*Noise (Level 3) + -1.47*Noise (Level 4) + -0.35*Forest Structure (Very Complex) + -1.23*Forest Structure (Complex) + 1.00*Habitat (Forest) + 0.33*Habitat (Open Forest)

Clark's Nutcracker Competitive Occupancy Models

331.08	0.00	0.13	logit Occupancy	-3.49 + -3.47*Distance to Nearest Whitebark Pine + 2.46*Average Number of Visitors + 43.46*Contrast-weighted Edge Density within 2 km + -12.23*Forest Structure (Very Complex) + -4.40*Forest Structure (Complex) + 7.25*Food (With) + 6.45*Habitat (Forest) + 8.36*Habitat (Open Forest)
			logit Detection	-0.80 + -0.74*Noise (Level 2) + -1.12*Noise (Level 3) + -0.62*Noise (Level 4) + 22.02*Forest Structure (Very Complex) + 17.98*Forest Structure (Complex) + -18.25*Canopy Cover (71-100%) + -20.82*Canopy Cover (41-70%) + -20.96*Canopy Cover (11-40%) + -0.19*Habitat (Forest) + -1.13*Habitat (Open Forest) + 3.08*Time After Sunrise
331.86	0.78	0.09	logit Occupancy	47.38 + -3.33*Distance to Nearest Whitebark Pine + 2.33*Average Number of Visitors + 44.84*Contrast-weighted Edge Density within 2 km + -12.58*Forest Structure (Very Complex) + -4.92*Forest Structure (Complex) + 6.88*Food (With) + 6.87*Habitat (Forest) + 8.62*Habitat (Open Forest) + -85.42*Patch Richness within 5 km
			logit Detection	-0.81 + -0.73*Noise (Level 2) + -1.09*Noise (Level 3) + -0.61*Noise (Level 4) + 27.59*Forest Structure (Very Complex) + 23.57*Forest Structure (Complex) + -23.85*Canopy Cover (71-100%) + -26.41*Canopy Cover (41-70%) + -26.56*Canopy Cover (11-40%) + -0.19*Habitat (Forest) + -1.12*Habitat (Open Forest) + 3.07*Time After Sunrise
332.82	1.74	0.06	logit Occupancy	-2.97 + -4.38*Distance to Nearest Whitebark Pine + 3.43*Average Number of Visitors + 50.43*Contrast-weighted Edge Density within 2 km + -15.22*Forest Structure (Very Complex) + -4.43*Forest Structure (Complex) + 10.04*Food (With) + 7.62*Habitat (Forest) + 10.38*Habitat (Open Forest) + -2.59*Visitor Use (High)
			logit Detection	-0.82 + -0.75*Noise (Level 2) + -1.12*Noise (Level 3) + -0.65*Noise (Level 4) + 26.77*Forest Structure (Very Complex) + 22.74*Forest Structure (Complex) + -22.96*Canopy Cover (71-100%) + -25.56*Canopy Cover (41-70%) + -25.70*Canopy Cover (11-40%) + -0.19*Habitat (Forest) + 1.13*Habitat (Open Forest) + 3.11*Time After Sunrise

Appendix 1.D. continued

				Common Raven Competitive Occupancy Models
982.87	0.00	0.10	logit Occupancy	-84.86 + 192.92*Contrast-weighted Edge Density within 2 km + 81.33*Percent Forest within 5 km + 38.52*Average Number of Visitors + -4.15*Forest Structure (Very Complex) + -14.30*Forest Structure (Complex)
			logit Detection	-1.59 + 0.03*Noise (Level 2) + -0.89*Noise (Level 3) + -1.64*Noise (Level 4) + -3.30*Time After Sunrise + 0.41*Canopy Cover (71-100%) + 0.78*Canopy Cover (41-70%) + 0.03*Canopy Cover (11-40%) + 0.39*Wind (Level 2) + 0.37*Wind (Level 3)
983.73	0.86	0.06	logit Occupancy	-98.20 + 235.53*Contrast-weighted Edge Density within 2 km + 97.99*Percent Forest within 5 km + 51.66*Average Number of Visitors + -5.57*Forest Structure (Very Complex) + -17.38*Forest Structure (Complex) + -8.72*Zone Type (Day Use) + -4.55*Zone Type (Trail Zone)
			logit Detection	-1.59 + 0.04*Noise (Level 2) + -0.88*Noise (Level 3) + -1.60*Noise (Level 4) + -3.32*Time After Sunrise + 0.41*Canopy Cover (71-100%) + 0.80*Canopy Cover (41-70%) + 0.03*Canopy Cover (11-40%) + 0.37*Wind (Level 2) + 0.36*Wind (Level 3)
983.98	1.11	0.06	logit Occupancy	-107.35 + 241.57*Contrast-weighted Edge Density within 2 km + 102.98*Percent Forest within 5 km + 47.08*Average Number of Visitors + -4.66*Forest Structure (Very Complex) + -17.60*Forest Structure (Complex)
			logit Detection	-1.58 + 0.02*Noise (Level 2) + -0.87*Noise (Level 3) + -1.58*Noise (Level 4) + -3.31*Time After Sunrise + 0.09*Canopy Cover (71-100%) + 0.63*Canopy Cover (41-70%) + -0.17*Canopy Cover (11-40%) + 0.37*Wind (Level 2) + 0.36*Wind (Level 3) + 0.07*Forest Structure (Very Complex) + 0.49*Forest Structure (Complex)