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Common raven occurrence in relation to energy transmission line corridors transiting human-altered sagebrush steppe

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ABSTRACT

Energy-related infrastructure and other human enterprises within sagebrush steppe of the American West often results in changes that promote common raven (*Corvus corax*; hereafter, raven) populations. Ravens, a generalist predator capable of behavioral innovation, present a threat to many species of conservation concern. We evaluate the effects of detailed features of an altered landscape on the probability of raven occurrence using extensive raven survey (n = 1045) and mapping data from southern Idaho, USA. We found nonlinear relationships between raven occurrence and distances to transmission lines, roads, and facilities. Most importantly, raven occurrence was greater with presence of transmission lines up to 2.2 km from the corridor. We further explain variation in raven occurrence along anthropogenic features based on the amount of non-native vegetation and cover type edge, such that ravens select fragmented sagebrush stands with patchy, exotic vegetative introgression. Raven occurrence also increased with greater length of edge formed by the contact of big sagebrush (*Artemisia tridentata* spp.) with non-native vegetation cover types. In consideration of increasing alteration of sagebrush steppe, these findings will be useful for planning energy transmission corridor placement and other management activities where conservation of sagebrush obligate species is a priority.

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1. Introduction

Common raven (*Corvus corax*; hereafter, raven) numbers have been increasing every year in semiarid environments across most of the western United States for the past several decades (Sauer et al., 2011). In Idaho, statewide raven abundance has increased five-fold since the 1960s (Sauer et al., 2011) and from 1985 to 2009 raven abundance has increased 11-fold within a remote energy research complex that occupies semiarid sagebrush steppe in southeastern Idaho, known as Idaho National Laboratory (INL; Gonzales-Stoller Surveillance, LLC, Idaho Falls, Idaho; ESER Breeding Bird Survey, unpublished data).

As a generalist species with a great capacity for behavioral modification, ravens take advantage of newly available resources placed in the environment as a result of human enterprises. Human alteration of semiarid landscapes often provides unintended food and water resources beneficial to raven survival and reproduction (Boarman and Heinrich, 1999; Boarman et al., 2006; Kristan and Boarman, 2003), an outcome referred to as an "anthropogenic subsidy" effect. In addition, tall structures such as energy transmission towers provide ravens with elevated perches from which to hunt and also serve as nesting substrate where natural tall nesting substrates like trees are rare or nonexistent (Howe et al., 2014; Knight and Kawashima, 1993; Steenhof et al. 1993). These unintended subsidies to ravens are thought to increase raven population size, density, and range by promoting raven survival and reproduction (Kristan et al., 2004; Webb et al., 2004).

Increased presence of ravens can be deleterious to other species, causing conservation problems. For example, ravens prey on the eggs and young of endangered desert tortoise (*Gopherus agassizii*; Boarman, 1993), California condor (*Gymnogyps californianus*; Snyder and Snyder, 1989), California least tern (*Sterna antillarum browni*; Avery et al., 1995), Western Snowy Plover (*Charadrius nivosus*; Burrell and Colwell, 2012), and Marbled Murrelet (*Brachyramphus marmoratus*; Peery et al., 2004). Raven abundance is positively correlated with depredation of eggs and nestlings of birds (Andrén, 1992; Luginbuhl et al., 2001), including greater sage-

Abbreviations: AIC, Akaike's Information Criterion; CI, Confidence interval; DOE, Department of Energy; ER, Evidence ratio; GLMM, Generalized linear mixed model; INL, Idaho National Laboratory; Km, kilometer; RSPF, Resource selection probability function.

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grouse (*Centrocercus urophasianus*; hereafter, sage-grouse; Coates et al., 2008; Coates and Delehanty, 2010; Lockyer et al., 2013). Furthermore, recent evidence suggests that sage-grouse incubation behavior is influenced by presence of ravens (Coates and Delehanty, 2008) and sage-grouse avoid avian predators when selecting nesting and brood rearing locations (Dinkins et al., 2012). Increased raven abundance may limit available high-quality nesting and brood-rearing habitat for sage-grouse.

To better understand these processes and to increase our ability to anticipate the degree to which future habitat alterations in the semiarid American West will subsidize further raven expansion, careful analysis of current raven occurrence within altered landscapes is necessary. A recent investigation of nest site selection by ravens on the INL (Howe et al., 2014) found ravens selected nest sites in close proximity to transmission lines and areas with increased land cover edge and multiple edge types associated with human disturbance, wildfire, and the introduction of non-native plant species. While resource selection by territorial breeding ravens is centered on nest site location (Howe et al., 2014), non-breeding migrants and juvenile dispersers often congregate at food and water sources and exhibit nomadic movements to follow food supplies (Heinrich et al., 1994). As such, raven occurrence can differ spatially and temporally based on life-history stage. Especially useful would be to assess the probability of occurrence for ravens across different life-history stages (breeding and non-breeding) relative to specific human alterations of sagebrush steppe and how the effects of subsidies vary under different landscape conditions. These findings can then be compared to those of only breeding ravens (Howe et al., 2014) to help further our understanding of factors that influence raven resource selection.

An important future alteration is the anticipated development of a national energy transmission grid intersecting continuous sagebrush steppe of the western United States and the placement of transmission towers integral to this grid. Such a network of transmission towers and power lines has the potential to promote further expansion of raven populations in those areas leading to further conservation conflicts with numerous prey species including sage-grouse. Our primary objective was to conduct a multi-scale, comprehensive analysis that identified associations between vegetation communities, anthropogenic features, and raven occurrence within an altered sagebrush steppe ecosystem. Specifically, we modeled resource selection probability functions for ravens using a combination of covariates that included land cover types at multiple spatial scales, edge (interface between two land cover types) indices, energy infrastructure, and other anthropogenic subsidies. Our secondary objective was to use the predictive indicators to develop spatially-explicit maps that depicted variation in the probability of raven occurrence across the study landscape, as well as uncertainty of the predicted value. Findings from this analysis provide land managers with information with which to assess environmental impacts for proposed land use changes associated with energy transmission corridors.

2. Materials and methods

2.1. Study site

The study area was within the INL, located along the Snake River Plain of southeastern Idaho, USA (Fig. 1A), and encompassing approximately 231,500 ha of cold desert sagebrush steppe. The study area and neighboring lands, topography, climate, and vegetation communities have been described in detail elsewhere (Howe et al., 2014; Shive et al., 2011). Briefly, the study area consisted of areas with differing degrees of anthropogenic alterations including the development of nuclear research facilities, 230 km of paved roads and 297 km of electrical transmission and distribution lines (Fig. 1B) that lie within otherwise relatively intact sagebrush steppe. On our study site, transmission line poles were wooden post structures ranging in height from 15.2 to 21.3 m with double wooden cross arms ranging in height from 11.9 to 17.4 m. Distribution line poles consisted of wooden post structures ranging in height from 15.2 to 16.8 m. For the purpose of this study we refer to both types of energy lines as transmission lines.

Human activities and numerous wildfires have influenced the composition of portions of the vegetation communities within the study area. Some post-fire communities were characterized by resprouting native shrubs, perennial grasses and forbs, while other disturbed areas were colonized by invasive species, such as cheatgrass (*Bromus tectorum*), desert alyssum (*Alyssum desertorum*), and crested wheatgrass (*Agropyron cristatum*). Together,

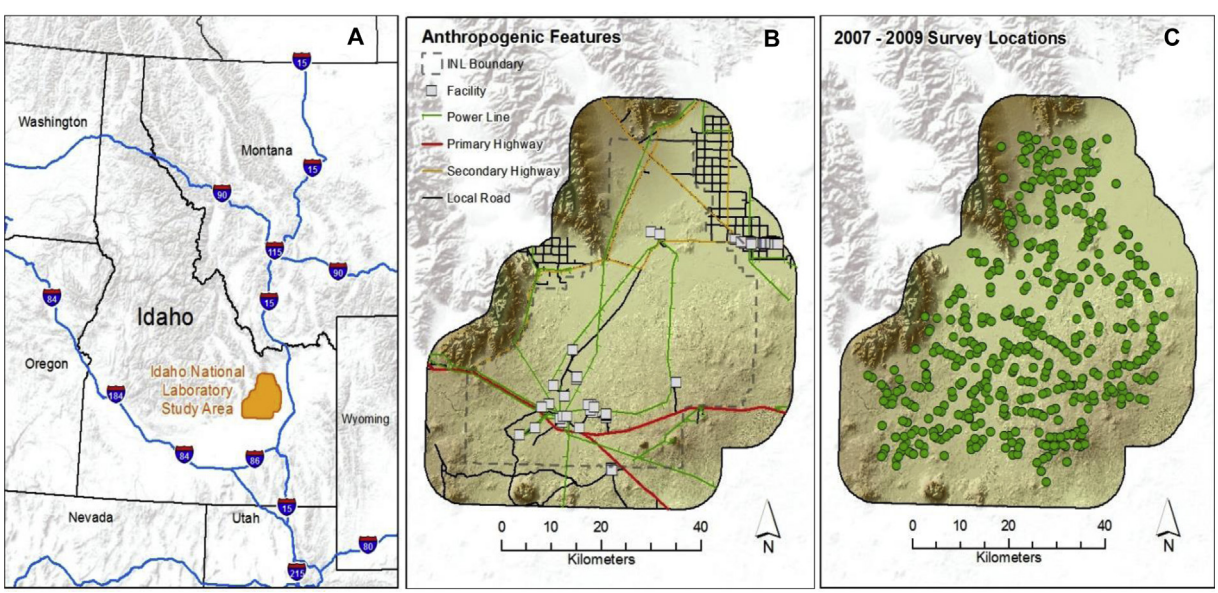

Fig. 1. Study area (A), anthropogenic factors (B), and raven surveys (C) used as covariates in common raven resource selection analysis. Data were collected within and near Idaho National Laboratory in southeastern Idaho during 2007 – 2009.

these disturbances have resulted in areas with increased vegetation edge (i.e. interface between two land cover types) and reduced shrub cover.

2.2. Field survey methods

We conducted 1045 raven point count surveys ($n = 387$, 2007; $n = 330$, 2008; $n = 328$, 2009; Fig. 1C). Surveys were conducted during each study year during 3 April – 15 July, which corresponded to the nesting season of sage-grouse. Our overall survey design was similar to variable radius point count techniques suggested by Ralph et al. (1995). Survey duration was ten minutes and all counts were conducted between sunrise and 1400 h (Luginbuhl et al., 2001) under favorable weather conditions, defined as sustained winds of <40 km/h and no more than a light precipitation. We employed a stratified random sampling design across the study area. Points were stratified by land cover type to include equal representation point counts per unit area of cover type. This random stratified assignment also resulted in variation in distances from anthropogenic sources. Survey points located within 3 km of each other were not surveyed on the same day to prevent double counting. Nearly all surveys were located along two-track trails, which had rare vehicle use (approximately 1 or 2 slow moving vehicles per month). To address whether or not trails influenced probability of raven occurrence, we assigned a subset (approximately 10%) of points between 0.5 and 2.0 km away from two-track trails and carried out a test of frequencies in raven observations between points located on and off two-track trails. We found no difference in observations ($\chi^2 = 1.82$, $P = 0.18$).

For each survey point, we scanned the area with both binoculars and unaided eyes, and listened for raven calls. For each raven, we estimated the distance from the survey point when first detected using a rangefinder (Nikon 1200 Rangefinder, Melville, NY). Raven observations used in the analysis consisted of ravens engaging in behaviors such as perching, standing on ground, performing foraging flights defined as flying $\leq$100 m above the ground with movement path and posture consistent with searching the ground below, copulating, nest incubation, and nest sentry behavior. Ravens observed in directed flight, defined as flying $\geq$100 m above the ground in a straight line direction, were not used in the resource selection analysis because they were not considered to be using the habitat near the survey point.

2.3. Model covariates

We derived multiple landscape-level covariates into the resource selection models from high-resolution land cover maps described by Shive et al. (2011). We condensed the 27 vegetation types of Shive et al. (2011) into nine landscape-level cover types based on the dominant overstory cover. The cover types were: Sage, consisting of Wyoming big sagebrush (*A. t. wyomingensis*), basin big sagebrush and their hybrids (*A. t. tridentata*); Rab, consisting of green rabbitbrush (*Chrysothamnus viscidiflorus*); Grass, consisting of grassland dominated by native perennial grasses and native forbs; Dwarf, consisting of dwarf sagebrush including little sagebrush (*A. arbuscula*) or black sagebrush (*A. nova*); 3tip, consisting of three-tip sagebrush (*A. tripartita*); Salt, consisting of shadscale saltbush (*Atriplex confertifolia*); Exot, consisting of exotic non-native perennial grasses and forbs; Wood, consisting of Utah juniper (*Juniperus osteosperma*); and Mix, consisting of mixed and intermingled juniper and shrubland.

We evaluated evidence of selection for land cover types at two spatial scales (Table 1), which were based on published raven movement parameter estimates. For example, the larger spatial extent was based on average home range or territory size for ravens (660.5 ha; Smith and Murphy, 1973), and the smaller extent (330.0 ha) was half that size to approximate a core use area. We then created two circular buffers that represented these spatial scales, centered on the survey points, and calculated the area of each land cover type within those buffers.

We also evaluate the effects of edge, defined as the interface between two different land cover types, by creating an edge index (Edge) covariate (Table 1). We first categorized all edge types, for example Sage abutting Grass. Then, we pooled all edge types and summed the length of edge within each spatial scale around each survey point. Because selection may be a function of proximity to edge, we also calculated the shortest straight-line (Euclidean) distance (Conner et al., 2003) between survey points and edge (DEdge). In addition to linear distances, we evaluated nonlinear metrics as exponential decay functions for the distance to edge (Nielsen et al., 2009). Specifically, we used $e^{-d/\alpha}$ where d was the distance to an edge, and α was the mean distance of the points where ravens were present. The decay function allowed us to estimate the effect of a feature to weaken as distance from edge increases. Covariates were standardized to compare across spatial scales.

We developed multiple anthropogenic feature covariates that were hypothesized to provide resource subsidies for ravens (Boarman et al., 2006; Engel and Young, 1992). For example, we calculated Euclidean distances between the survey points and anthropogenic features by deriving the distance between survey points and the nearest electrical transmission line (DTrans), paved road (DRoad), and facility (DFac; Table 1). Exponential decay functions were also calculated and evaluated for these distance variables as described above. Model parameter estimates (i.e., constants and coefficients) were then back-calculated and expressed in original measurement units to facilitate interpretation.

Using these covariates, we carried out a three-part modeling approach to meet our study objectives. First, we modeled resource selection probability functions (Boyce et al., 2002; Johnson et al., 2006; Manly et al., 2002) and identified relative importance of covariates on the probability of occurrence of ravens. We then developed spatially-explicit maps that reflected predicted probabilities and illustrated variation in occurrence across the landscape as a result of additive covariate effects. In a post-hoc analysis of edge effects (edge analysis), we measured the effects of edges associated with specific land cover types. The purpose of this analysis was to identify the abutment of two specific land cover types that had the greatest influence on increasing raven occurrence. All statistical analyses were conducted using Program R with package 'lme4' for model parameter estimation (Bates and Maechler, 2010) and package 'AICcmodavg' for multi-model inferences (Mazerolle, 2011). For some variables, we report means (±SE) at sites with and without raven sightings, and we calculated 95% confidence intervals (CI) for differences between those means.

2.4. Model development

We used a generalized linear mixed model approach (GLMM; specified the binomial error distribution using logit link function; Zuur et al., 2009) to estimate resource selection by ravens. We fit combinations of multiple explanatory variables to a response that took a binary form (scored as zero for no raven observations and one for $\geq$1 observation). Year of study and survey location were implemented as random effects to account for variance explained by temporal and spatial correlation (Zuur et al., 2009). To reduce effects of multicollinearity, we planned to exclude variables that covaried ($r \geq |0.65|$) using variance inflation factors (criterion < 10; Menard, 1995) and biological rationale. However, no variables covaried.

Table 1
Means ± SE of covariates used in model analyses of resource selection of common ravens in southeastern Idaho, 2007–2009.

Measure	Scale (ha)	Abbreviation	Description	Ravens absent		Ravens present	
				Mean	SE	Mean	SE
Distance	N/A	DRoad	Distance (km) to nearest road	3.00	0.09	2.27	0.13
		DTrans	Distance (km) to nearest transmission line	3.02	0.09	2.21	0.13
		DFacility	Distance (km) to nearest facility	6.39	0.14	5.10	0.24
		DEdge	Distance (km) to nearest edge	0.64	0.03	0.55	0.04
Edge	330.0 ha	Edge330	Length (km) of edge	6.01	0.20	7.17	0.39
	660.5 ha	Edge660	Length (km) of edge	12.25	0.38	14.32	0.74
Land Cover	330.0 ha	Sage330	Area (ha) of big sagebrush species	168.09	3.76	159.75	6.27
		Grass330	Area (ha) of native grassland	20.15	1.61	19.14	2.40
		Rab330	Area (ha) of rabbitbrush	59.17	3.16	54.70	5.19
		Wood330	Area (ha) of juniper woodland	6.45	1.00	3.79	1.12
		Mix330	Area (ha) of mixed juniper-shrubland	2.77	0.66	2.96	1.21
		Dwarf330	Area (ha) of dwarf sagebrush species	3.34	0.66	1.21	0.70
		Exot330	Area (ha) of non-native	9.05	0.91	14.68	2.14
		Salt330	Area (ha) of saltbush shrubland	6.47	0.92	5.48	1.48
		3Tip330	Area (ha) of three-tip sagebrush	17.60	1.93	17.96	3.47
Land Cover	660.5 ha	Sage660	Area (ha) of big sagebrush species	361.08	7.45	349.15	12.39
		Grass660	Area (ha) of native grassland	40.92	2.96	37.03	4.16
		Rab660	Area (ha) of rabbitbrush	125.78	6.30	122.19	10.66
		Wood660	Area (ha) of juniper woodland	13.90	2.03	8.92	2.34
		Mix660	Area (ha) of mixed juniper-shrubland	5.72	1.23	6.28	2.26
		Dwarf660	Area (ha) of dwarf sagebrush species	7.60	1.31	2.79	1.50
		Exot660	Area (ha) of non-native	19.49	1.56	30.66	3.55
		Salt660	Area (ha) of saltbush shrubland	13.73	1.83	10.64	2.77
		3tip660	Area (ha) of three-tip sagebrush	36.38	3.85	36.55	6.81

Our analytical approach was carried out in multiple steps. First, we reduced the number of variables by eliminating those that lacked evidence (described in Appendix A). Using variables that demonstrated support from the data, we developed models with all possible combinations of covariates, not allowing >3 covariates per model. This step allowed us to evaluate models with additive effects and identify those that were most influential. We evaluated model evidence by calculating differences (Δ) in Akaike's Information Criterion with second-order bias correction (AIC_c; Anderson, 2008) between the most parsimonious model and other models within the set. We calculated model probabilities ($w_{\text{model } i}$) and reported evidence ratios ($ER_{\text{model } j} = w_{\text{model } i}/w_{\text{model } j}$; Anderson, 2008).

We then model averaged parameter estimates (βs; Anderson 2008) and calculated 95% and 85% CIs (Arnold, 2010) based on unconditional standard errors. Confidence intervals that overlapped zero lacked evidence from the data. We also estimated the relative importance of each variable in terms of its contribution (Burnham and Anderson, 2002). We lastly used the averaged βs to calculate a resource selection probability function (RSPF) and further develop a spatially-explicit map of raven occurrence. Specifically, we modeled the probability of observing a raven within a 10-min survey given the environmental covariates across the INL. The RSPF followed the form:

$$w\left(x\right) = \frac{\exp(\beta_0 + \beta_1 X_1 \ldots \beta_k X_k)}{1 + \exp(\beta_0 + \beta_1 X_1 \ldots \beta_k X_k)}$$

Where w(x) is the probability of use, β_0 represents the averaged y-intercept, and $\beta_1 \ldots \beta_k$ represents the averaged parameter estimate for each covariate (1 … k). The surfaces were depicted on a color spectrum from low (blue) to high (red) probability. We also developed two more surfaces to illustrate uncertainty in the parameter estimates and variation in the predicted values. Specifically, we developed these surfaces based on the upper and lower limit of an 85% CI for each β. Although the surfaces did not directly depict the 85% CI of the predicted value derived from the model-averaged βs, areas that shared similar colors across the three surfaces illustrated a greater degree of certainty in the predictions of those averaged βs.

2.5. Post hoc edge analysis

To investigate if specific edge types were driving an overall edge effect, we developed *a posteriori* models consisting of specific edge covariates to evaluate evidence that certain edge types were more influential than others. We were particularly interested in the interface between Sage and each of the following cover types: Grass, Rab, Exot, Wood, and 3tip because as sagebrush steppe is altered these edge types appear within formerly contiguous stands of sagebrush. We developed 20 models representing edge effects. Because edge was found to be influential at both spatial scales, we measured the extent of edges within each scale (Table 2). We evaluated uncertainty among models using the same procedures described above for the resource selection analysis. Models with the lowest AIC_c scores were those for which specific edge types demonstrated the strongest associations with occurrence of ravens.

2.6. Model assumptions

Developing the probability of occurrence models for ravens was not without multiple assumptions. First, we assumed that raven resource selection was independent of selection by other ravens. Specifically, this means that each raven was assumed to make its own behavioral decision on resource selection rather than selecting a resource because another raven did or did not select that resource. Also, because the analysis was conducted at the population level, we assumed that all individuals had the capacity to access all resources across the study area. This assumption refers to the mobility of ravens relative to the size of the study area, not an assumption that social behavior such as territoriality was absent. This assumption likely was met because ravens are capable of long distance movements (e.g., 320 km; Mahringer, 1970). We assumed that resource availability of plant communities, edges, and human structures were constant across the three years of our study. Not only do shrub-steppe communities tend to change slowly barring

Table 2
Means ± SE of length of land cover edge type used in model analyses of resource selection of common ravens in southeastern Idaho, 2007 – 2009.

Juxtaposed cover types	Description	Ravens absent		Ravens present	
		Mean	SE	Mean	SE
Sage/Grass330	Length (km) of edge interfacing big sagebrush and native grassland	0.88	0.10	1.25	0.24
Sage/Rab330	Length (km) of edge interfacing big sagebrush and rabbitbrush	0.76	0.06	0.70	0.09
Sage/Exot330	Length (km) of edge interfacing big sagebrush and non-native vegetation	0.47	0.04	0.68	0.09
Rab/Exot330	Length (km) of edge interfacing rabbitbrush and non-native vegetation	0.09	0.02	0.06	0.02
Sage/Grass_Rab330	Length (km) of edge interfacing big sagebrush and native grassland plus big sagebrush and rabbitbrush	1.64	0.12	1.95	0.25
Grass/Rab330	Length (km) of edge interfacing native grassland and rabbitbrush	0.41	0.05	0.40	0.09
Sage/Grass_Exot330	Length (km) of edge interfacing big sagebrush and native grassland plus big sagebrush and non-native vegetation	1.35	0.11	1.93	0.24
Sage/Grass_Rab_Exot330	Length (km) of edge interfacing big sagebrush and native grassland plus big sagebrush and rabbitbrush plus big sagebrush and non-native vegetation	2.11	0.12	2.63	0.25
Sage/3tip330	Length (km) of edge interfacing big sagebrush and three-tip Sagebrush	0.16	0.02	0.13	0.03
Sage/Wood330	Length (km) of edge interfacing big sagebrush and juniper woodland	0.23	0.05	0.14	0.07
Sage/Grass660	Length (km) of edge interfacing big sagebrush and native grassland	1.63	0.17	2.20	0.39
Sage/Rab660	Length (km) of edge interfacing big sagebrush and rabbitbrush	1.76	0.11	1.65	0.19
Sage/Exot660	Length (km) of edge interfacing big sagebrush and non-native vegetation	1.08	0.08	1.57	0.16
Rab/Exot660	Length (km) of edge interfacing rabbitbrush and non-native vegetation	0.24	0.03	0.18	0.04
Sage/Grass_Rab660	Length (km) of edge interfacing big sagebrush and native grassland plus big sagebrush and rabbitbrush	3.40	0.20	3.84	0.41
Grass/Rab660	Length (km) of edge interfacing native grassland and rabbitbrush	0.74	0.08	0.70	0.14
Sage/Grass_Exot660	Length (km) of edge interfacing big sagebrush and native grassland plus big sagebrush and non-native vegetation	2.72	0.18	3.77	0.41
Sage/Grass_Rab_Exot660	Length (km) of edge interfacing big sagebrush and native grassland plus big sagebrush and rabbitbrush plus big sagebrush and non-native vegetation	4.48	0.21	5.41	0.43
Sage/3tip660	Length (km) of edge interfacing big sagebrush and three-tip sagebrush	0.28	0.04	0.28	0.06
Sage/Wood660	Length (km) of edge interfacing big sagebrush and juniper woodland	0.44	0.09	0.31	0.14

major perturbations like fire, the imagery and mapping process that defined spatial configurations of resources for our analyses were conducted during the same three-year period that we conducted our raven surveys, meaning that raven survey results were analyzed against concurrent resource distribution. Last, we assumed that the detection probability at each survey point was one or the difference between the probability and one was negligible and survey points had equal detection probabilities across vegetation communities within the sagebrush steppe ecosystem. These were reasonable assumptions within this broad, flat study site dominated by communities of short shrubs. Ravens are large and black and often very vocal, making detection unproblematic within the sagebrush ecosystem. Furthermore, we truncated data by the largest spatial scale of analysis to eliminate misclassification and because beyond that distance detection may become lower.

3. Results

3.1. Resource selection analysis

Multiple environmental covariates were supported and retained following the variable reduction approach (detailed in Appendix A) and, thus, we carried these variables forward to models with combined effects. Specifically, the land cover type variables that were carried forward consisted of Mix (330 ha), 3tip (330 ha), Dwarf (330 and 660.5 ha), Wood (330 and 660.5 ha), Exot (330 and 660.5 ha), Sage (330 and 660.5 ha), and Salt (330 and 660.5 ha scale). We also found evidence for Edge (330 and 660.5 ha) and the exponential decay form of distance to transmission line, road, and facility.

Following the modeling of combined effects, we found the most parsimonious model consisted of the distance to transmission line, distance to facility, and Exot (660.5 ha; Table 3). Among all models ($n = 130$), exponential decay functions of distances to transmission line, facility, road, and Exot (660.5 ha scale) and Edge (330 ha scale; Fig. 2) had the greatest relative importance (Table 4). These variables were used to develop a probability surface based on model averaged point predictions (Fig. 3A), as well as surfaces that represented variation in predictions based on upper and lower 85% CIs of parameter estimates (Fig. 3B and C).

To facilitate interpretation of distance variables based on exponential decay functions, we calculated the average percent decrease in probability of occurrence before and after α. On average, the odds of occurrence decreased by 12.2% (95% CI = 9.6–14.1%) for each km away from the transmission line up to $\alpha = 2.2$ km (Fig. 2A). The average decrease in occurrence was 1.9% (95% CI = 1.2–2.7%)

Table 3
Resource selection models for common ravens from survey data collected in southeastern Idaho, 2007–2009. Models with $\Delta AIC_c > 2$ are not shown. K = number of parameters; LL = log-likelihood; ΔAIC_c = difference between model of interest and most parsimonious model with second-order bias correction; w = model probability; ER = evidence ratio (e.g., $w_{model\ 1}/w_{model\ 2}$; Anderson 2008); χ^2 = Chi-square statistic from likelihood ratio test to assess model fit relative to null.

Model no.	Description[a]	K	LL	ΔAIC_c	w	ER	χ^{2b}
1	DTrans(exp), DFac(exp), Exot660	6	−752.31	0	0.10	–	38.4
2	DTrans(exp), DFac(exp), Edge330	6	−752.44	0.3	0.08	1.15	38.1
3	DTrans(exp), DFac(exp)	5	−753.55	0.5	0.08	1.26	35.9
4	DTrans(exp),DRoad(exp), Dwarf660	6	−752.56	0.5	0.07	1.29	37.9
5	DTrans(exp), DFac(exp), Dwarf660	6	−752.68	0.7	0.07	1.45	37.6
6	DTrans(exp),DRoad(exp), Exot660	6	−752.93	1.2	0.05	1.87	37.1
7	DTrans(exp),DRoad(exp), DFac(exp)	6	−753.03	1.5	0.05	2.07	36.9
8	DTrans(exp), DFac(exp), Wood660	6	−753.08	1.6	0.04	2.18	36.8
9	DTrans(exp), DRoad(exp)	5	−754.24	1.8	0.04	2.51	34.5
10	DTrans(exp), DFac(exp), Salt660	6	−753.24	1.9	0.04	2.53	36.5

[a] Total candidate set consisted of 130 models. Fixed model covariates are listed in column and models consisted of random intercept for year. Abbreviations: DTrans(exp) = exponential decay function for distance to transmission line; DFac = exponential decay function for distance to facility; DRoad(exp) = exponential decay functions for distance to road; Exot660 = amount of non-native vegetation at 660 ha scale; Edge330 = amount of edge at 330 ha scale; Dwarf660 = amount of dwarf sagebrush at 660 ha scale; Wood660 = amount of juniper woodland at 660 ha scale; Salt660 = amount of saltbush at 660 ha; Sage660 = amount of big sagebrush at 660 ha scale.
[b] All models in table had associated $P < 0.05$.

per km thereafter to a maximum distance of $\alpha = 11.7$ km. For distance to facilities $\alpha = 5.1$ km, resulting in a decrease in odds of occurrence of ravens by 4.4% (95% CI = 2.6–5.6%) for every km up to 5.1 km (Fig. 2B). After 5.1 km, the estimated average decrease was 0.7% (95% CI = 0.4–1.0%) to a maximum of 27.0 km. For distance to roads, $\alpha = 2.3$ km, resulting in a 10.0% (95% CI = 6.9–12.1%) decrease in odds of raven occurrence for each km within 2.3 km (Fig. 2C). At greater distances, the odds of occurrence decreased to an average of 1.8% (95% CI = 1.0–2.7%) per km away from roads to maximum distance of $\alpha = 10.5$ km. For the area covariate, every 100-ha increase in non-native vegetation at the 660.5 ha scale increased the odds of occurrence of ravens by 22.1% (95% CI = 0.4–48.5%; Fig. 2D). We also found an increase in odds of occurrence with greater edge (Fig. 2E). For each of these covariates, the estimated 95% CIs for the coefficient did not include zero.

3.2. Post hoc edge analysis

Of the 20 models considered, the most parsimonious model was a single covariate model consisting of the interface between Sage and Exot (660.5 ha; $w_{\text{edge model 1}} = 0.41$; Table 5). Points with ravens had greater lengths of these edge type interfaces than points without ravens (Table 2). A well supported alternative model consisted of the interface between Sage and Exot (660.5 ha) plus the interface of Sage and Grass (660.5 ha; $w_{\text{edge model 2}} = 0.16$). Model 1 was nearly 2.6 times ($w_{\text{edge model 1}}/w_{\text{edge model 2}}$) more likely to be the best-approximating model than model 2 in explaining selection for types of edge.

Table 4
Model-averaged parameter estimates and relative importance of explanatory variables used to model resource selection of common ravens in southeastern Idaho during 2007–2009.

Model covariate[a]	Parameter estimate[b]	Parameter likelihood[c]	Interpretation
DTrans(exp)	0.76**	0.97	Selected transmission lines
DFacility(exp)	0.57**	0.50	Selected facilities
DRoad(exp)	0.48*	0.32	Selected roads
Exot660	0.20*	0.25	Selected areas with non-native vegetation
Edge330	0.02*	0.25	Selected areas with increased edge
Dwarf660	−0.36*	0.23	Avoided areas dominated by dwarf sagebrush
Wood660	−0.15	0.14	–
Salt660	−0.14	<0.05	–
Sage660	−0.01	<0.05	-

[a] Abbreviations: DTrans(exp) = exponential decay function for distance to transmission line; DFac(exp) = exponential decay function for distance to facility; DRoad(exp) = exponential decay functions for distance to road; Exot660 = amount of non-native vegetation at 660 ha scale; Edge330 = amount of edge at 330 ha scale; Dwarf660 = amount of dwarf sagebrush at 660 ha scale; Wood660 = amount of juniper woodland at 660 ha scale; Salt660 = amount of saltbush at 660 ha; Sage660 = amount of big sagebrush at 660 ha scale.
[b] All listed model covariates had some level of support from the data by being carried forward from step 1. Double asterisk (**) indicates the averaged 95% CI of parameter estimate did not overlap zero, while single asterisk (*) indicates 85% CI did not overlap zero (Arnold 2010).
[c] Likelihood value represents the relative importance of explanatory variable (Anderson 2008).

4. Discussion

The ability of ravens to exploit a broad range of resources made available by human enterprise within sagebrush steppe, and the potential for increased raven numbers to harm sensitive species, speaks to a need for detailed understanding of the relationships between prevailing habitat features and raven occurrence (Boarman et al., 2006; Sauer et al., 2011). We found multiple, evidenced associations between presence of energy-related features within sagebrush steppe and raven occurrence. Our findings

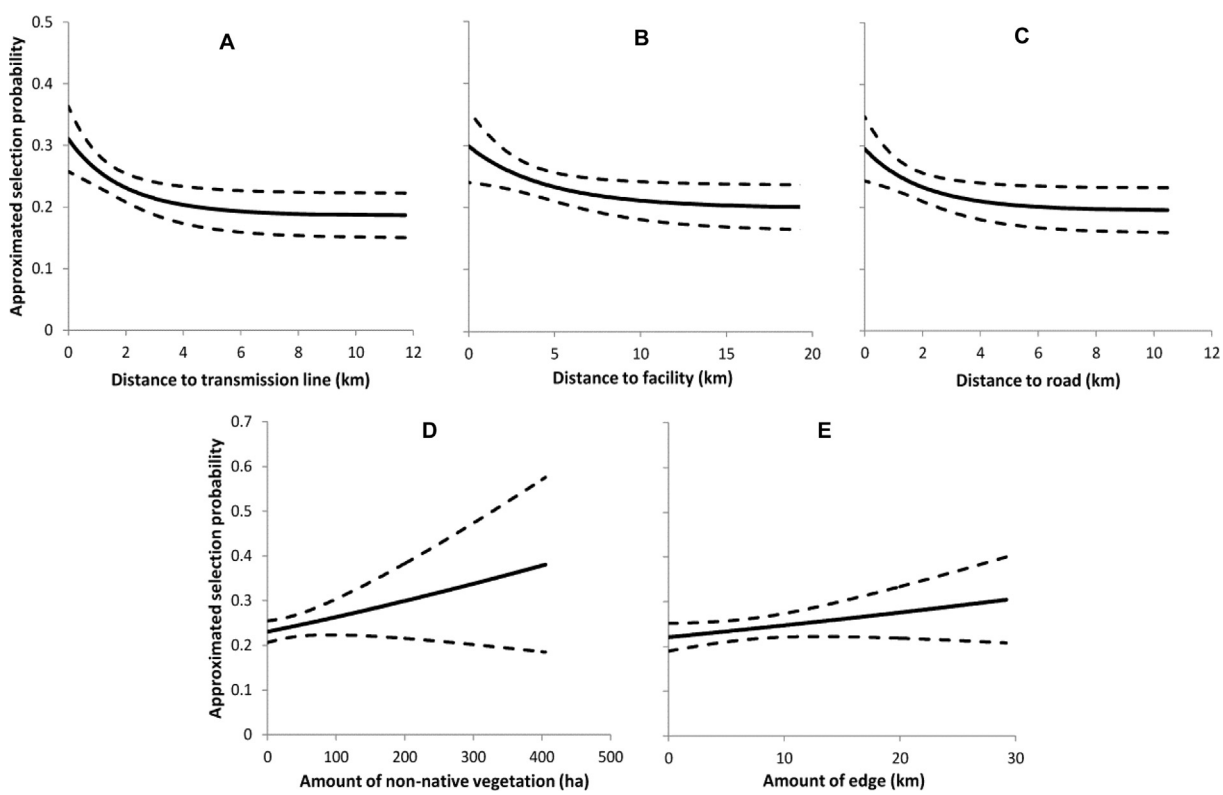

Fig. 2. Approximated selection probability for common ravens in relation to distance to transmission line (A), distance to facility (B), distance to road (C), amount of non-native vegetation at 660.5 ha scale (D), and length of land cover edge (E).

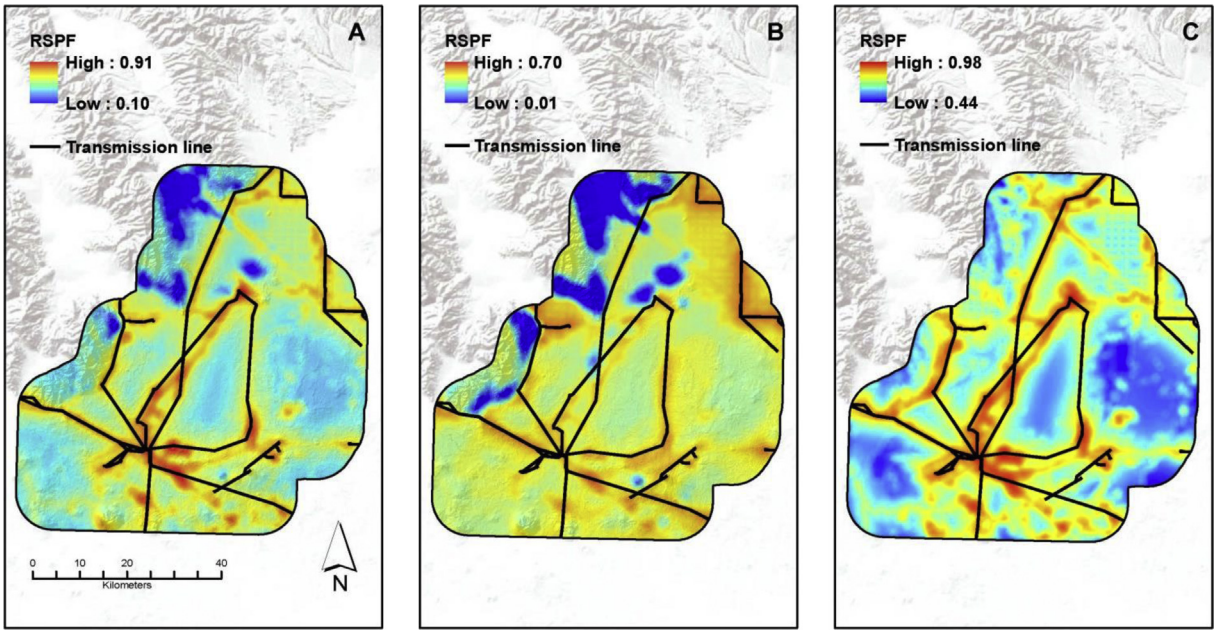

Fig. 3. Predictive surfaces of resource selection of common ravens in southeastern Idaho within and near the Idaho National Laboratory in southeastern Idaho during 2007–2009. Surfaces were derived from averaged point estimates of model parameters (A), and to represent uncertainty in the probability of occurrence, the lower (B) and upper (C) limits of 85% averaged parameter confidence intervals were mapped. Areas that shared similar colors across the three surfaces depict a greater degree of certainty.

corroborate previous findings indicating the significance of anthropogenic factors to raven populations (Engel et al., 1992; Knight and Kawashima, 1993; Steenhof et al., 1993). Here, we contribute additional information by identifying nonlinear relationships with anthropogenic features and the additive effects of vegetative habitat edges and non-native vegetation that co-occur with energy infrastructure placement, which should be of interest to conservationists and wildlife managers.

Table 5
Resource selection models of land cover edge type ($n = 20$) for common ravens in southeastern Idaho, 2007–2009. LL = log-likelihood; ΔAIC_c = difference between model of interest and most parsimonious model with second-order bias correction; w = model probability, ER = evidence ratio (e.g., $w_{model\ 1}/w_{model\ 2}$; Anderson 2008); χ^2 = Chi-square statistic for likelihood ratio test (asterisks indicates $P < 0.05$), which compared model fit relative to null (intercept-only model).

Model[a]	LL	ΔAIC_c	w	ER	χ^2
Sage/Exot660	−767.44	0.00	0.41	–	8.12*
Sage/Grass_Exot660	−768.41	1.90	0.16	2.59	6.18*
Sage/Grass_Exot330	−768.91	2.90	0.10	4.26	5.17*
Sage/Exot330	−769.17	3.40	0.07	5.47	4.65*
Sage/Grass_Rab _Exot660	−769.43	4.00	0.06	7.39	4.14*
Sage/Grass_Rab _Exot330	−769.69	4.50	0.04	9.49	3.61
Sage/Grass330	−770.32	5.70	0.02	17.29	2.36
Sage/Grass660	−770.50	6.10	0.02	21.12	1.99
Sage/Grass_Rab330	−770.80	6.70	0.01	28.50	1.39
Sage/Wood330	−770.94	7.00	0.01	33.12	1.11
Rab/Exot330	−770.99	7.10	0.01	34.81	1.01
Sage/Grass_Rab660	−770.99	7.10	0.01	34.81	1.02
Rab/Exot660	−771.03	7.20	0.01	36.60	0.94
Sage/Wood660	−771.20	7.50	0.01	42.52	0.60
Sage/3tip330	−771.31	7.70	0.01	46.99	0.36
Sage/Rab330	−771.35	7.80	0.01	49.40	0.29
Sage/Rab660	−771.39	7.90	0.01	51.94	0.22
Sage/3tip660	−771.41	7.90	0.01	51.94	0.18
Grass/Rab660	−771.47	8.00	0.01	54.60	0.05
Grass/Rab330	−771.49	8.10	0.01	57.40	0.01

[a] Model statement represent fixed covariates in each binomial model and random intercept for year was fit to each model. Number of parameters for each model was four. Covariates represent length of edge type (interface between two cover types). Abbreviations: Sage = big sagebrush; Exot = non-native vegetation; Dwarf = dwarf sagebrush; Wood = juniper woodland; Grass = perennial grassland; Salt = saltbush; Rab = rabbitbrush; 3tip = three-tip sagebrush; 330 = 330 ha scale; 660 = 660.5 ha scale.

Energy transmission lines are an especially important new environmental feature associated with raven numbers and occurrence. Although the greatest probability of raven occurrence was directly within the transmission line path (Fig. 3), the effect of distance to transmission line was nonlinear with effect size greatest at distances of 2.2 km or closer. These findings suggest that placement of a transmission line in sagebrush steppe has a substantial impact on raven occurrence within a 4.5 km corridor centered on the transmission line. In other words, transmission lines may cause the greatest human footprint (Leu et al., 2008) up to a theoretical threshold of approximately 2 km away from the line, by which prey species may be impacted, and beyond that distance the effect weakens substantially.

Large high-voltage transmission towers are often used by ravens (Knight and Kawashima, 1993; Steenhof et al., 1993) and transmission poles at our study site provided some of the tallest roosting and perching substrates for ravens. However, we also provided evidence that even smaller, low-voltage transmission lines significantly influence raven occurrence in sagebrush steppe habitat.

We observed variation in the estimated probability of raven occurrence within transmission corridors (Fig. 3), which we attribute to the additive effects of energy infrastructure serving as an unintended subsidy to ravens that is further augmented by other anthropogenic factors and altered vegetation characteristics. Of particular interest is the positive relationship between raven occurrence and alteration of vegetation communities resulting in the creation of cover-type edges and introgression of non-native vegetation. Vegetation cover type alteration within the study site was the direct result of wildfire and human disturbance. Importantly, transmission line distance effects in areas where transmission lines intersected land cover types that retained contiguous native shrub canopy cover such as sagebrush and saltbush were associated with relatively less influence on raven occurrence. Conversely, the tall structures associated with transmission lines,

coupled with conversion to non-native cover type and creation of cover type edges expressed strong, positive additive effects in probability of raven occurrence.

Interestingly, we found strong evidence for selection of the cover type variables at the largest spatial scale (660.5 ha) among those that we evaluated. Our study did not discriminate between territorial (breeding) and nomadic (non-breeding) ravens and, thus, provides general inferences about raven habitat selection across the entire raven population. However, we might expect ravens to function at smaller spatial scales during the breeding season if they are nesting and have established territories. Indeed, a recent study that focused only on nesting ravens within our study area indicated that land cover types were selected at a much smaller scale (102.1 ha; Howe et al., 2014). Some evidence indicates that territorial ravens may pose more threat to sensitive species like sage-grouse in sagebrush steppe (Bui et al., 2010). However, research is needed that identifies differences in habitat selection and deleterious impacts between breeding and non-breeding ravens.

Cheatgrass and other invasive species accounted for some of the non-native cover type effects we observed, but a considerable amount of non-native cover consisted of crested wheatgrass resulting from the land management practices as described in Howe et al. (2014). Our results indicate that ravens are selecting areas with reduced shrub canopy cover in altered sagebrush steppe habitat. In an altered sagebrush habitat of northeastern Nevada, ravens were more likely to depredate sage-grouse nests in areas with reduced shrub canopy cover (Coates and Delehanty, 2010). It is possible that ravens are attracted to prey species associated with non-native grassland environments, such as higher densities of Horned larks (*Eremophila alpestris*), the western harvest mouse (*Reithrodontomys megalotis*) (Reynolds and Trost, 1980), and grass-feeding grasshoppers (Fielding and Brusven, 1993). Grasshopper and other insect remains, as well as bird and small mammal remains, were prevalent in raven pellets collected in southwestern Idaho (Engel and Young, 1989). Alternatively, raven occurrence in areas dominated by non-native vegetation could reflect an attraction to other resources from land use practices coincidently associated with cover type such as animal husbandry or other agricultural practices. Further investigations are warranted to identify specific resources exploited by ravens in areas dominated by non-native vegetation.

The amount of land cover edge, specifically the interface between sagebrush and non-native vegetation, influenced raven use as well. Selection for edge-dominated areas suggests that ravens are taking advantage of new habitat conditions caused by habitat fragmentation and conversion. Fragmentation of contiguous landscapes affects a suite of biotic and abiotic parameters including alternating flux of radiation, wind, and water. These disturbances can influence the remaining native vegetation by altering resource availability and species composition; particularly at the edge between the two cover types (Saunders et al., 1991).

Ravens are visually-cued predators and edge-dominated areas may provide ravens with greater visual detection of prey than those with contiguous stands of sagebrush. For example, edges may provide ravens greater opportunity to detect and depredate nests of other bird species. Birds nesting near edges often experience increased rates of nest predation. For instance, Vander Haegen et al. (2002) found that fragmentation in shrub-steppe landscapes positively influenced predation rates for real and artificial nests. Nests in fragmented habitats were approximately nine times more likely to be depredated than those in contiguous habitats, and the majority of nests in fragments were depredated by corvids (Vander Haegen et al., 2002).

Centers of human activity, in this case presence of INL research facilities, also appear to be an important resource for ravens. Surveyed ravens were, on average, closer to centers of human activity than expected based on availability. This result supports the hypothesis that raven populations are closely associated with humans in exurban environments. Raven abundance has been found to fluctuate in response to predictable patterns in human abundance, with raven numbers peaking in concordance with peak human numbers (Boarman et al., 2006). Facilities on the INL are occupied by humans year round and provide continually replenished food subsidies, mainly from dumpsters, but also water resources such as evaporative pools and sewage ponds. Buildings, cooling towers, landscaping trees, and high concentrations of power distribution lines associated with INL facilities also provided numerous tall perches for ravens.

Ravens were detected closer to paved roads than expected. Paved roads provide road-killed carrion and refuse for scavenging by ravens providing valuable food. Carrion from road-killed animals provides prey species to ravens that otherwise would be unavailable (Boarman and Heinrich, 1999). We regularly observed ravens flying directly over roads, particularly in the early morning hours, presumably searching for road-killed carrion. Reports of similar observations of ravens flying along road networks have been reported elsewhere (Bui et al., 2010).

Increased raven abundance is positively correlated with common alterations within sagebrush steppe, helping to explain widespread raven population increases across the American West. Our results will be useful in predicting potential outcomes to forthcoming disturbances anticipated to occur with the placement of a continental scale energy grid network. Assuming that sagebrush steppe at our study area reasonably represents sagebrush steppe ecosystems elsewhere in the American West, results suggest that raven occurrence will likely increase as contiguous stands of sagebrush are fragmented by energy transmission corridors — especially considering these areas will likely also experience non-native cover type introgression and increased cover type edges.

5. Conclusions

Our analyses provide empirical evidence for additive effects of energy-related infrastructure and alterations to landscape vegetation on probability of raven occurrence in semiarid sagebrush steppe. Most importantly, the presence of a transmission line corridor appears to positively influence raven occurrence up to about 2.2 km from the line but this effect varies based on presence of other landscape alterations. For example, cover type fragmentation and conversion from sagebrush to non-native grasses result in landscapes selected by ravens, probably as a result of unintended subsidies these changes provide for ravens. This study suggests that ravens will benefit from further energy corridor expansion in the western United States expected with the development of western energy grid systems and renewable energy sources. For example, wind energy is the fastest growing sector of renewable energy in the United States and developing rapidly throughout sagebrush steppe ecosystems, with 20% of the nation's energy expected to be from wind point sources by 2030 (DOE, 2008). Energy corridor development could result in significant deleterious impacts to some native species of conservation concern within sagebrush steppe ecosystems, not only through direct habitat loss but also by the increased presence of ravens. As corridor placement and other cover type changes reduce contiguous sagebrush cover, our results indicate that raven occurrence will increase, promoting potentially negative impacts to prey species. This study also indicates that protecting the remaining contiguous sagebrush habitat from fragmentation by transmission lines, roads, human structures, wildfire, and the invasion of non-native vegetation could be an integral component of efforts to stem the rapid increase and range

expansion of ravens in the sagebrush steppe. Further, rehabilitation could be used as a tool in fragmented landscapes to reduce the amount of edge associated with patches, to connect those patches, and reduce the benefits that edge-dominated areas currently provide to ravens, especially in areas intersected by transmission lines. The removal or control of non-native vegetation, especially in areas with diminished sagebrush canopy cover, could potentially reduce resources exploited by ravens in those areas. The use of perch deterrents on transmission poles has not been shown to be effective (Prather and Messmer, 2010), but continued research seeking effective perch deterrent designs may yield an effective deterrent. The removal and disposal of road-killed animals would likely reduce the attraction of ravens to paved roads, and future studies that are designed to test this hypothesis would be valued. Finally, centers of human activity, such as the facilities in this study located in otherwise undeveloped sagebrush habitats, could be managed to limit the availability of refuse or other unintentional food and water subsidies for ravens.

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Appendix A

We conducted an initial analysis to reduce the number of variables and identify the most influential spatial scale of measurement for those variables measured at both scales. We identified the most parsimonious models within sets of models formed around three measurement themes. The three themes consisted of: (1) distance to environmental factor such as transmission lines, roads, facilities, and edge of cover types; (2) amount of edge at each spatial scale; and (3) area of land cover type at each spatial scales. Within each theme, we developed sets of models in which each model consisted of one or two covariates as additive effects. Models consisting of single covariates or pairwise combinations of covariates within a theme were compared to one another to identify covariates most associated with resource selection. We evaluated a total of 100 models across all themes. However, for those factors measured at multiple spatial scales, we did not allow more than one scale within the same model. This technique allowed us to identify the most appropriate scale by comparing models at one scale to models at the other. Models were evaluated using Akaike's information criterion with second-order bias correction (AIC_c; Anderson, 2008) and compared the relative utility of models using the AIC_c differences (ΔAIC_c) between models. We calculated model probabilities ($w_{\text{model } i}$; Anderson 2008) and reported evidence ratios ($ER = w_{\text{model } i}/w_{\text{model } j}$) of the most parsimonious model compared to other models in the set (Anderson, 2008). We used likelihood ratio tests (Anderson, 2008) to evaluate each model fit relative to a null model (random intercepts only; $\alpha = 0.05$). Specifically, we used covariates from models in step 1 that fulfilled two criteria: (1) ΔAIC_c was ≤ 4; and (2) the model fit the data significantly better than the null model using the likelihood ratio test.

We found the exponential decay functions of distances represented raven resource selection better than the linear analogue and, thus, we used the exponential decay functions in the additive model combinations within this initial modeling step. Within the group of additive models for distances, the most parsimonious model consisted of two distance covariates: distance to transmission line and distance to facility (Table A). However, another model that was competitive and supported by the data included distance to transmission line and distance to road (Table A). The former model was 2.0 times more likely to represent resource selection of ravens than the latter model. In addition, former model was 19.1 times more likely to explain selection than a model consisting solely of distance to transmission line, and 86.5 times more likely than a model consisting solely of distance to facility.

Within the edge theme of models, both spatial scales showed similar evidence of support (Table A). Amount of edge for the 330 ha scale averaged nearly 1.2 times greater at points with raven detection (7.17 ± 0.39 km) than at points without raven detection (6.01 ± 0.20 km; difference = 1.16 km; 95% CI = 0.30–2.02 km). On average, for the 660.5 ha scale, the amount of edge was also 1.2 times greater at points with ravens (14.32 ± 0.74 km) than points without (12.25 ± 0.38 km; difference = 2.07 km; 95% CI = 0.43–3.72 km). Both models were competitive and carried forward to development of more complex additive models.

For the land cover type models, the most parsimonious model considered dwarf sagebrush and non-native vegetation at the 660.5 ha scale (Table A). This model provided evidence that ravens selected areas with non-native vegetation and did not select areas with dwarf sagebrush. Specifically, we found greater non-native vegetation at points with ravens (30.66 ± 3.55 ha) than at points without ravens (19.49 ± 1.56 ha; difference = 11.17; 95% CI = 18.79–35.41 ha), and less dwarf sagebrush at points with ravens (2.79 ± 1.50 ha) than points without (7.60 ± 1.31 ha; difference = 4.81 ha; 95% CI = 0.91–8.70 ha). Non-native vegetation was the strongest covariate based on its presence in all five of the top models where the $\Delta AIC_c \leq 4$ (Table A). We also found other land cover covariates met the criteria to be carried forward, including dwarf sagebrush, juniper woodland, saltbush, and big sagebrush (Table A).

Table A
Top resource selection models identified in preliminary analysis. Models with $\Delta AIC_c > 4$ are not shown. Resource selection models for common ravens from survey data collected in southeastern Idaho, 2007–2009. K = number of parameters; LL = log-likelihood; ΔAIC_c = difference between model of interest and most parsimonious model with second-order bias correction; w = model probability, ER = evidence ratio (e.g., $w_{\text{model } 1}/w_{\text{model } 2}$; Anderson 2008).

Analysis[a]	No.	Model[b]	K	LL	$\Delta AICc$	w	ER	$\chi 2$
Distance	1	DTrans(exp),DFac(exp)	5	−753.55	0	0.61	–	35.9
	2	DTrans(exp),DRoad(exp)	5	−754.24	1.4	0.31	2.0	34.5
Edge	1	Edge330	4	−768.05	0	0.53	–	6.9
	2	Edge660	4	−768.33	0.6	0.40	1.3	6.3
Land Cover 330 ha	1	Dwarf330, Exot330	5	−766.30	1.4	0.25	–	10.4
	2	Exot330	4	−768.02	1.6	0.12	1.5	7.0

Table A (*continued*)

Analysis[a]	No.	Model[b]	*K*	LL	ΔAIC*c*	w	ER	χ2
	3	Wood330, Exot330	5	−767.12	2.5	0.10	1.9	8.8
	4	Sage330, Exot330	5	−767.57	3.3	0.07	2.2	7.8
	5	Exot330, Salt330	5	−767.95	3.3	0.05	2.4	7.1
	6	Rab330, Exot330	5	−767.97	3.3	0.05	2.6	7.1
	7	Exot330, 3tip330	5	−767.97	3.3	0.05	2.8	7.1
	8	Mix330, Exot330	5	−767.99	3.3	0.05	3.0	7.0
	9	Grass330, Exot330	5	−768.01	3.4	0.04	3.1	7.0
Land Cover 660 ha	1	Dwarf660, Exot660	5	−764.61	0	0.40	–	13.8
	2	Exot660	4	−766.77	2.3	0.12	3.2	9.5
	3	Wood660, Exot660	5	−766.14	3.1	0.09	4.6	10.7
	4	Sage660, Exot660	5	−766.42	3.6	0.06	6.2	10.2
	5	Exot660, Salt660	5	−766.55	3.9	0.06	7.0	9.9

[a] This initial step of the analysis evaluated 100 models to assess evidence of covariates. The exponential decay function of distance variables ($e^{-d/\alpha}$ where d was the distance to a landscape feature, and α was the mean distance of the points where ravens were present) showed substantially greater support than the linear form.

[b] All variables shown here were carried forward to more complex additive models because these models fulfilled two criteria: (1) ΔAIC_c was ≤ 4 and (2) the model fit the data significantly better than the null model using the likelihood ratio test.

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