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RESEARCH ARTICLE

Recreation changes the use of a wild landscape by corvids

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ABSTRACT

As urban areas have grown in population, use of nearby natural areas for outdoor recreation has also increased, potentially influencing bird distribution in landscapes managed for conservation. Members of the family Corvidae (crows, ravens, jays, and magpies) have strong interactions with humans and may be directly affected by recreation in wild landscapes. In Mount Rainier National Park, we evaluated the effects of vegetation, visitor use, and the availability of human-subsidized food on the use of landscape features by 4 corvid species: Steller's Jay (*Cyanocitta stelleri*), Gray Jay (*Perisoreus canadensis*), Common Raven (*Corvus corax*), and Clark's Nutcracker (*Nucifraga columbiana*). We conducted $>$1,400 point counts across areas that varied in habitat and in the degree of human recreational impact. We calculated predicted occupancy values while allowing for variation in detection probability. In addition to species-specific suites of vegetation and landscape variables, we found that patterns of human recreation, such as visitor use, food subsidy, and amount of road edge, were also significant in explaining corvid distribution. The number of visitors present during point counts was positively associated with Steller's Jay and Clark's Nutcracker use. Common Ravens used areas with fewer people but with a high density of road edge. Gray Jays, Common Ravens, and Clark's Nutcrackers were each more likely to use sites with anthropogenic food subsidy than sites without subsidies. These changes in landscape use may affect the performance of ecosystem services by corvids and could serve as useful and easily measured bioindicators of the impacts of recreation.

Keywords: Clark's Nutcracker, Common Raven, corvid, Gray Jay, Mount Rainier National Park, PRESENCE, recreation, Steller's Jay

La recreación cambia el uso de los córvidos de un paisaje silvestre

RESUMEN

A medida que la población de las áreas urbanas crece, el uso recreativo de las áreas naturales vecinas también crece, influyendo potencialmente la distribución de las aves en los paisajes manejados para la conservación. Los miembros de la Familia Corvidae tienen interacciones intensas con los humanos y pueden ser afectados directamente por las actividades recreativas en los paisajes silvestres. En el Parque Nacional Mount Rainier, evaluamos los efectos de la vegetación, el uso de los visitantes y la disponibilidad de alimentos subsidiados por los humanos sobre el uso de los rasgos del paisaje por parte de 4 especies de córvidos: *Cyanocitta stelleri*, *Perisoreus canadensis*, *Corvus corax* y *Nucifraga columbiana*. Realizamos más de 1,400 conteos por punto en áreas con distintos hábitats y nivel de impacto humano recreativo y calculamos los valores predictivos de ocupación con distintos niveles de probabilidad de detección. Además de series de vegetación y variables de paisaje específicos para cada especie, encontramos que los patrones de recreación humana, como el uso de los visitantes, el alimento subsidiado y la cantidad de borde de caminos, también afectaron significativamente la distribución de los córvidos. El número de visitantes presentes durante los conteos por punto estuvo asociado positivamente con el uso por parte de *C. stelleri* y *N. columbiana*. *C. corax* usó áreas con menos cantidad de gente pero con una alta densidad de bordes de camino. *P. canadensis*, *C. corax* y *N. columbiana* presentaron una mayor probabilidad de uso de sitios con alimentos humanos subsidiados que sitios sin subsidios. Estos cambios en el uso del paisaje pueden afectar el desempeño de los servicios ecosistémicos por parte de los córvidos y pueden servir como bio-indicadores útiles y fácilmente medibles de los impactos de la recreación.

Palabras clave: córvidos, *Corvus corax*, *Cyanocitta stelleri*, *Nucifraga columbiana*, Parque Nacional Mount Rainier, *Perisoreus canadensis*, PRESENCE, recreación.

INTRODUCTION

Recreation, ecotourism, and other nonconsumptive human activities affect native wildlife communities and the ecosystems to which they belong (Edington and Edington 1986, Knight and Gutzwiller 1995, Liddle 1997). Human recreation in natural areas (e.g., by outdoor photographers, rock climbers, hikers, and horseback riders) exposes wildlife to direct human disturbance, while the creation of recreational infrastructure (e.g., access roads, bike paths, campgrounds, and picnic areas) affects the composition and pattern of native landscapes. Although many native species of wildlife are negatively affected by human recreation in natural areas (Anderson 1995, Knight and Cole 1995b, Czech and Krausman 1997), the magnitude and direction of these impacts 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 of wildlife, both positive and negative, to recreation are well documented (Burger and Gochfeld 1998, Gutzwiller et al. 1998, 2002, Marzluff and Neatherlin 2006), population-level responses over broad spatial scales to patterns of human recreation have not been evaluated.

Avian communities may be especially sensitive to nonconsumptive wildland recreation (Anderson 1995, Knight and Cole 1995b, Miller et al. 1998). The repeated presence of humans in the environment (e.g., hikers along a trail) may affect avian richness and abundance (Riffell et al. 1996). 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, 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). Additionally, there may be an increase in egg and chick predation (the primary cause of nest failure in songbirds; Martin 1993) due to the attraction of mammalian (Bradley and Marzluff 2003, Martin and Joron 2003, Gutzwiller and Riffell 2008) and avian (Gutzwiller et al. 2002, Marzluff and Neatherlin 2006, Piper and Catterall 2006) predators. Alternatively, human disturbance of some landscapes may directly deter predators or confound predatory behavior and result in inflated nest success for more tolerant avian species (Sandvik and Barrett 2001, Francis et al. 2009).

The vulnerability of particular species to impacts of recreation such as nest desertion or increased predation is likely to depend on various life history traits as well as their resource requirements (Knight and Cole 1995a, Hill et al. 1997). Bird species that are likely to be negatively affected by an increase in nonconsumptive recreation include those that require specialized resources, ground nesters, rare species, and those that require large contiguous home ranges (Knight and Cole 1995a, Neatherlin and Marzluff 2004, Marzluff and Neatherlin 2006). By contrast, human recreation in 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. Avian predators, including corvids, may benefit from increased visibility and juxtaposition of diverse resources (e.g., edge habitats; Martin and Joron 2003). Corvids are intelligent generalist-omnivores that are well adapted to human presence, 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, Huhta and Sulkava 2014). 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, Marzluff and Neatherlin 2006).

Changing corvid communities may also affect important ecosystem functions, including carrion decomposition (Knight and Kawashima 1993, Mason and MacDonald 1995), seed dispersal (Vander Wall and Balda 1977, Tomback and Taylor 1987, Johnson et al. 1997), and nest predation (Andrén 1992, Marzluff and Restani 1999, Ibarzabal and Desrochers 2004). Increasing the spatial perspective on the response of corvids to human recreation may increase our understanding of recreation's effect on ecosystem processes and afford managers the information they need 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.

Although corvids are already known to be highly associated with humans and with man-made habitat features on the landscape (Neatherlin and Marzluff 2004, Marzluff and Angell 2005, Marzluff and Neatherlin 2006, Huhta and Sulkava 2014), no research has explicitly investigated the effects of food subsidy on the distribution patterns of corvids and their use of landscape habitat features in wildland ecosystems. We evaluated the impact of anthropogenic food subsidy and other aspects of human recreation on the distribution patterns and landscape-scale habitat use of 4 corvid species in Mount Rainier National Park, Washington, USA: Steller's Jay (*Cyanocitta stelleri*), Gray Jay (*Perisoreus canadensis*), Common Raven (*Corvus corax*), and Clark's Nutcracker (*Nucifraga columbiana*).

We expected corvid presence to increase near areas of high visitor use (e.g., visitor centers, picnic areas, and drive-up campgrounds) and with food subsidy. Although we expected the provision of anthropogenic food subsidy to be important in explaining landscape-scale distribution

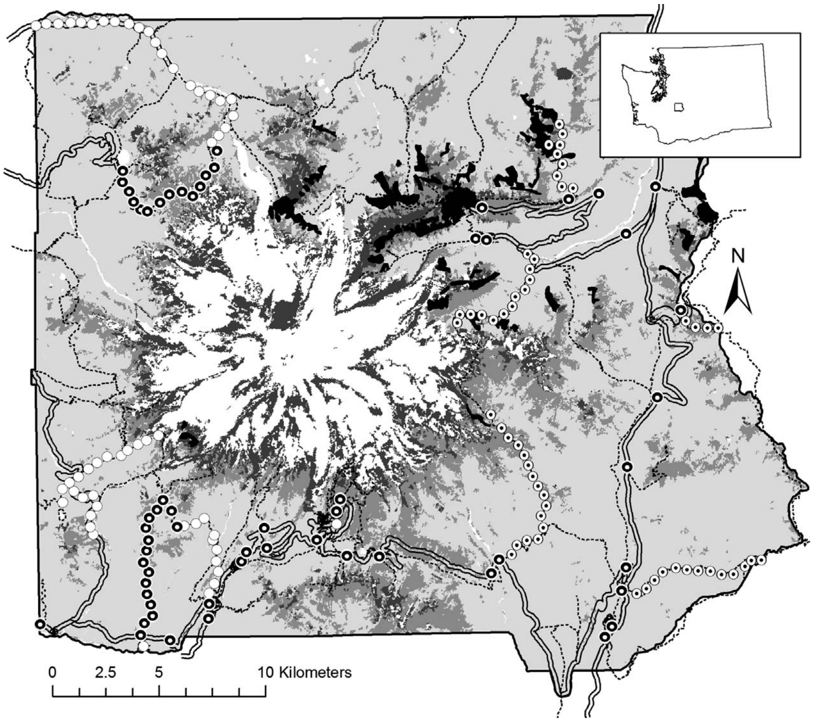

FIGURE 1. Mount Rainier National Park, Washington, USA, with locations of our corvid surveys. Open circles are sites that were surveyed only in 2009. White circles with black centers were surveyed only in 2010. Black circles with white centers are sites that were surveyed during both years. Roads are indicated by double lines and trails by dashed lines. Shading represents 5 landcover types, from white to darkest gray: open water–glacier, forest, meadow–shrub, barren rock, and stands of whitebark pine.

patterns of all 4 corvid species, we suspected that this relationship might be most apparent for species whose typical habitat requirements commonly occur in areas of relatively low human impact (e.g., high elevations). The habitat preferences of Steller's Jays naturally coincide with areas of relatively high human impact in the park (i.e. low-elevation forests with lots of edge; Vigallon and Marzluff 2005a), and we predicted that patterns of Steller's Jay use might best be explained by a model including both natural and human-influenced landscape features, such as edge, campgrounds, or park zones restricted to day use. Gray Jays tend to use higher-elevation contiguous forests away from most human-affected landscape features (Luginbuhl et al. 2001), and we predicted that a model including natural landscape features and food availability would best explain this species' distribution patterns. By contrast, we predicted that recreational landscape features (particularly roads; Knight et al. 1995) and anthropogenic food availability would be most important in explaining patterns of Common Raven distribution. We suspected that vegetation characteristics, most notably the presence of whitebark pine (*Pinus albicaulis*; Hutchins and Lanner 1982, Tomback 1982), would explain the distribution patterns of Clark's Nutcrackers. However, 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

We surveyed corvids throughout Mount Rainier National Park (Figure 1), a 95,354-ha reserve on a 4,392-m volcanic peak located on the west side of the Cascade Range, ~100 km southeast of Seattle in southwestern Washington. The park is 97% designated wilderness (Public Law 100–668). It has long, cool, wet winters and relatively warm, dry summers. Vegetation and habitat features vary widely throughout the park, due to the combined effects of the steep elevation gradient and precipitation levels that change with elevation and the east–west rain-shadow effect. Elevations below 1,000 m are characterized by mature forests dominated by Douglas-fir (*Pseudotsuga menziesii*), western redcedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) (Franklin et al. 1988). Mixed forests of western white pine (*Pinus monticola*), western hemlock, and Pacific silver fir (*Abies amabilis*) are found at midlevel elevations between 1,000 and 1,500 m. Relatively open mixed forests and subalpine meadows characterize elevations from 1,500 to 2,000 m, where dominant tree species include subalpine fir (*Abies lasiocarpa*), mountain hemlock (*Tsuga mertensiana*), Alaska cedar (*Callitropsis nootkatensis*), and whitebark pine (Hamann 1972, Henderson 1974). Subalpine meadow vegetation may include heather species (*Cassiope* sp. or *Phyllodoce* sp.), huckleberry (*Vaccinium* sp.), subalpine lupine (*Lupinus arcticus* ssp. *subalpinus*), false hellebore (*Veratrum viride*), sedges, alpine aster (*Aster alpinus*), paintbrush (*Castilleja* sp.), western anemone (*Anemone occidentalis*), or fescues (*Festuca* sp.). Above 2,000 m is an alpine zone covered mostly by heather communities, snow, glaciers, rock outcrops, and talus fields (Hamann 1972, Edwards 1980). In total, ~58% of the park is forested, ~23% 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. During the study period, the park had >2 million visitors each year (http://www.nps.gov/mora). The park maintains 4 visitor centers, 3 wilderness information centers, 4 drive-up campgrounds, 41 hike-in campgrounds, and >400 km of trail.

Corvid Surveys

Incorporating a variety of vegetation types, recreational impacts, and park management uses, we surveyed 168 sites for corvid presence throughout Mount Rainier National Park during the summer seasons (mid-June through late September) of 2009 and 2010. On Mount Rainier, heavy snow covered most of our survey sites during the rest of the year, and summer was the only season when many of our sites were accessible. We surveyed a total of 168 sites, including 113 sites sampled in 2009, 114 sampled in 2010, and 59 sampled in both survey seasons (Figure 1). During each year, we visited survey sites between 2 and 10 times, totaling 639 visits in 2009 and 774 visits in 2010. Although the number of visits to each site ranged from 2 to 18 across both seasons, the analysis program PRESENCE (we used version 2.4) allows unequal survey effort (MacKenzie et al. 2006; see Acknowledgments). 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. 2006). Most sites (84%) received ≥6 visits ($n = 141$). Although we made efforts to visit sites in each of 3 periods within the season—early (mid-June through mid-July), middle (mid-July through mid-August), and late (mid-August through late September)—whenever possible, visits were highly constrained by snow conditions (higher elevations in the park are often snow-covered through late July). Given the specific conditions for each site, however, we attempted to make visits at varying times throughout the accessible, snow-free portion of the season to minimize within-season differences in detectability.

We chose survey locations that reflected a variety of human impacts and recreational intensities. Site selection was logistically constrained by snow level and by physical accessibility. It is possible that our results will have limited applicability to high-elevation sites, which may be used increasingly as temperatures rise and snowfall declines in response to climate change. For sites accessible by vehicle, we compiled lists of sites with and without food subsidy (defined by the presence or absence of at least 1 campsite, trash can, or picnic table) after analyzing park maps and consulting with park personnel, and we randomly chose a selection from each list. For hike-in-only sites, we randomly selected hikes from a list comprising all 1- or 2-day hikes, excluding those that were snow-covered during much of the field season or required the use of specialty equipment (e.g., crampons or ice axes). We then placed survey sites along each of the trails and at each backcountry campground encountered along the hike. In total, we included 35 sites accessible by car and 133 that were hike-in-only; 31 sites had anthropogenic food subsidies, and 137 did not have food available. Approximately half of vehicle-accessible sites had food subsidy available ($n = 17$). Most hike-in sites did not have human-subsidized food available ($n = 119$), but food subsidy was available at hike-in campgrounds ($n = 14$).

We intended to survey sites in areas of high human use and areas that provided human food subsidy to capture corvid presence in human-altered landscapes. Therefore, at campgrounds, administrative areas, and visitor centers, survey sites were located at the approximate center of the human use area. Likewise, along roads, we conducted point counts in pullouts or parking areas. We conducted surveys along low-human-use trail corridors to measure corvid presence and abundance in areas minimally affected by human recreational intrusion on otherwise natural landscapes. Additionally, linearity of the visual field can bias detectability during surveys, and the forested trail corridors were characterized by linear vegetation. Thus, to remove the influence of the trail corridor on visual corvid detections, we surveyed forested trail sites at a random distance (10–50 m) and right-angle direction off the trail. Observers remained within sight of the trail corridor, however, so that counts of visitors were not influenced. We separated all survey sites by ≥500 m and assumed that sites were independent (i.e. corvids detected at a site were not detected at any other site).

During each visit to a survey site, we conducted one 20-min point count, during which we recorded all corvids detected visually or audibly, following standard point-count techniques (Ralph et al. 1993, 1995). We conducted surveys on days with only light wind (<19 kph) and no more than light precipitation (National Oceanic and Atmospheric Administration 1995), between sunrise and

TABLE 1. Point-count, site, and landscape-scale variables included in analyses of detection and habitat use by 4 corvid species in Mount Rainier National Park, Washington, USA, 2009–2010.

Variable	Definition
Point-count features [a]	
Cloud Cover	Percentage of cloud cover in visible sky at beginning of point count: 0–100%
Noise	Measure of noise level at beginning of point count: 1 (no noise), 2 (gentle babbling brook noise), 3 (babbling creek noise), 4 (rushing creek and river noise)
Observer	1 of 3 observers: MW, LS, and JS
Precipitation	Presence of precipitation during $\geq$5 min (25%) of point count: no rain or light rain
Time after Sunrise	Time elapsed between sunrise and the start of point count, number of minutes converted to decimal fraction of a day
Wind	Measure of wind level at beginning of point count, Beaufort scale (0–6); wind levels 0 and 1 and levels 3 and greater aggregated for analyses
Site features	
Average Visitors	Average number of visitors observed across all visits to site
Canopy Cover [b]	Canopy cover directly above survey site: <11%, 11–40%, 41–70%, 71–100%; estimated using a moosehorn
Elevation	Elevation at survey site (m)
Food	Availability of anthropogenic food at site: with picnic tables, trash cans, and/or campsites or without facilities
Forest Structure [b]	Description of general forest structure within 50 m: very complex (VC; 2 or more canopy layers and multiple openings), complex (C; 1 or 2 canopy layers with few openings), simple (S; 1 canopy layer and no openings or meadow habitat with few or no trees) (Luginbuhl et al. 2001)
Zone Type	As defined by 2001 General Management Plan: backcountry camp, backcountry trail, or day use
Landscape metrics	
Distance to Camp	Distance to nearest campground (m)
Distance to Whitebark Pine [c]	Distance to nearest stand of whitebark pine (m); location of stands based on shapefile provided by National Park Service
Edge Density (2 km)	Contrast-weighted density of important edges within 2-km radius of survey site (m ha^{-1}): forest-developed edge weight = 1, forest-meadow edge weight = 0.5, other = 0
Edge Density (5 km)	Contrast-weighted density of important edges within 5-km radius of survey site (m ha^{-1}); weights described above
Patch Richness (2 km)	Number of different types of landcover patches within 2 km
Patch Richness (5 km)	Number of different types of landcover patches within 5 km
Percent Forest (2 km)	Percentage of forest landcover within 2-km radius of survey site
Percent Forest (5 km)	Percentage of forest landcover within 5-km radius of survey site
Road Edge (2 km) [d]	2 × length of road within 2 km of survey site (m)
Road Edge (5 km) [d]	2 × length of road within 5 km of survey site (m)

[a] Point-count features were only used to model detection.
[b] Canopy cover and structure were used to model detection in addition to use.
[c] Distance to whitebark pine was used only in Clark's Nutcracker analyses.
[d] Length of road edge was used only in Common Raven analyses.

early afternoon (the time of day when corvids are most active; Luginbuhl et al. 2001). Across 2 field seasons, 3 observers conducted all corvid surveys and each observer surveyed the majority of the sites at least once.

Variable field conditions during wildlife surveys can create differences in detectability between both survey sites and point counts (Rosenstock et al. 2002, and references therein). Bird, and specifically corvid, detection may vary by wind, ambient noise, precipitation, time after sunrise, and light intensity (Anderson and Ohmart 1977, Luginbuhl et al. 2001, Donnelly and Marzluff 2006). Therefore, during each point count, we noted the observer and recorded the percentage of cloud cover, the level of noise and wind, the presence of precipitation, and the start time (used to calculate the time after sunrise); at each survey site, we also measured canopy cover using a moosehorn and noted the structure of the surrounding forest (Table 1).

To help assess the relationship between corvid distribution and habitat use, we measured numerous recreation and landscape variables during each of our surveys. We counted the number of visitors observed within 100 m of the survey site during each point count (Table 1); we did not count vehicles. We measured the elevation of each survey site and classified each site by zone type, a classification of the type of visitor use (Table 1) based on designations outlined in Mount Rainier National Park's 2001 General Management Plan. Using ArcGIS version 9.3.0 (ESRI, Redlands, California, USA), we measured the distance from each survey site to the nearest campground and the nearest stand of whitebark pine (Table 1). We used the distance to whitebark pine only in the analyses of Clark's Nutcracker observations. We used the NPScape 2001 landcover dataset (Homer et al. 2004, National Park Service 2010), which classified landcover in Mount Rainier National Park by 30-m cells, to represent the landcover patterns surrounding each survey site within buffer areas of 2-km and 5-km radii. Corvid home-range sizes may vary across habitats and between wild and developed areas (Marzluff and Neatherlin 2006), and these buffer areas encompass the average home-range sizes of the targeted corvid species (Marzluff and Neatherlin 2006, Lorenz and Sullivan 2009, Strickland and Ouellet 2011). Using FRAGSTATS version 3.3 (see Acknowledgments) and the landcover dataset, we calculated landscape metrics within each buffer area for each survey site, including contrast-weighted edge density, patch richness, percent forest, length of road edge, Shannon's diversity index, and contagion. We chose these metrics 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 (Marzluff et al. 2000, 2004, Vigallon and Marzluff 2005b). For contrast-weighted edge density, edges between forest and developed land received a weight of 1.0, edges between forest and meadow–shrub received a weight of 0.5, and all other landcover edges received a zero weight. 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: $r^2 > 0.93$, $P < 0.001$); thus, we included only contrast-weighted edge density, patch richness, percent forest, and length of road edge in our final analyses (Table 1). We used length of road edge only in the analyses of Common Raven observations.

Analyses

We used PRESENCE to model occupancy, while allowing for varying detectability, and to predict site-specific occupancy values for each corvid species (MacKenzie et al. 2006). Because some birds may disperse between sites, there is a potential lack of closure across our surveys; therefore, we interpret our model results as reflecting corvid use rather than occupancy (MacKenzie et al. 2006). We scaled values of some variables to avoid numerical convergence issues with the logit link function in PRESENCE. We converted percent forest and cloud cover to proportions and expressed elevation and distance measurements in kilometers, with the exception of length of road edge, which we scaled to hundreds of kilometers. We divided values for average number of visitors and patch richness by 10. To evaluate variables for multicollinearity, we calculated variance inflation factors using the HH package in R version 3.1.1 (R Core Development Team, Vienna, Austria; Heiberger 2015). We found limited evidence of multicollinearity (no variance inflation factors were >10; Belsley et al. 1980) and did not exclude any variables from further analyses.

For all PRESENCE analyses, we used Akaike's Information Criterion, corrected for small sample size (AIC_c; Akaike 1974), to rank models and identify the most parsimonious model that best explained the data collected for each species (Burnham and Anderson 1998, Arnold 2010). We considered a model to be competitive if its ΔAIC_c with respect to the top model was <2 (Burnham and Anderson 1998, 2002). We calculated model weights (w_i) and evidence ratios, comparing the most parsimonious model with others in each dataset. We used odds ratios (ORs) to examine the effect of beta parameters in competitive models. We calculated ORs using the equation $\text{OR} = e^{\beta}$, and 95% confidence intervals (CIs) using the equation $\text{CI} = e^{\beta \pm 2^{*}\text{SE}\beta}$ (MacKenzie et al. 2006). For continuous variables, ORs >1 indicate a positive association between corvid use and covariate value, and ORs <1 indicate a negative association (MacKenzie et al. 2006). When a categorical covariate has an OR between zero and 1, birds are less likely to use areas representative of that covariate compared to the covariate indicated by the intercept parameter (MacKenzie et al. 2006). Categorical covariates with an OR >1 are positively associated with corvid use compared to the intercept state.

Detection. Before investigating patterns of corvid landscape use, we determined a detection model for each species. Using AIC_c and a null occupancy model, we compared models incorporating all possible combinations of 8 detection variables: observer, cloud cover, wind, noise, canopy cover, forest structure, precipitation, and time after sunrise (Table 1). We chose the single best detection model to proceed with occupancy modeling for each species.

Year. In our investigation of corvid use, we first tested for the significance of survey year in explaining the distribution of corvids at 59 sites surveyed in both seasons. We compared 2 models: a null model with no explanatory use variables and a model considering only year. For each species, the null model was the most parsimonious (Steller's Jay: $w_i = 0.82$; Gray Jay: $w_i = 0.84$; Common Raven: $w_{\text{i}} = 0.82$; Clark's Nutcracker: $w_i = 0.80$). Thus, in all subsequent analyses, we did not consider the effect of year on corvid landscape use.

Extent. We analyzed whether landscape metrics at the 2-km or the 5-km extent best explained patterns of corvid use. For each of the 4 species, we compared 3 models: a null model with no explanatory variables; a model that considered contrast-weighted edge density, percent forest, and patch richness within 2 km; and a model that considered the metrics within 5 km (Table 1). We then used the spatial extent (2 or 5 km) indicated by the most parsimonious model in further analyses of each species.

Variable selection. We reduced the number of variables by considering 3 model sets designed to test explicit hypotheses (natural landscape features, aspects of recreation, and food availability) and then evaluated the evidence for variables within each model set using forward model selection. We included all variables identified in competitive models of each set in a single comprehensive analysis of corvid use (for similar methods, see Coates et al. 2014).

Model set 1: Vegetation and natural landscape features. We tested the hypothesis that the use of each species responds to vegetation and natural landscape features by comparing the null model to those including canopy cover, forest structure, and elevation as well as contrast-weighted edge density, percent forest, and patch richness within the appropriate spatial extent for each species (Table 1). For Clark's Nutcracker analyses, we additionally considered the distance to the nearest whitebark pine stand.

Model set 2: Recreation. We tested the hypothesis that corvid use increases in proximity to recreational activity by comparing the null model to models combining 3 explanatory variables: average number of visitors, the park administrative zone type (backcountry camp, backcountry trail, or day use), and the distance to the nearest campground (Table 1). For Common Raven analyses, we also considered the length of road edge within the appropriate spatial extent.

Model set 3: Food subsidy. We tested the hypothesis that corvid use increases in proximity to anthropogenic food by comparing the null model to a model considering food availability (Table 1). We considered food to be available at sites where picnic tables and/or trash cans were present.

Use within the national park. To describe the environments inhabited by each corvid, we used forward model selection to relate use to landscape, recreation, and food-availability variables previously identified as important (see above). For species for which anthropogenic food availability was important in explaining overall distribution patterns, we additionally compared models that included interactions between food and each landscape variable important to that species.

Spatial Autocorrelation

Although we assumed that our sites were independent, spatial autocorrelation (Legendre 1993) was a potential limitation of our survey design because some of our sites were separated by only 500 m while some of our habitat variables considered areas up to 5 km surrounding each site. To assess the degree of spatial autocorrelation, we calculated residuals for each site as the observed presence value (presence = 1, absence = 0; presence indicates that the species was detected during $\geq$1 visit to the site over the 2 study years) minus the probability of detecting the species at least once as predicted by the top occupancy model for each species (for detailed residual equations, see Moore and Swihart 2005). For each species, we then used correlograms to calculate Moran's I (in R version 2.15.1; http://www.r-project.org) for residuals across a number of distance categories (Cliff and Ord 1981, Moore and Swihart 2005); we chose distance categories of 1,000 m because this was twice the minimum separation distance between sites.

RESULTS

We detected Steller's Jays, Gray Jays, and Common Ravens at approximately half of the total 168 survey sites (Steller's Jay: $n = 81$; Gray Jay: $n = 89$; Common Raven: $n = 89$). We observed Steller's Jays ($n = 413$) most often and had 395 and 273 observations of Gray Jays and Common Ravens, respectively. We observed 176 Clark's Nutcrackers at only 28 different survey sites. We had no detections of American Crow (*Corvus brachyrhynchos*), the only other corvid native to the region.

Spatial Autocorrelation

We found no evidence of consistent spatial autocorrelation in the residual values for any of the 4 study species, based on Moran's I (see Appendix Figure 2). Therefore, we present results for all species without further consideration of spatial autocorrelation.

Occupancy Modeling: Identifying Patterns in Corvid Use Detection

Several variables proved important for corvid detection in general (Table 2), and these occurred in top models as well as in competitive models (see Appendix Table 5). Forest structure and canopy cover were important for detection of all species except Common Raven. Noise was an important variable for all species except Clark's Nutcracker. Cloud cover and precipitation were not included in the most parsimonious detection model for any species. The odds of detecting a Steller's Jay was greater in complex (OR = 2.48; Table 2) or very complex forests (OR = 1.49) compared to simply structured forests, and detection was most likely during counts with at least some noise (OR $\geq$ 1.01) compared to very quiet counts. Steller's Jay detection was 105% more likely in forests with moderate canopy cover (OR = 2.05) and 57% more likely with high canopy cover (OR = 1.57) compared to forests with no canopy cover. The odds of detecting Gray Jays in complex (OR = 5.45E–10) or very complex forests (OR = 9.74E–10) were much less than in simply structured forests, and the likelihood of detection increased in forests with at least some canopy cover (OR $\geq$ 9.87E+08) compared to open sites with little or no canopy

TABLE 2. Landscape attributes associated with detection of 4 corvid species in Mount Rainier National Park, Washington, USA, 2009–2010. Only the results from the top model are shown, although there were several competitive models for each species (Steller's Jay: 6 competitive models; Gray Jay: 3 models; Common Raven: 3 models; Clark's Nutcrackers: 4 models). Full specifications of all competitive models for each species are provided in Appendix Table 5. The parameter estimates (β values) are untransformed logit values of variables, w_i is the weight of the top model, and OR is the odds ratio of the parameter estimate. The confidence intervals (CI) are the 95% confidence limits of the odds ratio.

Species	w_i	Variable	β	SE	OR	CI
Steller's Jay	0.16	Intercept	−2.09	0.31	0.12	0.07, 0.23
		Canopy Cover (71–100%)	0.45	1.12	1.57	0.17, 14.73
		Canopy Cover (41–70%)	0.72	1.11	2.05	0.22, 18.92
		Canopy Cover (11–40%)	−0.17	1.14	0.84	0.09, 8.25
		Forest Structure (Very Complex)	0.4	1.13	1.49	0.16, 14.30
		Forest Structure (Complex)	0.91	1.16	2.48	0.24, 25.28
		Noise (Level 2)	0.44	0.19	1.55	1.06, 2.27
		Noise (Level 3)	0.01	0.22	1.01	0.65, 1.57
		Noise (Level 4)	0.4	0.33	1.49	0.77, 2.89
Gray Jay	0.32	Intercept	−0.45	0.24	0.64	0.39, 1.03
		Noise (Level 2)	−0.28	0.19	0.76	0.52, 1.11
		Noise (Level 3)	−1.1	0.25	0.33	0.20, 0.55
		Noise (Level 4)	−1.98	0.48	0.14	0.05, 0.36
		Observer 1	−0.74	0.32	0.48	0.25, 0.90
		Observer 2	−0.84	0.2	0.43	0.29, 0.64
		Forest Structure (Very Complex)	−20.75	1.51	9.74E−10	4.75E−11, 2.00E−08
		Forest Structure (Complex)	−21.33	1.53	5.45E−10	2.56E−11, 1.16E−08
		Canopy Cover (71–100%)	20.87	1.52	1.16E+09	5.54E+07, 2.42E+10
		Canopy Cover (41–70%)	21.4	1.51	1.97E+09	9.601E+07, 4.03E+10
		Canopy Cover (11–40%)	20.71	1.54	9.87E+08	4.54E+07, 2.15E+10
Common Raven	0.31	Intercept	−1.76	0.31	0.17	0.09, 0.32
		Noise (Level 2)	0.12	0.19	1.13	0.77, 1.65
		Noise (Level 3)	−0.7	0.25	0.50	0.30, 0.82
		Noise (Level 4)	−1.66	0.55	0.19	0.06, 0.57
		Observer 1	−0.43	0.4	0.65	0.29, 1.45
		Observer 2	0.64	0.25	1.90	1.15, 3.13
		Time after Sunrise	−3.67	1.15	0.03	0.003, 0.25
		Wind (Level 2)	0.55	0.2	1.73	1.16, 2.59
		Wind (Level 3)	0.47	0.33	1.60	0.83, 3.10
Clark's Nutcracker	0.21	Intercept	−1.19	0.32	0.30	0.16, 0.58
		Forest Structure (Very Complex)	25	2.26	7.20E+10	7.84E+08, 6.61E+12
		Forest Structure (Complex)	21.74	2.51	2.76E+09	1.83E+07, 4.19E+11
		Canopy Cover (71–100%)	−23.03	2.47	9.96E−11	7.12E−13, 1.39E−08
		Canopy Cover (41–70%)	−24.44	2.26	2.43E−11	2.65E−13, 2.23E−09
		Canopy Cover (11–40%)	−25.33	2.33	9.98E−12	9.45E−14, 1.05E−09
		Time after Sunrise	2.89	1.89	17.99	0.41, 788.40

cover. Detection of Gray Jays was most likely during relatively quiet counts compared to counts with at least moderate noise (OR $\leq$ 0.76). The odds of Common Raven detection improved in breezy (OR = 1.73) or windy conditions (OR = 1.60) compared to still conditions and declined with time after sunrise (OR = 0.03). The odds of Common Raven detection also changed between observers; observer 2 was 90% more likely to detect Common Ravens (OR = 1.90) than observer 3. For Clark's Nutcrackers, detection odds were much greater in complex (OR = 2.76E+09) and very complexly structured forests (OR = 7.20E+10) than in simple forests. Detection of Clark's Nutcrackers was much less likely, however, in forests with greater amounts of canopy cover (OR $<$ 2.43E–11) than in areas with little or no canopy cover. Contrary to the pattern observed in Common Ravens, the odds of Clark's Nutcracker detection improved with time after sunrise (OR = 17.99).

Extent

For each study species, 1 spatial extent was clearly best for explaining patterns of corvid use (see Appendix Table 6). For both jays, landscape metrics with a buffer extent of 5 km comprised the most parsimonious model (Steller's Jay: $w_i = 1.00$; Gray Jay: $w_i = 0.87$). For Common Ravens and Clark's Nutcrackers, a model considering a 2-km extent was most parsimonious (Common Raven: $w_i = 1.00$; Clark's Nutcracker: $w_i = 1.00$).

TABLE 3. Vegetation and landscape features, recreation, and food availability associated with habitat use of 4 corvid species in Mount Rainier National Park, Washington, USA, 2009–2010. Full specifications of all competitive models for each species are provided in Appendix Tables 7–9.

Species	Model set	Variables in competitive models
Steller's Jay	Landscape	Edge Density (5 km),[a] Elevation,[a] Patch Richness (5 km),[a] Canopy Cover, Percent Forest (5 km)
	Recreation	Zone Type,[a] Average Number of Visitors,[a] Distance to Campground
	Food	Food Availability
Gray Jay	Landscape	Elevation,[a] Forest Structure, Patch Richness (5 km), Percent Forest (5 km)
	Recreation	Zone Type,[a] Average Number of Visitors,[a] Distance to Campground
	Food	Food Availability
Common Raven	Landscape	Edge Density (2 km),[a] Percent Forest (2 km),[a] Forest Structure
	Recreation	Road Length (2 km),[a] Average Number of Visitors,[a] Distance to Campground,[a] Zone Type
	Food	Food Availability [a]
Clark's Nutcracker	Landscape	Distance to Whitebark Pine,[a] Edge Density (2 km),[a] Forest Structure,[a] Elevation,[a] Patch Richness (2 km) [a]
	Recreation	Average Number of Visitors,[a] Zone Type [a]
	Food	Food Availability [a]

[a] Variable included in the top model.

Independent Effects of Landscape Features, Recreation, and Food

Within each model set, each corvid responded to distinct natural and anthropogenic aspects of the montane environment (Table 3; for details on all competitive models, see Appendix Tables 7–9). However, as with detection, we found several features in each category to be important across several species.

We first related corvid use to natural landscape features, independent of recreation or food availability, and found that at least 1 corvid responded to each landscape feature we considered (Table 3; Appendix Table 7). Steller's Jays, Common Ravens, and Clark's Nutcrackers were more likely to use areas with frequent nearby edges (Steller's Jay: OR = 2.09E+08; Common Raven: OR = 6.62E+35; Clark's Nutcracker: OR = 3.29), and the odds of the jays and Clark's Nutcrackers using an area improved with greater patch richness (Steller's Jay: OR = 6.72E+06; Gray Jay: OR = 2.49E+10; Clark's Nutcracker: OR = 5.26E+08). Jays and Common Ravens were most likely to use areas with high nearby percent forest cover (Steller's Jay: OR = 3.60; Gray Jay: OR = 10.59; Common Raven: OR = 1.91E+06), although, within these forests, the odds of Steller's Jay use decreased with elevation (OR = 0.15) and in areas with moderate (OR = 0.53) and high canopy cover (OR = 0.25). Common Ravens were less likely to use areas with complex (OR = 1.68E–04) or very complex forests (OR = 0.04) compared to simply structured forests, whereas the odds of Gray Jay and Clark's Nutcracker use was greatest at complexly structured sites (Gray Jay: OR = 22.00; Clark's Nutcracker: OR = 19.30) compared to simple forest structures. Both Gray Jays and Clark's Nutcrackers were more likely to use high elevations compared to low (Gray Jay: OR = 144.03; Clark's Nutcracker: OR = 0.05E+04). Finally, and as expected, the odds of Clark's Nutcrackers using an area decreased with distance from whitebark pine (OR = 0.52).

The presence of both jays and of Common Ravens depended on all 3 recreation variables when natural landscape features and food availability were not considered (Table 3; Appendix Table 8). The odds of Steller's Jay use was greatest in day-use (OR = 12.06) and trail zones (OR = 5.58) compared to backcountry zones, and their use increased with distance from campgrounds (OR = 1.28) and with greater numbers of visitors (OR = 3.59). The odds of Gray Jay use were greatest in trail zones (OR = 1.11) and least in day-use areas (OR = 0.18) compared to backcountry zones, and Gray Jays were 118% more likely to use areas with greater amounts of visitors (OR = 2.18). Common Ravens were most likely to use areas with abundant nearby roads (OR = 1.10E+19), but their odds of use decreased with the number of average visitors (OR = 0.05). Both Gray Jay and Common Raven use decreased with distance to the nearest campground (Gray Jay: OR = 0.83; Common Raven: OR = 0.55). Clark's Nutcrackers were less likely to use the day-use (OR = 0.16) or trail zones (OR = 0.52) compared to backcountry zones, and the odds of Clark's Nutcracker use increased with average visitor presence (OR = 2.92).

When assessed independently, food availability was within the competitive model sets of each species compared against the null model and improved upon the null model for both Common Ravens and Clark's Nutcrackers (Table 3; Appendix Table 9). All species were more likely to use areas where food subsidies were available (Steller's Jay: OR = 1.75; Gray Jay: OR = 1.62; Common Raven: OR = 21.33; Clark's Nutcrackers: OR = 3.35) compared to areas where subsidies were absent.

Combined Effects of Landscape, Recreation, and Food

The joint importance of natural landscape features and environmental aspects related to human recreation (as identified in Table 3) explained significant variation in the use of Mount Rainier National Park by all corvids. In general, corvids most often used sites of high visitor use, including campgrounds, roads, and edgy areas at low elevations (Table 4; for details on all competitive models,

TABLE 4. Top models describing corvid habitat use across all survey points, considering important landscape features, aspects of recreation, and food availability. Variables considered for each species (Table 3) were identified using a process outlined in the text and detailed in Appendix Tables 7–9. Only the results from the top model are shown, although there were several competitive models for each species (Steller's Jay: 5 competitive models; Gray Jay: 8 models; Common Raven: 2 models; Clark's Nutcrackers: 3 models). Full specifications of all competitive models for each species are provided in Appendix Table 10. Parameter estimates (β values) are untransformed logit values of variables, w_i is the weight of the top model, and OR is the odds ratio of the parameter estimate. Confidence limits (CL) are the 95% confidence limits of the odds ratio. For each species, all models additionally considered the top detection model identified in Table 2.

Species	w_i	Variable	β	SE	OR	CL
Steller's Jay	0.18	Intercept	−10.74	3.14	2.17E−05	4.06E−08, 0.01
		Edge Density (5 km) [a]	14.71	6.04	2.45E+06	13.87, 4.31
		Average Number of Visitors [a]	4.02	1.60	55.70	2.27, 1366.49
		Patch Richness (5 km) [a]	20.35	5.20	6.88E+08	2.10E+04, 2.26E+13
		Elevation [a]	−2.77	0.92	0.06	0.01, 0.39
		Canopy Cover (71–100%)	−2.21	0.89	0.11	0.02, 0.65
		Canopy Cover (41–70%)	−1.27	0.84	0.28	0.05, 1.51
		Canopy Cover (11–40%)	−0.34	1.04	0.71	0.09, 5.70
Gray Jay	0.14	Intercept	−11.15	3.47	1.44E−05	1.39E−08, 0.01
		Elevation [a]	9.64	2.95	1.54E+04	42.10, 5.61E+06
		Distance to Campground [a]	0.84	0.36	2.32	1.13, 4.76
		Food Availability	1.51	0.97	4.53	0.65, 31.50
Common Raven	0.27	Intercept	−21.72	12.92	3.69E−10	2.21E−21, 61.56
		Edge Density (2 km) [a]	59.15	30.71	4.88E+25	0.10, 2.31E+52
		Road Length (2 km) [a]	41.48	21.11	1.03E+18	0.48, 2.24E+36
		Percent Forest (2 km) [a]	15.63	10.59	6.14E+06	0.004, 9.69E+15
		Average Number of Visitors [a]	−4.13	2.96	0.02	4.32E−05, 5.99
		Food Availability	4.78	5.87	119.10	0.001, 1.49E+07
Clark's Nutcracker	0.43	Intercept	−2.85	2.13	0.06	0.001, 4.10
		Distance to Whitebark Pine [a]	−2.07	0.63	0.13	0.04, 0.44
		Edge Density (2 km) [a]	28.84	10.74	3.35E+12	1571.84, 7.14E+21
		Average Number of Visitors [a]	1.63	0.83	5.10	0.97, 26.84
		Forest Structure (Very Complex) [a]	−3.24	1.55	0.04	0.002, 0.87
		Forest Structure (Complex) [a]	1.76	1.81	5.81	0.16, 217.02
		Food Availability [a]	4.29	1.93	72.97	1.54, 3463.38

[a] Variable included in all competitive models.

see Appendix Table 10). Gray Jays, Common Ravens, and Clark's Nutcrackers also used areas where food subsidy was available, even after we controlled for natural habitat associations.

The odds of a Steller's Jay using a location decreased with elevation (OR = 0.06) and increased with the amount of nearby edge (OR = 2.45E+06), patch richness of the surrounding landscape (OR = 6.88E+08), and average visitor presence (OR = 55.70; Table 4). Steller's Jays were also less likely to use areas with at least some canopy cover (OR ≤ 0.71) compared to areas of little or no canopy cover. By contrast, Gray Jays utilized high-elevation areas (OR = 1.54E+04), and the odds of use increased with the availability of anthropogenic food (OR = 4.53). Gray Jay use also increased with distance to the nearest campground (OR = 2.32). Common Raven use was associated with fragmented forests, and the odds of Common Raven use increased with greater nearby edge density (OR = 4.88E+25), road length (OR = 1.03E+18), and percent forest cover (OR = 6.14E+06). Common Ravens were also more likely to use areas with anthropogenic food subsidies (OR = 119.10), but, conversely, the odds of use decreased with average visitor presence (OR = 0.02). Clark's Nutcrackers also used fragmented forests with high nearby edge density (OR = 3.35E+12), and they were more likely to use complexly structured forests (OR = 5.81) than simply structured forests. The odds of use by Clark's Nutcrackers decreased with distance from stands of whitebark pine (OR = 0.13) but increased with both visitor presence (OR = 5.10) and the availability of anthropogenic food (OR = 72.97). Clark's Nutcrackers were the only corvid species for which food was included in all competitive models.

Based on the inclusion of anthropogenic food in the comprehensive model for Gray Jays, Common Ravens, and Clark's Nutcrackers, we investigated the importance of the interaction between food and vegetation variables. Models considering these interactions were not competitive, however, and food availability and natural landscape features did not interact to affect the use patterns of any species (we also evaluated the differences in raw variables at occupied sites with and without food, using a frequentist approach; see Appendix Table 11).

DISCUSSION

Recreational activity and infrastructure were important to the distribution of all 4 corvid species that regularly occur in Mount Rainier National Park. Particularly, Gray Jays, Common Ravens, and Clark's Nutcrackers use areas where anthropogenic food resources are available. Consequences of wilderness recreation and ecotourism, including increased human presence and food availability, are among the leading causes of species endangerment (Czech and Krausman 1997). For adaptable and relatively common species like corvids, recreation in wilderness areas may affect their distribution, which in turn may affect important ecosystem functions.

Patterns of Corvid Distribution

Variation in the relationship between recreation and corvid distribution likely stems from species-specific life history traits and behaviors. Flexible foraging strategies may enable some species to utilize areas of high visitor use and change their use of other landscape features in areas of food subsidy (Knight and Kawashima 1993, Knight et al. 1995, Marzluff and Neatherlin 2006). Additionally, species that naturally use vegetative features similar to those created by human development (e.g., use of edges by Steller's Jays; Sieving and Willson 1998, Brand and George 2001) may be more likely to use developed areas with high visitor use in wildland preserves such as Mount Rainier (Kluza et al. 2000). Alternatively, forest interior species such as Gray Jays utilize contiguous habitat (Raphael et al. 2002), which may help account for the lack of association on Mount Rainier between Gray Jays and landscape features heavily affected by recreation, despite their reputation as "camp robbers."

Home-range size may also affect the variables associated with each species' use of landscape features. Although we expected the presence of corvids with smaller home ranges to be correlated with landscape features at the smaller, 2-km scale, we found the opposite. Common Raven, the species with the largest home range, responded to the smaller landscape scale. This result matched previous observations in the Redwood National and State Parks, California, USA, where Common Raven home ranges were never >2 km from a road or other feature of recreational infrastructure (Scarpignato and George 2013). Likewise, although the jays have relatively small home ranges, these species responded to the broader landscape scale. We are unsure how to explain this result, although it is possible that we captured a population-level effect for the smaller species, but trends more representative of individual birds for the larger corvids.

Although we did not look directly at patterns of corvid density in the present study, we did observe Clark's Nutcrackers traveling in large flocks (>10 birds) during 2 surveys of areas without food subsidies. We did not observe this behavior in areas where anthropogenic food was available. Vander Wall and Balda (1977) also observed Clark's Nutcrackers flocking as the birds harvested seeds in the San Francisco Peaks during the nonbreeding season. If Clark's Nutcrackers flock during seed harvesting to increase the efficiency of seed collection (Vander Wall and Balda 1977), this could explain our observations at sites that both meet traditional Clark's Nutcracker summer habitat requirements (open, high-elevation forests near stands of whitebark pine; Tomback 1998) as well as provide anthropogenic food subsidy, where foraging by Clark's Nutcrackers may be less focused on pine seeds. However, we made relatively fewer observations of Clark's Nutcrackers than of the other corvid species; further study with more observations, as well as direct analyses of density patterns, will likely elucidate a clearer relationship. Additionally, Clark's Nutcrackers collect and cache pine seeds mostly in the late summer and fall (Vander Wall and Balda 1977), and, thus, future Clark's Nutcracker surveys should consider season as a potentially important variable in explaining Clark's Nutcracker distribution.

Measuring Occupancy or Density

Here, we report the results of occupancy analyses alone in explaining patterns of corvid distribution in Mount Rainier National Park. However, anecdotal observations (see above) and previous work on Common Raven (Bui et al. 2010) suggest that research should consider the specific behavioral traits of targeted species (food specialization, territoriality, juvenile flocking, etc.) when designing surveys to measure either occupancy or density (or both). The distribution and abundance of territorial species, such as Steller's Jays, is likely to be fairly consistent, and either occupancy or density alone may adequately describe the species' use of landscape features. For flocking (e.g., Clark's Nutcrackers) or wide-ranging (e.g., Common Raven) species, however, occupancy and density may reveal different patterns in landscape use. This was not the case in our study area (Seckel 2011). Density and occupancy estimates were closely correlated for Steller's Jays, Gray Jays, and Clark's Nutcrackers (Seckel 2011). Although Common Ravens on Mount Rainier displayed only a weak correlation between occupancy and density estimates, variables important to Common Raven abundance were similar to those identified here: Density increased at sites near road edges, with high levels of visitor use, and with food subsidy (Seckel 2011).

Changing Use of the Landscape

Although we observed corvids using human-influenced landscape features as well as areas with anthropogenic food resources, we did not observe any changes in their use of natural landscape features in response to food availability. This suggests that the level of food provisioning in Mount Rainier National Park remains low enough to sustain natural habitat associations for this group of species. However, the use of areas with recreational development may affect the performance of ecosystem services by corvids.

In Mount Rainier National Park, Steller's Jays are generalist predators that use areas of fragmented forest landscapes with nearby edges and high visitor presence. Although we did not find that food subsidy specifically was important to Steller's Jays, this species uses areas likely to have the most visitor traffic and, thus, likely to have abundant supplemental food resources. Our observations are generally consistent with previous studies in a similar habitat in Olympic National Park, Washington, USA, where Steller's Jays used forest edges, especially along campgrounds and other areas of human development and where Common Ravens foraged at greater densities at campgrounds (Marzluff et al. 2004, Marzluff and Neatherlin 2006). Similarly, campgrounds in the Redwood National and State Parks affected space use by Steller's Jays during the breeding season (Goldenberg 2013). Although the home ranges of Steller's Jays at campground and non-campground sites were equivalent in size, home ranges overlapped more at campgrounds, which suggests that they are able to live and breed at higher densities in these areas. Although we do not present direct evidence of changes in predation levels near human-use areas, Steller's Jays shift their landscape use in response to recreational infrastructure and anthropogenic food provisioning, which suggests that localized increases in predation near human-use areas may occur.

Common Ravens use edgy areas with nearby roads on Mount Rainier and in other wilderness areas (Marzluff et al. 2004, Marzluff and Neatherlin 2006, Scarpignato and George 2013). Previous studies found that Common Ravens are drawn to roads, in particular, for the easy foraging opportunities for carrion (Knight and Kawashima 1993, Knight et al. 1995). Thus, roads provide an indirect anthropogenic food subsidy to Common Ravens and other carrion eaters (i.e. vultures). Similar patterns were observed in Olympic National Park, where Common Ravens also used forest edges, particularly along campgrounds (Marzluff et al. 2004, Marzluff and Neatherlin 2006), and in the Redwood park system, where Common Ravens used edgy roaded areas (Scarpignato and George 2013). In fact, Common Raven home ranges in California never extended beyond 2 km away from a road (Scarpignato and George 2013), though this was not the case on the Olympic Peninsula (Marzluff and Neatherlin 2006, Webb et al. 2012). Notably, although Common Raven home ranges rarely overlapped, they did so most at areas with anthropogenic food resources. Roads and other human-supplied food resources may draw Common Ravens away from contiguous forest patches and reduce carrion removal in less disturbed areas.

On Mount Rainier, Gray Jays (generalists that, like Common Ravens, may forage on carrion) use areas with food subsidy in high-elevation forests away from most recreational infrastructure. By contrast, Siberian Jays (*Perisoreus infaustus*, a close European relative of the Gray Jay) were more abundant near urban areas and campsites than in surrounding forests in Pallas-Yllästunturi National Park in Finland (Huhta and Sulkava 2014). Although we found that food subsidies were important for Gray Jays, there is no evidence that this species is shifting its use of landscape features in favor of greater food resources at lower elevations in areas with greater visitor impact. Instead, food availability may allow for localized increases in Gray Jay presence (e.g., near backcountry campgrounds), potentially increasing predation levels in these areas or reducing the jays' use of carrion farther from these sources of anthropogenic food subsidies.

Clark's Nutcrackers coevolved with large-seeded pines, including the whitebark pine in the Pacific Northwest (Lanner 1996), and it is not surprising that, in Mount Rainier National Park, Clark's Nutcrackers use areas near stands of whitebark pine. We also found, however, that Clark's Nutcrackers are associated with the presence of anthropogenic food subsidies, and we anecdotally observed Clark's Nutcrackers foraging on anthropogenic food refuse during point counts at some high-visitor-use sites. When in areas generally near whitebark pine stands, Clark's Nutcracker distribution may shift slightly to encompass areas with food subsidies, perhaps indicating a general need for Clark's Nutcrackers to forage more widely when anthropogenic foods are not available. This may increase the dispersal of the pine, but it may also increase the energetic demands on Clark's Nutcrackers. Although we found no evidence that food subsidies negatively affect the use of whitebark pine by Clark's Nutcrackers in Mount Rainier National Park, food subsidy may still be an important energy source for Clark's Nutcrackers in years with low seed crops. Because Clark's Nutcrackers, like many granivorous birds, respond to cone crop failures and seed shortages with emigration or irruption (Davis and Williams 1957, 1964, Bock and Lepthien 1976), food subsidy from visitors to Mount Rainier could help prevent localized population extinctions and lower the risk of mutualism disruption (McKinney et al. 2009). This may be especially relevant because persistent threats to whitebark pine trees and cone production, particularly white pine blister rust, are widespread in western North America and throughout the range of whitebark pine (Kendall and Keane 2001, Smith et al. 2008, Tomback and Achuff 2010).

Management Implications

Land managers of reserved public natural areas are challenged with both providing the public with recreational opportunities and preserving native landscapes for ecosystem function and service, a compromise legally mandated in the United States by the Wilderness Act of

1964 (Public Law 88–577). By monitoring patterns in the occupancy of synanthropic species, particularly corvids, managers can access a suite of useful bioindicators that are easy to measure, are responsive to human influence, and may reflect changes in important ecosystem functions. Changes in corvid distribution through time, or differences in corvid use in areas near and far from human impact, can be measured against a set threshold. For example, on Mount Rainier, Steller's Jays presently use lower-elevation edgy sites. An increase in Steller's Jay presence at backcountry campgrounds or along trails, typically in less fragmented higher-elevation habitats, could indicate an increase in visitor use or food provisioning in these areas and the crossing of a "visitor-impact threshold." In many cases, management may wish to take action to avoid exceeding set thresholds, including increased fines for direct food provisioning, implementation of wildlife-proof garbage cans, improved policing of backcountry "leave no trace" rules, and an increased effort to improve and increase both public awareness and visitors' sense of responsibility (e.g., outlining risks to wildlife and visitors in park newspapers or through presentations and visitor programs; Mount Rainier National Park has an excellent "Keep Wildlife Wild Day"). Alternatively, in some specific circumstances, food provisioning may help maintain otherwise threatened corvid populations. If local whitebark pine populations decline, targeted food subsidies may help maintain resident populations of Clark's Nutcrackers.

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APPENDIX

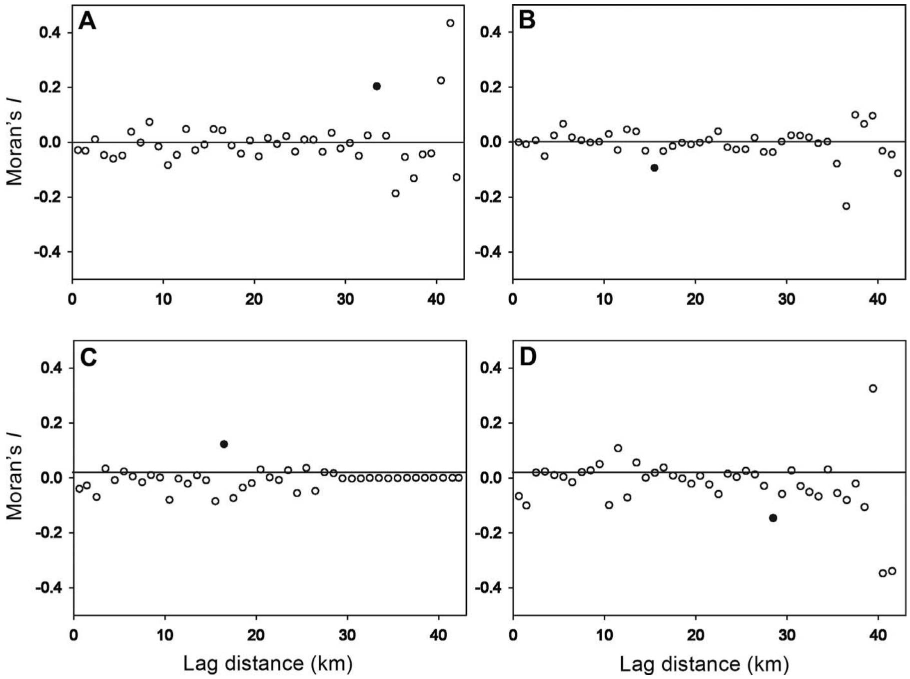

FIGURE 2. Moran's *I* correlograms of residuals from top models of corvid occupancy in Mount Rainier National Park, Washington, USA, 2009–2010. We calculated residuals for each site as the observed presence value (presence = 1, absence = 0) minus the probability of detecting the species at least once as predicted by the top occupancy model (for detailed residual equations, see Moore and Swihart 2005). For each species, we then calculated Moran's *I* in the program R for residuals across a number of distance categories (Cliff and Ord 1981, Moore and Swihart 2005). We chose distance categories of 1,000 m because this was twice the minimum separation distance between sites. Only 1 distance category for each species (filled circles) exhibited evidence of significant spatial autocorrelation (using a 2-sided test and an alpha level of 0.05).

TABLE 5. Landscape attributes associated with corvid detection across all survey points for (A) Steller's Jay, (B) Gray Jay, (C) Common Raven, and (D) Clark's Nutcracker in Mount Rainier National Park, Washington, USA, 2009–2010. Using PRESENCE, we evaluated the importance of 8 variables (Table 1) for corvid detection by comparing logit link models considering all potential variable combinations. The coefficients are untransformed logit values of variables in competitive ($\Delta AIC_c < 2$) detection models. Standard errors are shown in brackets following coefficients. w_i is the model weight, and ER is the evidence ratio.

ΔAIC_c	w_i	ER	Logit link detection models
(A) Steller's Jay competitive detection models.			
0.00 [a]	0.16	–	−2.09[0.31] + 0.45[1.12]*Canopy Cover (71–100%) + 0.72[1.11]*Canopy Cover (41–70%) − 0.17[1.14]*Canopy Cover (11–40%) + 0.40[1.13]*Forest Structure (Very Complex) + 0.91[1.16]*Forest Structure (Complex) + 0.44[0.19]*Noise (Level 2) + 0.01[0.22]*Noise (Level 3) + 0.40[0.33]*Noise (Level 4)
0.41	0.13	1.23	−1.91[0.29] + 0.63[1.11]*Canopy Cover (71–100%) + 0.83[1.10]*Canopy Cover (41–70%) − 0.05[1.13]*Canopy Cover (11–40%) + 0.30[1.13]*Forest Structure (Very Complex) + 0.76[1.15]*Forest Structure (Complex)
0.94	0.10	1.60	−1.95[0.33] + 0.46[1.12]*Canopy Cover (71–100%) + 0.73[1.11]*Canopy Cover (41–70%) − 0.16[1.14]*Canopy Cover (11–40%) + 0.38[1.14]*Forest Structure (Very Complex) + 0.90[1.16]*Forest Structure (Complex) + 0.46[0.19]*Noise (Level 2) + 0.04[0.23]*Noise (Level 3) + 0.43[0.33]*Noise (Level 4) − 1.19[1.02]*Time after Sunrise
1.24	0.09	1.86	−1.89[0.28] + 1.19[0.30]*Canopy Cover (71–100%) + 1.16[0.31]*Canopy Cover (41–70%) + 0.37[0.39]*Canopy Cover (11–40%)
1.29	0.08	1.91	−2.05[0.30] + 1.16[0.30]*Canopy Cover (71–100%) + 1.15[0.31]*Canopy Cover (41–70%) + 0.35[0.39]*Canopy Cover (11–40%) + 0.42[0.19]*Noise (Level 2) − 0.001[0.22]*Noise (Level 3) + 0.18[0.32]*Noise (Level 4)
1.62	0.07	2.25	−1.78[0.32] + 0.65[1.11]*Canopy Cover (71–100%) + 0.85[1.10]*Canopy Cover (41–70%) − 0.03[1.13]*Canopy Cover (11–40%) + 0.28[1.13]* Forest Structure (Very Complex) + 0.75[1.15]*Forest Structure (Complex) − 1.00[1.01]*Time after Sunrise
(B) Gray Jay competitive detection models			
0.00 [b]	0.32	–	−0.45[0.24] − 0.28[0.19]*Noise (Level 2) − 1.10[0.25]*Noise (Level 3) − 1.98[0.48]*Noise (Level 4) − 0.74[0.32]*Observer (MW) − 0.84[0.20]Observer (LS) − 20.75[1.51]*Forest Structure (Very Complex) − 21.33[1.53]*Forest Structure (Complex) + 20.87[1.52]*Canopy Cover (71–100%) + 21.40[1.51]*Canopy Cover (41–70%) + 20.71[1.54]*Canopy Cover (11–40%)
1.33	0.17	1.95	−0.32[0.27] − 0.27[0.19]*Noise (Level 2) − 1.09[0.25]*Noise (Level 3) − 1.97[0.48]*Noise (Level 4) − 0.73[0.32]*Observer (MW) − 0.82[0.20]Observer (LS) − 20.86[1.49]*Forest Structure (Very Complex) − 21.42[1.51]*Forest Structure (Complex) + 20.97[1.50]*Canopy Cover (71–100%) + 21.50[1.49]*Canopy Cover (41–70%) + 20.80[1.10]*Canopy Cover (11–40%) − 1.11[1.10]*Time after Sunrise
1.49	0.15	2.11	−0.38[0.26] − 0.29[0.19]*Noise (Level 2) − 1.10[0.25]*Noise (Level 3) − 1.96[0.48]*Noise (Level 4) − 0.76[0.32]*Observer (MW) − 0.85[0.20]Observer (LS) − 27.74[1.16]*Forest Structure (Very Complex) − 28.32[1.18]*Forest Structure (Complex) + 27.88[1.17]*Canopy Cover (71–100%) + 28.40[1.16]*Canopy Cover (41–70%) + 27.70[1.19]*Canopy Cover (11–40%) − 0.17[0.19]*Cloud Cover
(C) Common Raven competitive detection models			
0.00 [c]	0.31	–	−1.76[0.31] + 0.12[0.19]*Noise (Level 2) − 0.70[0.25]*Noise (Level 3) − 1.66[0.55]*Noise (Level 4) − 0.43[0.40]*Observer (MW) + 0.64[0.25]Observer (LS) − 3.67[1.15]*Time after Sunrise + 0.55[0.20]*Wind (Level 2) + 0.47[0.33]*Wind (Level 3)
1.05	0.19	1.69	−1.94[0.34] + 0.05[0.20]*Noise (Level 2) − 0.76[0.26]*Noise (Level 3) − 1.74[0.55]*Noise (Level 4) − 0.48[0.40]*Observer (MW) + 0.56[0.25]Observer (LS) − 3.66[1.14]*Time after Sunrise + 0.54[0.20]*Wind (Level 2) + 0.56[0.34]*Wind (Level 3) + 0.28[0.25]*Forest Structure (Very Complex) + 0.50[0.27]*Forest Structure (Complex)
1.62	0.14	2.25	−1.98[0.34] + 0.06[0.20]*Noise (Level 2) − 0.78[0.26]*Noise (Level 3) − 1.74[0.55]*Noise (Level 4) − 0.45[0.40]*Observer (MW) + 0.59[0.25]Observer (LS) − 3.66[1.14]*Time after Sunrise + 0.58[0.20]*Wind (Level 2) + 0.61[0.34]*Wind (Level 3) + 0.26[0.26]*Canopy Cover (71–100%) + 0.55[0.26]*Canopy Cover (41–70%) + 0.07[0.38]*Canopy Cover (11–40%)
(D) Clark's Nutcracker competitive detection models			
0.00 [d]	0.21	–	−1.19[0.32] + 25.00[2.26]*Forest Structure (Very Complex) + 21.74[2.51]*Forest Structure (Complex) − 23.03[2.47]*Canopy Cover (71–100%) − 24.44[2.26]*Canopy Cover (41–70%) − 25.33[2.33]*Canopy Cover (11–40%) + 2.89[1.89]*Time after Sunrise
0.16	0.20	1.09	−0.82[0.21] + 25.13[2.21]*Forest Structure (Very Complex) + 21.98[2.48]*Forest Structure (Complex) − 23.18[2.44]*Canopy Cover (71–100%) − 24.55[2.21]*Canopy Cover (41–70%) − 25.43[2.28]*Canopy Cover (11–40%)
1.73	0.09	2.37	−1.00[0.34] + 25.20[3.05]*Forest Structure (Very Complex) + 22.07[3.44]*Forest Structure (Complex) − 22.87[3.40]*Canopy Cover (71–100%) − 24.59[3.04]*Canopy Cover (41–70%) − 25.28[3.10]*Canopy Cover (11–40%) + 3.37[1.98]*Time after Sunrise − 0.66[0.43]*Noise (Level 2) − 0.84[0.43]*Noise (Level 3) − 0.33[1.23]*Noise (Level 4)

TABLE 5. Continued.

ΔAIC_c	w_i	ER	Logit link detection models
1.99	0.08	2.71	−1.26[0.35] + 36.88[1.59]*Forest Structure (Very Complex) + 33.61[1.95]*Forest Structure (Complex) − 34.93[1.90]*Canopy Cover (71–100%) − 36.35[1.58]*Canopy Cover (41–70%) − 37.25[1.69]*Canopy Cover (11–40%) + 2.93[1.89]*Time after Sunrise + 0.17[0.36]*Cloud Cover

[a] $AIC_c = 1{,}175.08$
[b] $AIC_c = 1{,}089.37$
[c] $AIC_c = 1{,}017.91$
[d] $AIC_c = 418.41$

TABLE 6. Influence of the extent of landscape variables on corvid habitat use across all survey points for (A) Steller's Jay, (B) Gray Jay, (C) Common Raven, and (D) Clark's Nutcracker in Mount Rainier National Park, Washington, USA, 2009–2010. Using PRESENCE, we evaluated the importance of contrast-weighted edge density, patch richness, and percent forest cover within radii of 2 km and 5 km on corvid occupancy by comparing occupancy models considering all 3 variables at each extent. The coefficients are untransformed logit values of variables in competitive ($\Delta AIC_c < 2$) use models. Standard errors are shown in brackets following coefficients. For each species, all models additionally considered the top detection model identified in Table 5. w_i is the model weight, and ER is the evidence ratio.

ΔAIC_c	w_i	ER	Logit link use models
(A) Steller's Jay competitive habitat-use models			
0.00 [a]	1.00	–	−13.89[2.76] + 22.33[5.27]*Contrast-weighted Edge Density within 5 km + 12.66[3.83]*Patch Richness within 5 km + 2.76[1.32]*Percent Forest Cover within 5 km
16.00	0.00	2,980.96	−3.39[1.46] + 5.26[2.69]*Contrast-weighted Edge Density within 2 km + 1.90[2.02]*Patch Richness within 2 km + 2.18[1.27]*Percent Forest Cover within 2 km
(B) Gray Jay competitive habitat-use models			
0.00 [b]	0.87	–	−12.46[0.56] − 24.75[8.49]*Contrast-weighted Edge Density within 5 km + 45.83*Patch Richness within 5 km − 9.99[3.59]*Percent Forest Cover within 5 km
3.80	0.13	6.69	3.55[2.89] − 6.96[4.12]*Contrast-weighted Edge Density within 2 km + 2.78[2.86]*Patch Richness within 2 km − 3.01[2.71]*Percent Forest Cover within 2 km
(C) Common Raven competitive habitat-use models [c]			
0.00 [d]	1.00	–	−21.17[11.12] + 86.41[56.97]*Contrast-weighted Edge Density within 2 km – 0.95[11.09]*Patch Richness within 2 km + 15.04[9.13]*Percent Forest Cover within 2 km
21.19	0.00	39,920.03	−12.12[16.56] + 58.80[74.88]*Contrast-weighted Edge Density within 5 km + 4.76[7.86]*Percent Forest Cover within 5 km
22.69	0.00	84,510.70	−4.02[5.39] + 29.77[15.98]*Contrast-weighted Edge Density within 5 km − 0.32[7.73]*Patch Richness within 5 km
23.26	0.00	112,420.32	−16.54 + 63.33*Contrast-weighted Edge Density within 2 km + 4.91*Patch Richness within 2 km + 5.74*Percent Forest Cover within 2 km
(D) Clark's Nutcracker competitive habitat-use models			
0.00 [e]	1.00	–	−2.60[1.74] + 5.14[3.20]*Contrast-weighted Edge Density within 2 km + 6.91[3.83]*Patch Richness within 2 km + −5.02[1.60]*Percent Forest Cover within 2 km
20.26	0.00	25,084.36	7.57[4.41] + 2.30[5.09]*Contrast-weighted Edge Density within 5 km + −12.20[6.80]*Patch Richness within 5 km + −3.05[1.36]*Percent Forest Cover within 5 km

[a] $AIC_c = 1{,}157.71$
[b] $AIC_c = 1{,}086.80$
[c] The model considering all 3 variables at the 5-km extent converged, but PRESENCE was unable to calculate standard error. Therefore, we also provide results from 2 models, one considering edge density and percent forest and the other considering edge density and patch richness.
[d] $AIC_c = 990.87$
[e] $AIC_c = 396.87$

TABLE 7. Vegetative and natural landscape attributes associated with corvid habitat use across all survey points for (A) Steller's Jay, (B) Gray Jay, (C) Common Raven, and (D) Clark's Nutcracker in Mount Rainier National Park, Washington, USA, 2009–2010. Using PRESENCE, we evaluated the importance of variables (Table 1) on corvid habitat use by comparing logit link models using forward model selection. The coefficients are untransformed logit values of variables in competitive ($\Delta AIC_c < 2$) use models. Standard errors are shown in brackets following coefficients. For each species, all models additionally considered the top detection model identified in Table 5. w_i is the model weight, and ER is the evidence ratio.

ΔAIC_c	w_i	ER	Logit link use models
(A) Steller's Jay competitive habitat-use models			
0.00 [a]	0.37	–	−10.67[2.73] + 19.16[5.51]*Contrast-weighted Edge Density within 5 km − 1.90[0.70]*Elevation + 15.72[4.57]*Patch Richness within 5 km
1.69	0.16	2.33	−9.76[2.88] + 19.88[5.77]*Contrast-weighted Edge Density within 5 km − 2.82[0.92]*Elevation + 17.12[4.79]*Patch Richness within 5 km − 1.39[0.75]*Canopy Cover (71–100%) − 0.64[0.70]*Canopy Cover (41–70%) + 0.20[0.95]*Canopy Cover (11–40%)
1.76	0.15	2.41	−12.82[2.96] + 20.30[5.51]*Contrast-weighted Edge Density within 5 km − 1.67[0.77]*Elevation + 16.86[4.36]*Patch Richness within 5 km + 1.28[1.46]* Percent Forest within 5 km
(B) Gray Jay competitive habitat-use models			
0.00 [b]	0.30	–	−4.55[1.71] + 4.97[1.80]*Elevation
0.30	0.26	1.16	−8.22[3.26] + 6.59[2.72]*Elevation + 1.65[1.61]*Forest Structure (Very Complex) + 3.09[1.82]*Forest Structure (Complex)
0.95	0.19	1.61	19.12[9.25] + 5.37[1.66]*Elevation + 23.94[14.74]*Patch Richness within 5 km
1.76	0.13	2.41	−6.79[3.63] + 5.29[2.14]*Elevation + 2.36[2.90]*Percent Forest within 5 km
(C) Common Raven competitive habitat-use models			
0.00 [c]	0.36	–	−20.73[10.29] + 82.48[45.31]*Contrast-weighted Edge Density within 2 km + 14.46[7.45]*Percent Forest within 2 km
0.19	0.33	1.10	−36.98[16.39] + 156.68[70.90]*Contrast-weighted Edge Density within 2 km + 29.48[13.18]*Percent Forest within 2 km − 3.15[3.44]*Forest Structure (Very Complex) − 8.69[5.47]*Forest Structure (Complex)
(D) Clark's Nutcracker competitive habitat-use models			
0.00 [d]	0.60	–	−23.59[21.18] − 0.65[0.26]*Distance to Whitebark Pine + 1.19[11.67]*Contrast-weighted Edge Density within 2 km − 0.63[1.35]*Forest Structure (Very Complex) + 2.96[2.09]*Forest Structure (Complex) + 9.26[8.58]*Elevation + 20.08[22.00]*Patch Richness within 2 km

[a] $AIC_c = 1{,}153.65$
[b] $AIC_c = 1{,}071.03$
[c] $AIC_c = 988.53$
[d] $AIC_c = 344.07$

TABLE 8. Local and landscape features shaped by human presence and recreation patterns and associated with corvid habitat use across all survey points for (A) Steller's Jay, (B) Gray Jay, (C) Common Raven, and (D) Clark's Nutcracker in Mount Rainier National Park, Washington, USA, 2009–2010. Using PRESENCE, we evaluated the importance of variables (Table 1) on corvid habitat use by comparing logit link models using forward model selection. The coefficients are untransformed logit values of variables in competitive ($\Delta AIC_c < 2$) use models. Standard errors are shown in brackets following coefficients. For each species, all models additionally considered the top detection model identified in Table 5. w_i is the model weight, and ER is the evidence ratio.

ΔAIC_c	w_i	ER	Logit link use models
(A) Steller's Jay competitive habitat-use models			
0.00 [a]	0.43	–	−1.95[0.81] + 2.49[0.92]*Zone (Day Use) + 1.72[0.83]*Zone (Trail Zone) + 3.59[1.99]*Average Number of Visitors
0.24	0.38	1.13	−2.03[0.81] + 1.95[0.98]*Zone (Day Use) + 1.34[0.87]*Zone (Trail Zone) + 3.83[1.98]*Average Number of Visitors + 0.25[0.18]*Distance to Campground
(B) Gray Jay competitive habitat-use models			
0.00 [b]	0.36	–	1.42[1.02] − 1.71[1.10]*Zone (Day Use) + 0.10[1.10]*Zone (Trail Zone) + 0.78[0.50]*Average Number of Visitors
1.09	0.21	1.72	1.52[1.05] − 1.27[1.11]*Zone (Day Use) + 0.10[1.13]*Zone (Trail Zone)
1.53	0.17	2.15	1.45[1.00] − 1.34[1.15]*Zone (Day Use) + 0.46[1.16]*Zone (Trail Zone) + 0.81[0.50]*Average Number of Visitors − 0.19[0.19]*Distance to Campground
(C) Common Raven competitive habitat-use models			
0.00 [c]	0.24	–	1.67[0.95] + 43.84[23.87]*Length of Road Edge within 2 km − 3.04[2.01]*Average Number of Visitors − 0.60[0.43]*Distance to Campground
0.04	0.24	1.02	0.67[0.43] + 28.68[16.70]*Length of Road Edge within 2 km − 2.02[1.47]*Average Number of Visitors
0.70	0.17	1.42	0.52[0.39] + 14.19[7.59]*Length of Road Edge within 2 km
1.60	0.11	2.23	22.15[2.98] + 27.88[17.05]*Length of Road Edge within 2 km − 2.14[1.59]*Average Number of Visitors − 20.82[4.80]*Zone (Day Use) − 21.73[2.98]*Zone (Trail Zone)
(D) Clark's Nutcracker competitive habitat-use models			
0.00 [d]	0.37	–	−0.84[0.63] + 1.07[0.44]*Average Number of Visitors − 1.82[0.88]*Zone (Day Use) − 0.65[0.68]*Zone (Trail Zone)
0.72	0.26	1.43	−1.60[0.25] + 0.61[0.32]*Average Number of Visitors

[a] $AIC_c = 1{,}156.76$
[b] $AIC_c = 1{,}086.69$
[c] $AIC_c = 1{,}009.26$
[d] $AIC_c = 415.76$

TABLE 9. Influence of food availability on corvid habitat use across all survey points for (A) Steller's Jay, (B) Gray Jay, (C) Common Raven, and (D) Clark's Nutcracker in Mount Rainier National Park, Washington, USA, 2009–2010. Using PRESENCE, we evaluated the importance of food availability on corvid habitat use by comparing a null model with one considering food availability. The coefficients are untransformed logit values of variables in competitive ($\Delta AIC_c < 2$) use models. Standard errors are shown in brackets following coefficients. For each species, all models additionally considered the top detection model identified in Table 5. w_i is the model weight, and ER is the evidence ratio.

ΔAIC_c	w_i	ER	Logit link use models
(A) Steller's Jay competitive habitat-use models			
0.00 [a]	0.63	–	0.38[0.20]
1.04	0.37	1.68	0.28[0.22] + 0.56[0.52]*Food Availability
(B) Gray Jay competitive habitat-use models			
0.00 [b]	0.71	–	1.11[0.29]
1.80	0.29	2.46	1.00[0.31] + 0.48[0.68]*Food Availability
(C) Common Raven competitive habitat-use models			
0.00 [c]	0.64	–	1.30[0.43] + 3.06[5.07]*Food Availability
1.11	0.36	1.74	1.73[0.51]
(D) Clark's Nutcracker competitive habitat-use models			
0.00 [d]	0.86	–	−1.69[0.26] + 1.21[0.49]*Food Availability

[a] $AIC_c = 1{,}175.08$
[b] $AIC_c = 1{,}089.37$
[c] $AIC_c = 1{,}016.80$
[d] $AIC_c = 414.76$

TABLE 10. Variables influencing corvid habitat use across all survey points, considering predetermined suites (see Tables 7–9) of landscape features, aspects of recreation, and food availability for (A) Steller's Jay, (B) Gray Jay, (C) Common Raven, and (D) Clark's Nutcracker in Mount Rainier National Park, Washington, USA, 2009–2010. Using PRESENCE, we evaluated the importance of predetermined variables (Tables 7–9) on corvid habitat use by comparing logit link models using forward model selection. The coefficients are untransformed logit values of variables in competitive (ΔAIC$_c$ < 2) use models. Standard errors are shown in brackets following coefficients. For each species, all models additionally considered the top detection model identified in Table 5. w_i is the model weight, and ER is the evidence ratio.

ΔAIC$_c$	w_i	ER	Logit link use models
(A) Steller's Jay competitive habitat-use models			
0.00 [a]	0.18	–	−10.74[3.14] + 14.71[6.04]*Contrast-weighted Edge Density within 5 km + 4.02[1.60]*Average Number of Visitors + 20.35[5.20]*Patch Richness within 5 km − 2.77[0.92]*Elevation − 2.21[0.89]*Canopy Cover (71–100%) − 1.27[0.84]*Canopy Cover (41–70%) − 0.34[1.04]*Canopy Cover (11–40%)
0.87	0.11	1.54	−12.84[3.25] + 14.34[6.21]*Contrast-weighted Edge Density within 5 km + 3.99[1.83]*Average Number of Visitors + 20.92[5.40]*Patch Richness within 5 km − 2.65[1.01]*Elevation − 2.08[0.91]*Canopy Cover (71–100%) + 0.98[0.87]*Canopy Cover (41–70%) − 0.30[1.08]*Canopy Cover (11–40%) + 1.63[1.06]*Zone (Day Use) + 1.70[0.89]*Zone (Trail Zone)
1.14	0.10	1.77	−14.29[3.24] + 15.75[5.92]*Contrast-weighted Edge Density within 5 km + 4.38[1.70]*Average Number of Visitors + 22.18[4.85]*Patch Richness within 5 km − 2.32[0.97]*Elevation − 2.22[0.91]Canopy Cover (71–100%) − 1.24[0.85]*Canopy Cover (41–70%) − 0.34[1.04]*Canopy Cover (11–40%) + 2.20[1.71]*Percent Forest within 5 km
1.66	0.08	2.29	−11.27[3.14] + 13.59[6.18]*Contrast-weighted Edge Density within 5 km + 4.09[1.61]*Average Number of Visitors + 20.48[5.20]*Patch Richness within 5 km − 2.56[0.97]*Elevation − 2.08[0.90]*Canopy Cover (71–100%) − 1.19[0.84]*Canopy Cover (41–70%) − 0.20[1.06]*Canopy Cover (11–40%) + 0.19[0.21]*Distance to Campground
1.70	0.08	2.34	−13.36[2.87] + 13.64[5.92]*Contrast-weighted Edge Density within 5 km + 3.14[1.78]*Average Number of Visitors + 17.66[4.75]*Patch Richness within 5 km − 1.49[0.80]*Elevation + 1.75[1.01]*Zone (Day Use) + 1.78[0.85]*Zone (Trail Zone)
(B) Gray Jay competitive habitat-use models			
0.00 [b]	0.14	–	−11.15[3.47] + 9.64[2.95]*Elevation + 0.84[0.36]*Distance to Campground + 1.51[0.97]*Food Availability
0.21	0.12	1.11	−10.06[3.17] + 9.05[2.83]*Elevation + 0.64[0.31]*Distance to Campground + 1.12[0.83]*Average Number of Visitors
0.35	0.11	1.19	−9.28[3.11] + 8.56[2.79]*Elevation + 0.64[0.32]*Distance to Campground
0.72	0.09	1.44	−18.24[6.15] + 11.55[3.29]*Elevation + 0.92[0.36]*Distance to Campground + 1.86[0.99]*Food Availability + 6.25[4.12]*Percent Forest within 5 km
1.17	0.08	1.80	−12.85[4.55] + 10.08[3.16]*Elevation + 0.64[0.34]*Distance to Campground + 1.63[1.93]*Forest Structure (Very Complex) + 3.09[2.11]*Forest Structure (Complex)
1.42	0.07	2.04	−28.62[4.74] + 9.50[2.86]*Elevation + 0.82[0.36]*Distance to Campground + 1.47[0.95]*Food Availability + 29.55[8.19]*Patch Richness within 5 km
1.63	0.06	2.26	−24.29[5.36] + 8.81[2.72]*Elevation + 0.64[0.32]*Distance to Campground + 24.81[8.76]*Patch Richness within 5 km
1.81	0.06	2.48	−10.91[3.40] + 9.50[2.90]*Elevation + 0.76[0.36]*Distance to Campground + 0.97[1.11]*Food Availability + 0.71[0.95]*Average Number of Visitors
(C) Common Raven competitive habitat-use models			
0.00 [c]	0.27	–	−21.72[12.92] + 59.15[30.71]*Contrast-weighted Edge Density within 2 km + 41.48[21.11]*Road Length within 2 km + 15.63[10.59]*Percent Forest within 2 km − 4.13[2.96]*Average Number of Visitors + 4.78[5.87]*Food Availability
0.54	0.21	1.31	−19.75[53.54] + 54.86[126.66]*Contrast-weighted Edge Density within 2 km + 35.59[23.78]*Road Length within 2 km + 14.39[45.06]*Percent Forest within 2 km − 2.54[2.22]*Average Number of Visitors
(D) Clark's Nutcracker competitive habitat-use models			
0.00 [d]	0.43	–	−2.85[2.13] − 2.07[0.63]*Distance to Whitebark Pine + 28.84[10.74]*Contrast-weighted Edge Density within 2 km + 1.63[0.83]*Average Number of Visitors − 3.24[1.55]*Forest Structure (Very Complex) + 1.76[1.81]*Forest Structure (Complex) + 4.29[1.93]*Food
1.67	0.18	2.31	−7.32[5.71] − 1.88[0.66]*Distance to Whitebark Pine + 25.15[11.56]*Contrast-weighted Edge Density within 2 km + 1.62[0.94]*Average Number of Visitors − 2.40[1.77]*Forest Structure (Very Complex) + 3.07[2.46]*Forest Structure (Complex) + 4.13[2.04]*Food + 2.85[3.38]*Elevation
1.90	0.16	2.59	−4.66[3.47] − 2.07[0.63]*Distance to Whitebark Pine + 28.26[10.95]*Contrast-weighted Edge Density within 2 km + 1.49[0.81]*Average Number of Visitors − 3.57[1.68]*Forest Structure (Very Complex) + 1.43[1.90]*Forest Structure (Complex) + 4.48[2.00]*Food + 4.46[6.52]*Patch Richness within 2 km

[a] AIC$_c$ = 1,147.93
[b] AIC$_c$ = 1,068.22
[c] AIC$_c$ = 979.22
[d] AIC$_c$ = 335.26

TABLE 11. Effect of food subsidy (occupied sites with food − occupied sites without food) on corvid presence on the landscape in Mount Rainier National Park, Washington, USA, 2009–2010. For continuous variables, effect is equal to the difference between the average raw variable value at occupied sites in areas with and without food subsidy. For categorical variables, effect is the difference between the percentage of occupied sites in areas with and without food subsidy. We tested for significant differences between occupied sites with and without food for each species using Student's *t*-tests and an alpha level of 0.05. Occupied sites are those where the species was observed during ≥1 visit. Negative values indicate that the use of the landscape feature decreased in areas of food subsidy.

	Effect of food subsidy			
Variable	Steller's Jay	Gray Jay	Common Raven	Clark's Nutcracker
Average Visitors	9.95 [a]	8.52 [a]	6.49 [a]	11.82 [a]
Distance to Camp (m)	−382.71	−760.58 [a]	−763.45 [a]	−736.69
Distance to Whitebark Pine (m)				−152.48
Edge Density (2 km; m ha^{-1})	4.59	3.91	0.58	−3.04
Edge Density (5 km; m ha^{-1})	2.13	1.34	0.33	−1.07
Elevation (m)	−31.58	−12.83	−62.15	0.24
Patch Richness (2 km)	0.33	0.47	0.15	0.18
Patch Richness (5 km)	−0.06	−0.04	−0.06	−0.04
Percent Forest (2 km)	−3.60	−9.80 [a]	−2.21	−12.64 [a]
Percent Forest (5 km)	−4.34	−6.52	−2.05	−11.66
Road Edge (2 km; m)	13,259.73 [a]	9,039.44 [a]	3,801.59	6,579.18
Road Edge (5 km; m)	21,527.67	8,487.52	4,023.76	3,632.16
Percentage of Occupied Sites with:				
Canopy Cover (<11%)	−15.08	−8.99	−20.29	−26.67
Canopy Cover (11–40%)	−7.14	−1.59	−4.74	20.00
Canopy Cover (41–70%)	17.46	11.01	28.13	−2.22
Canopy Cover (71–100%)	4.76	−0.44	−3.10	8.89
Forest Structure (Simple)	−13.49	−8.99	−18.78	−21.11
Forest Structure (Complex)	15.08	11.16	15.09	−6.67
Forest Structure (Very Complex)	−1.59	−2.17	3.69	27.78
Zone Type (Backcountry Camp)	11.11	45.00	33.27	40.00
Zone Type (Day Use)	48.41	34.06	27.54	54.44
Zone Type (Trail)	−59.52 [a]	−79.06	−60.80	−94.44

[a] $P \leq 0.05$