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**Subject:** GRSG: sage-grouse indirect effects and transmission lines mini-workshop - call in #, webinar, and literature citations attached  
**Date:** Wednesday, December 03, 2014 2:45:13 PM  
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## FWS Sage-grouse Indirect Effects and Transmission Lines Mini-workshop

### Call-in Info:

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### Citations for workshop:

#### Reduced Recruitment:

Gibson, D. E. Blomberg, and J. Sedinger. 2013. Dynamics of greater sage-grouse (*Centrocercus urophasianus*) populations in response to transmission lines in central Nevada. Progress Report: Final. University of Reno, Unpublished Report. 68pp.

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**Avoidance:**

Gillan, J.K., E. Strand, J. Karl, K. Reese, and T. Laninga. 2013. Using spatial statistics and point-pattern simulations to assess the spatial dependency between greater sage-grouse and anthropogenic features. *Wildlife Society Bulletin* 37(2): 301-310.

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**Avian Predation:**

Howe, K.B., P.S. Coates, and D.J. Delehanty. 2014. Selection of Anthropogenic Features and Vegetation Characteristics by Nesting Common Ravens in the Sagebrush Ecosystem. *Condor Ornithological Applications* 116:35-49.

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Coates, P.S., K.B. Howe, M.L. Casazza, and D.J. Delehanty. 2014. Common raven occurrence in relation to energy transmission line corridors transiting human altered sagebrush steppe. *Journal of Arid Environments* 111:68-78

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## Original Article

# Using Spatial Statistics and Point-Pattern Simulations to Assess the Spatial Dependency Between Greater Sage-Grouse and Anthropogenic Features

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**ABSTRACT** The greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse), a candidate species for listing under the Endangered Species Act, has experienced population declines across its range in the sagebrush (*Artemisia* spp.) steppe ecosystems of western North America. One factor contributing to the loss of habitat is the expanding human population with associated development and infrastructure. Our objective was to use a spatial-statistical approach to assess the effect of roads, power transmission lines, and rural buildings on sage-grouse habitat use. We used the pair correlation function (PCF) spatial statistic to compare sage-grouse radiotelemetry locations in west-central Idaho, USA, to the locations of anthropogenic features to determine whether sage-grouse avoided these features, thus reducing available habitat. To determine significance, we compared empirical PCFs with Monte Carlo simulations that replicated the spatial autocorrelation of the sampled sage-grouse locations. We demonstrate the implications of selecting an appropriate null model for the spatial statistical analysis by comparing results using a spatially random and a clustered null model. Results indicated that sage-grouse avoided buildings by 150 m and power transmission lines by 600 m, because their PCFs were outside the bounds of a 95% significance envelope constructed from 1,000 iterations of a null model. Sage-grouse exhibited no detectable avoidance of major and minor roads. The methods used here are broadly applicable in conservation biology and wildlife management to evaluate spatial relationships between species occurrence and landscape features. Our results can directly inform planning of infrastructure and other development projects in or near sage-grouse habitat. © 2013 The Wildlife Society.

**KEY WORDS** *Centrocercus urophasianus*, Monte Carlo, pair correlation function, point pattern, Ripley's K, sage-grouse, spatial statistics.

The greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse), a candidate species for listing under the Endangered Species Act of 1973 (ESA; U.S. Department of the Interior 2010), has experienced population declines across its range in the sagebrush (*Artemisia* spp.) steppe ecosystems of western North America (Connelly and Braun 1997, Connelly et al. 2004). Sage-grouse now occupy only 56% of their pre-settlement range, though they still occur in 11 western states and 2 Canadian provinces (Schroeder et al. 2004). The conservation status of this wide-ranging species could have a

significant influence on public land policy regarding land use, energy and mineral development, transportation and communication corridors, and livestock grazing (Wambolt et al. 2002; US Bureau of Land Management 2004, 2011; Stiver et al. 2006, 2010), because two-thirds of remaining sagebrush lands (329,881 km<sup>2</sup>) are publicly managed (Knick 2011). The remaining one-third of sagebrush lands (150,186 km<sup>2</sup>) that are privately owned (Knick 2011) could be impacted if sage-grouse are listed under the ESA.

Causes for the species' decline have been attributed primarily to the removal and degradation of sagebrush-dominated lands essential for cover, nesting, and food (Connelly and Braun 1997, Braun 1998, Leonard et al. 2000, Connelly et al. 2004). Historically, conversion of sagebrush habitats to crop fields and livestock pastures was the primary driver of habitat reduction (Swenson et al. 1987, Beck and

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Mitchell 2000), but more recently wildfire, invasion of annual grasses, and infrastructure development have been responsible for habitat alteration in the sagebrush steppe biome (Knick et al. 2003, 2011; Connelly et al. 2004; Miller et al. 2011).

One factor contributing to current sage-grouse habitat threats is the continually expanding human population and footprint. From 1960 to 2000, the western United States was the fastest growing region of the country and during the 1990s grew at twice the national rate (Perry and Mackun 2001, Travis 2007). From 2000 to 2010, population growth in the region slowed only slightly and 3 of the 4 fastest growing states (NV, UT, and ID) were those with significant sage-grouse populations (Mackun and Wilson 2011). Development patterns spurred by increasing human populations have been characterized by extensive suburban development around major cities and rapid growth of exurban communities and “ranchettes” far removed from metropolitan centers (Brown et al. 2005, Hansen et al. 2005, Travis 2007). This type of growth consumes more land and fragments landscapes more significantly than concentrated urban development (Sullins et al. 2002, Connelly et al. 2004). Many ranches that were previously used for livestock production have been sold and subdivided into low-density housing (Knick et al. 2011). Associated infrastructure, including roads and power-lines, has also expanded on these landscapes (Leu et al. 2008, Leu and Hanser 2011). In some parts of the sage-grouse range, most notably Wyoming, USA, energy development has expanded (Walker et al. 2007, Naugle et al. 2011). Thousands of new natural gas wells have come on line in recent years and required the construction of roads, power lines, compressor stations, pipelines, and ponds (US Bureau of Land Management 2003).

Anthropogenic features can impact ecological processes and wildlife behavior beyond the immediately affected area. Typically, lower biodiversity and more human-adapted species persist adjacent to ranchettes (Theobald et al. 1997; Maestas et al. 2001, 2003; Odell and Knight 2001). The introduction of non-native plant species is one cause because it can change the ecological composition of surrounding land, effectively degrading habitat (Hansen et al. 2005). Wildlife may also avoid anthropogenic features because of noise and the presence of domestic animals such as dogs and cats (Hansen et al. 2005). This type of avoidance behavior can fragment habitat, shrink total available habitat, and create dispersal barriers (Marzluff and Ewing 2001). By assuming that anthropogenic features have some effect on the surrounding land, a recent study by Knick et al. (2011) concluded that power lines have an ecological influence on 39% of all remaining sagebrush lands in the American West, highways influence 38% of remaining sagebrush lands, and urban development influences 18.6% of sagebrush lands. Also, <5% of the entire sage-grouse range is farther than 2.5 km from a mapped road (Knick et al. 2011).

Although sage-grouse cannot tolerate the outright removal of sagebrush (Braun et al. 1977, Connelly et al. 2000), the extent to which proximity to anthropogenic features can negatively influence sage-grouse or cause avoidance behavior

is less understood. Some studies have observed negative associations of infrastructure on sage-grouse lek size and persistence (Braun 1986, Hall and Haney 1997, Harju et al. 2010, Holloran et al. 2010, Johnson et al. 2011) and also nest initiation rates (Lyon and Anderson 2003). Sage-grouse have been documented avoiding habitat adjacent to oil and gas wells and their associated infrastructure (Carpenter et al. 2010, Holloran et al. 2010). Sage-grouse are also thought to occur less often near power lines and major highways (Braun 1998, Hanser et al. 2011).

Most of the studies aimed at understanding sage-grouse habitat associations have not directly considered the clustered nature of sage-grouse populations and the impact of the resulting spatial autocorrelation of sage-grouse observations (only surveyed exception was Yost et al. 2008). Spatial autocorrelation refers to tendency of nearby observations to be more similar (positive autocorrelation) or less similar (negative autocorrelation) than distant observations (i.e., observations are not independent in space; Legendre and Fortin 1989, Legendre 1993). Almost all ecological data will exhibit some degree of autocorrelation as a result of processes (e.g., competition, succession, population genetics, predator-prey interactions), or underlying environmental patterns (e.g., vegetation, soils, topography, anthropogenic features; Legendre and Fortin 1989). Likewise, the species being sampled will often cluster because of habitat features or social structures within the population (Lieske and Bender 2009). Spatial autocorrelation inherent in ecological data by itself is not a problem; in fact, it is very useful for resource usage estimations that use interpolation techniques (Aarts et al. 2008).

Problems can arise when autocorrelated data are used in classical statistical models and significance testing that assumes independent samples (Legendre and Fortin 1989, Legendre et al. 1990, Fortin and Jacquez 2000). Spatial autocorrelation in sample data can reduce the effective sample size and the degrees of freedom for tests of statistical significance (Dale and Fortin 2002). As a consequence, results can be classified as significant when they are actually not (i.e., type I error; Dale and Fortin 2002, Klute et al. 2002, Lieske and Bender 2009). In logistic regression analysis, a popular modeling technique for species-habitat associations, spatially autocorrelated data can overestimate the effects of independent variables on the response (Klute et al. 2002, Dormann et al. 2007, Aarts et al. 2008, Lieske and Bender 2009). Similarly, “Monte Carlo” studies that compare observed data with many different computer-generated random permutations can also result in Type I errors if spatial autocorrelation of the observed data is not included in the null model (Fortin and Payette 2002).

Previous studies on sage-grouse habitat associations should not be disregarded and may be highly accurate if the parameters capture the spatial dependency inherent in the data. But frequently, non-environmental processes that cannot be modeled may be partly responsible for the species’ distribution. Accordingly, all ecological studies should consider the potential of spatial autocorrelation in their data and how it might affect results.

Our objectives were to employ a spatial-statistical approach to determine whether sage-grouse in an isolated population in west-central Idaho, USA, were avoiding anthropogenic features (i.e., roads, power transmission lines, and rural buildings) and, if so, how far from the feature was the zone of influence. This study explicitly accounted for the spatial autocorrelation of sage-grouse observations to evaluate their association with anthropogenic features. This research incorporates spatial analysis techniques, including considerations for null model selection, that are broadly applicable for evaluating relationships between species occurrence and landscape features within the species' environment across large areas. The results can inform planning and decision making for rural development including infrastructure routes that minimize negative impacts to sage-grouse and their habitats.

## STUDY AREA

This study was conducted in the West Central Sage-grouse planning area in west-central Idaho, which included parts of Washington, Adams, Gem, and Payette counties (centered at 44°26'N, 116°38'W). The 374,700 ha planning area was established to conserve a small and isolated population of sage-grouse that was considered the most likely to be extirpated within the state (Idaho Sage-grouse Advisory Committee 2006). Exact population numbers are unknown but it was estimated that the population was significantly lower than in 1970 due to the abandonment of many leks (Idaho Sage-grouse Advisory Committee 2006, West Central Sage-grouse Local Working Group 2008). Currently, 14 leks are being monitored each year. The major potential threats to sage-grouse in this area were geographic isolation, private property development, wildfire, expansion of annual grasslands, and West Nile Virus (Idaho Sage-grouse Advisory Committee 2006).

The study area consisted primarily of rolling hills of sagebrush steppe and grassland vegetation. The shrub component was mainly xeric big sagebrush (*Artemisia tridentata* sp. *xericensis*), stiff sagebrush (*A. rigida*) and three-tip sagebrush (*A. tripartita*). Native perennial grasses included bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), Sandberg bluegrass (*Poa secunda*), and Thurber needlegrass (*Achnatherum thurberianum*). Elevations ranged from 630 m at the Snake River near Brownlee reservoir to >1,220 m at the southern boundary of Payette National Forest. The greatest proportion of the area and of occupied sage-grouse habitat lay between 760 m and 1,070 m in elevation (West Central Sage-grouse Local Working Group 2008). The climate was characterized by cold, wet winters and hot, dry summers. Mean annual precipitation was about 28 cm at lower elevations near the city of Weiser, Idaho, but increased quickly with elevation to >51 cm over much of the planning area. Seventy-five percent of the planning area was considered intact shrub and bunchgrass communities dominated by sagebrush species. Of the 25% that had been altered, 50% was due to invasive annual grasslands thought to have originated from contaminated wheat crops, 49% was in farmland, and only 1% was

developed (West Central Sage-grouse Local Working Group 2008).

The study area was rural and had experienced slow human population growth compared with other regions of Idaho. The valley bottoms support irrigated farmland while the uplands were primarily used for livestock grazing. Most settlements, including the small towns of Midvale and Cambridge, occurred along the U.S. 95 highway corridor (Fig. 1). Land speculation and ranchette style housing, however, had become increasingly popular outside of city limits (Adams County, Idaho 2006, West Central Sage-grouse Local Working Group 2008).

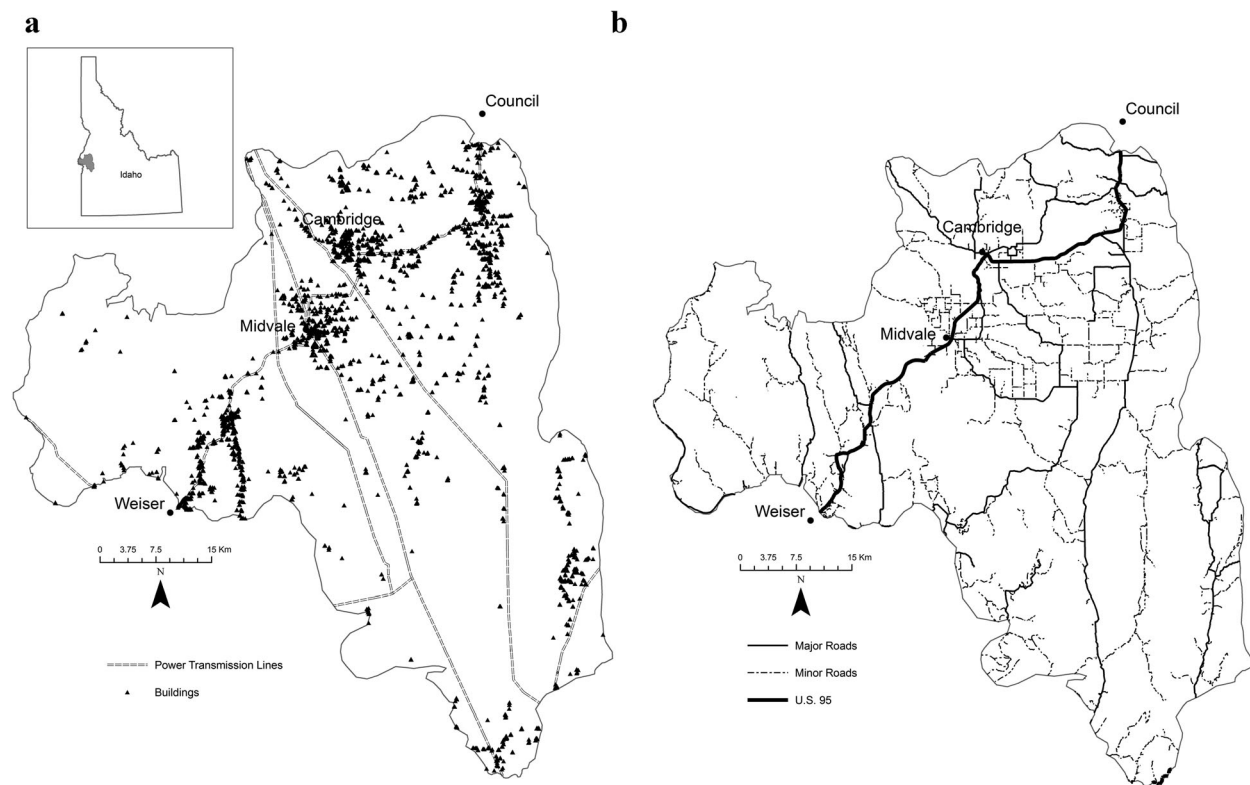
## METHODS

### Sage-grouse Telemetry

We obtained sage-grouse location data from the Idaho Department of Fish and Game, who used radiotelemetry to locate sage-grouse in the study area from April 2005 to December 2007 (Gray 2009). Fourteen females and 44 males captured on 14 different leks were used in this study. To ensure a representative sample of the population, leks were selected to have a range of habitats, a mix of private and public lands, and geographic separation. Sage-grouse were monitored every 2–3 weeks from March through September and once per month from October through February. With this sampling method, bias from serially correlated individual sage-grouse should be small. Location coordinates were recorded using a Garmin (Olathe, Kansas, USA) 76CS Global Positioning System (GPS) where the bird was first seen, but 26 of the locations were obtained through triangulation to prevent flushing. Average accuracy of the GPS was 2–10 m, while the triangulation error could be up to 150 m. Four-hundred ninety-six locations, collected between the months of March and November across all years, were used for the analysis. We excluded the few locations obtained during the winter (Dec–Feb) because sage-grouse habitat use is greatly dependent on snow depth and topography and may not accurately reflect behavior toward anthropogenic features (Connelly et al. 2011). We treated all sage-grouse locations equally with no attempt to depict behavior based on sex, age, or lek of capture. Though it is likely that sage-grouse behavior is partially dependent on seasonal habitat requirements and sex (Patterson 1952; Gill and Glover 1965; Wallestad et al. 1975; Connelly et al. 1981, 1988, 2000, 2011; Gates 1985), we did not examine avoidance behavior distinguished by season or sex because of small sample sizes.

### Anthropogenic Features

We compared sage-grouse locations with the mapped locations of major roads, minor roads, power transmission lines, and buildings within the study area (Fig. 1). Major roads were defined as any road receiving average daily traffic counts from the Idaho Transportation Department (2004a, b). The major roads could be paved or dirt and represented the most frequently used roads. Included in the major roads category was the only 2-lane highway in the study area, U.S.



**Figure 1.** The west central sage-grouse planning area, Idaho, USA (Washington, Adams, Gem, and Payette counties) (a) power transmission lines and buildings, and (b) major and minor roads.

95. Minor roads consisted of all remaining mapped roads excluding 2-tracks. Mapped power lines included only the major transmission lines (>138 kV), and excluded the distribution lines (National Geographic Maps 2004, US Bureau of Land Management 2007). These transmission lines were usually supported by large structures, including the steel lattice (25 m ht) and steel H-frame (17 m ht). The buildings polygon layer included all structures in the study area and was created through digitizing (at a scale of 1:3,000) on aerial imagery from the National Agriculture Image Program (USDA-FSA-APFO 2004). Because the sage-grouse location data were collected 2005–2007, it is possible that some anthropogenic features were omitted or committed in the analysis.

For the analysis, we transformed each anthropogenic feature layer originally modeled as lines and polygons into point features. For linear features, we placed a point every 125 m, which was determined largely by computing limitations. The point frequency should not affect the results comparing the observed point pattern with the null model. For the buildings layer, a centroid point was placed in each polygon.

### Analysis

To determine geographic relationships between sage-grouse locations and each of the anthropogenic feature types, we employed a multi-scale measure of spatial dependence for point patterns. We used the pair correlation function (PCF)

to compare observed with expected number of anthropogenic feature points within concentric rings surrounding sage-grouse locations.

In the bivariate form, the PCF is defined (Stoyan and Stoyan 1994, Schurr et al. 2004):

$$\hat{g}_{12}(r) = \frac{1}{2\pi r} \frac{A^2}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij}^{-1} k_b(r - |x_i - y_j|)$$

where  $\hat{g}_{12}(r)$  is the PCF at a specified radius,  $A$  is the total point-pattern area, and  $n_1$  and  $n_2$  are the number of sage-grouse points and anthropogenic feature points, respectively. The  $x_i$  are locations of sage-grouse points,  $y_j$  are the locations of anthropogenic feature points, and  $w_{ij}$  is a weighting function that accounts for edge effect bias created by unobservable anthropogenic feature points outside the study area. We used the “translation” edge correction described by Torquato (2002) and Pommerening and Stoyan (2006), which extrapolates the point-pattern spatial structure within the study area to infinitely outside the study area. This edge correction is also recommended for study areas with complex shapes (Baddeley and Turner 2005). The PCF looks at a neighborhood of points surrounding the specified radius and gives greater weight to points near the radius and less weight to points further away. This type of weighting is known as an Epinečnikov kernel and is specified by  $k_b$ , where  $b$  is the bandwidth parameter specifying the size of the radius neighborhood that will receive weighting. Points lying

outside the bandwidth will not be considered in the calculation at that radius.

The PCF is a variation of Ripley's  $K$  (Ripley 1981), which measures spatial association within cumulative circles rather than rings. For this application, PCF is the preferred method because it is a more responsive analysis at multiple scales and can identify specific distances of avoidance or clustering. In a Ripley's  $K$  analysis, the results at larger distances are influenced by the shorter distances, which may obscure the spatial association at any given scale.

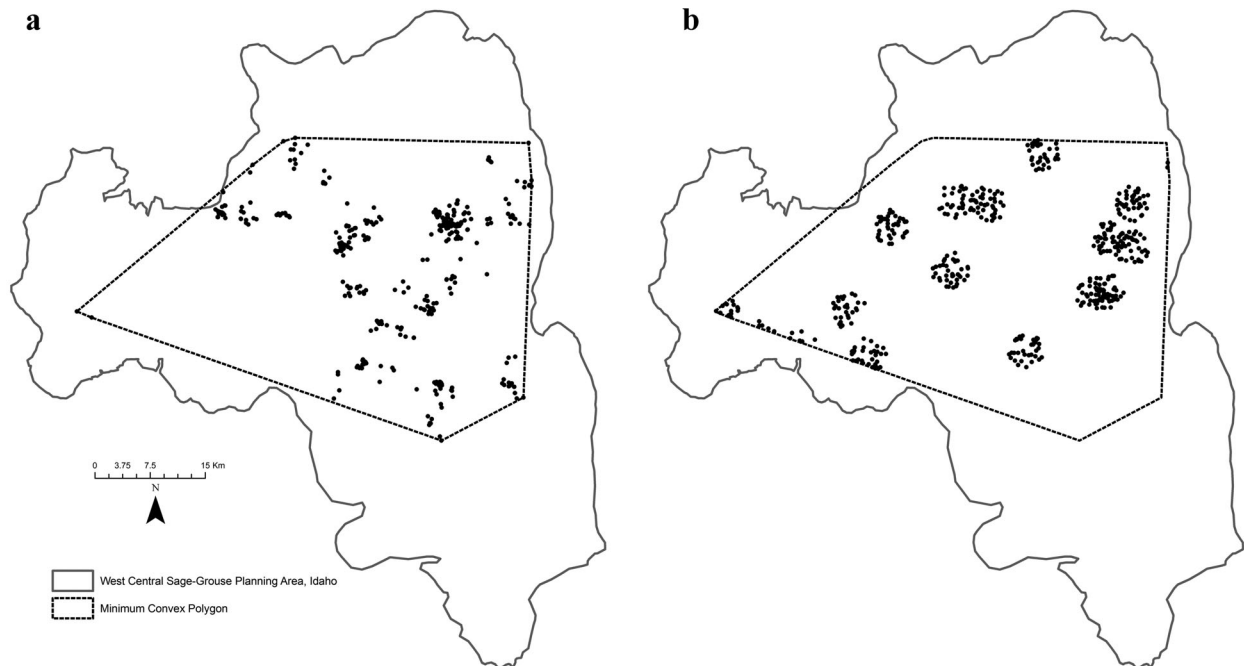
We computed the PCF function initially with  $r = 150$  m, because this is the estimated largest possible location error associated with GPS and radio triangulation (Garmin 2011, Shepherd et al. 2011). We subsequently computed the PCF function every 150 m to a maximum of  $r = 5$  km to assess the spatial relationship at different scales across the study area. We chose a bandwidth of 75 m because it was half the distance between PCF calculations, and because it provided enough smoothing to the PCF graph to aid in interpretation while not over-smoothing the results.

The empirical  $\hat{g}_{12}(r)$  considers all the points of type 1 (sage-grouse) and calculates the intensity of points of type 2 (anthropogenic feature) surrounding it in a ring with a specified radius. The empirical value can then be compared with the expected number of points at the same radius, which is derived from a null PCF model constructed from Monte Carlo point simulations. A deviation between the empirical and expected curves suggests dependence between points of type 1 and 2. Empirical values larger than the expected curve at a given distance suggest that the 2-point types are clustering around each other at that scale. Smaller values than

expected suggests the point types are exhibiting avoidance at that scale.

To test the significance of the spatial association between sage-grouse locations and anthropogenic features, we compared the empirical plot of  $\hat{g}_{12}(r)$  to a null model constructed from 1,000 Monte Carlo simulations. We simulated point patterns designed to mimic the observed spatial pattern of sage-grouse habitat use. The map of sage-grouse telemetry points exhibited strong clustering (Fig. 2a). This strong spatial autocorrelation is a violation of sample independence (see Legendre and Fortin 1989), so a completely spatially random (CSR) null model or parametric statistical test is inappropriate. Therefore, the simulated points used in comparison with the spatially dependent data reflected the same intensity of clustering to prevent false positive findings of significance (Fig. 2b; Fortin and Payette 2002). We also ran the simulations using a CSR model for comparison purposes.

Computation of  $\hat{g}_{12}(r)$  and the simulations were carried out using the Spatstat package (Baddeley and Turner 2005) in the statistics program R 2.10.1 (R Development Core Team 2009). Using the "Kppm" command in Spatstat, we fitted a homogenous Poisson cluster point process model to the sage-grouse data using the PCF function with the same parameters described previously. The simulated cluster patterns were realized following the Matern cluster process (see Møller and Waagepetersen 2003), which creates point patterns using 3 parameters:  $\kappa$  is the intensity of parent points generated through a Poisson process;  $\mu$  is the average number of offspring points surrounding each parent point; and  $R$  is the radius of the cluster of offspring points centered



**Figure 2.** (a) Known sage-grouse locations in the west central sage-grouse planning area, Idaho, USA (Washington, Adams, Gem, and Payette counties) observed April 2005 to December 2007. The locations are bounded by a minimum convex polygon that served as the simulation boundary. (b) Example of a simulated cluster-point pattern created from a homogenous Poisson cluster-point process model. We used 1,000 realizations of the simulated cluster-point patterns as a null model to assess spatial dependency between observed sage-grouse locations and anthropogenic features.

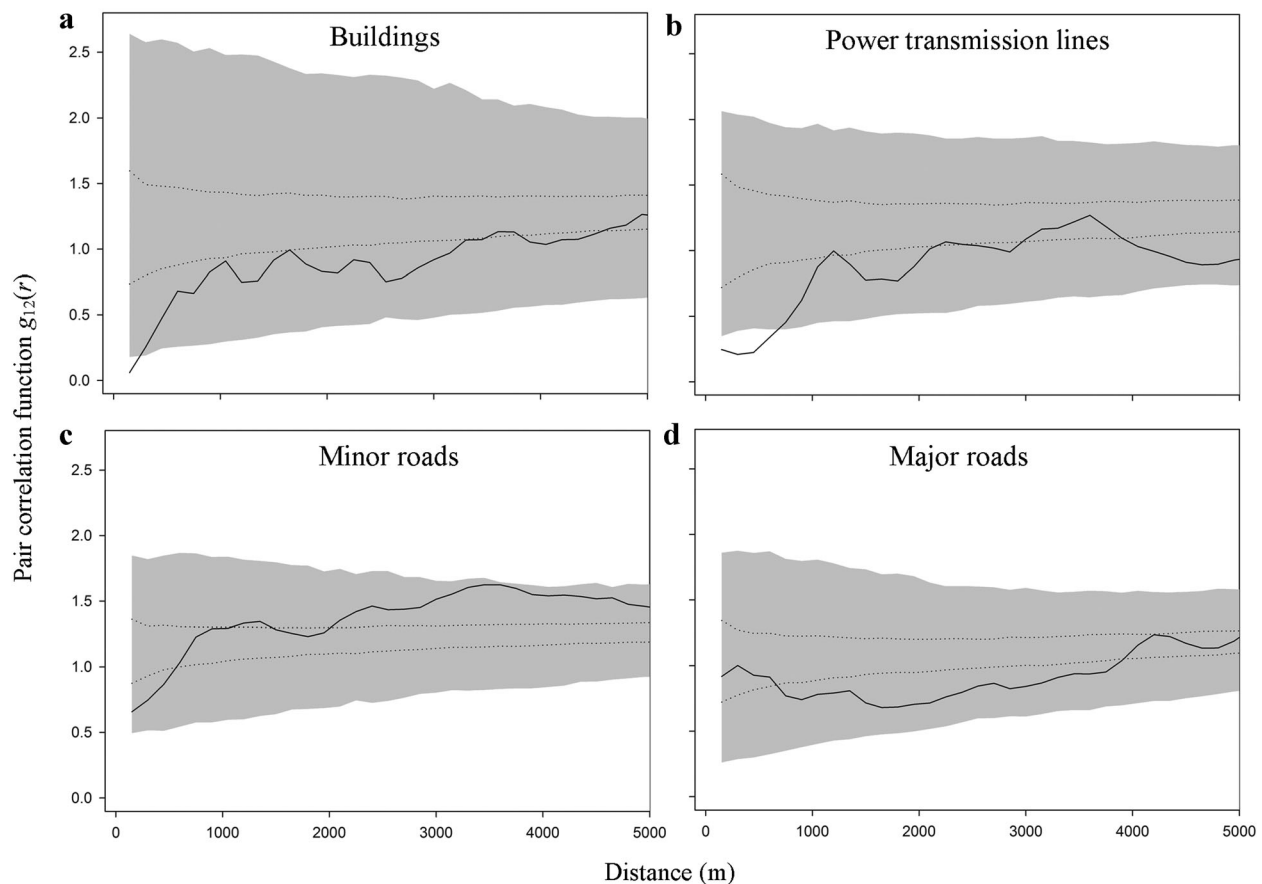
on the parent point. The simulated points were allowed to occur only within available habitat, which we defined as a minimum convex polygon surrounding all of the sage-grouse locations. The Bureau of Land Management, Idaho, considers nearly all of the land within the minimum convex polygon to be sage-grouse habitat (US Bureau of Land Management 2009). Accordingly, simulated points were permitted to occur anywhere within the minimum convex polygon except in water bodies or towns. From the simulations, we created 95% significance envelopes for the clustered and CSR null models to illustrate the difference in statistically significant findings between the 2 simulation methods. For a given radius, values of  $\hat{g}_{12}(r)$  outside of the clustered significance envelope were considered to be significantly different from random arrangements of points showing the same spatial dependence as the sage-grouse locations. This would indicate clustering around or avoidance of anthropogenic features by sage-grouse at those distances.

## RESULTS

Fitting a homogenous Poisson cluster point process model to the sage-grouse data using the PCF function produced a clustered point pattern with  $\kappa = 6.200333\text{e-}09$ ,

$\mu = 47.51922$ , and  $R = 1,748$  m. The significance envelopes exhibited a typical funnel shape where PCF variability was greatest at near distances and shrinks at larger scales (Fig. 3). This was due to the fact that closer concentric rings have less total area and thus a greater opportunity for PCF variability. The funnel-shaped envelopes also tilted upward as scale increased. This is caused by the spatial clustering of the anthropogenic features we are testing. In the study area, there is more open space than there is developed space, so the simulated points were, on average, farther away from anthropogenic features than closer.

Selection of the null model proved to highly influence the statistical inference. The results indicated that observed sage-grouse exhibited avoidance of buildings by 150 m (Fig. 3a) because the PCF value at that distance was less than the clustered 95% significance envelope. The CSR null model produced a much narrower significance envelope, which equates to a much lower standard of statistical significance. The CSR null model indicated that sage-grouse were avoiding buildings by up to 3.45 km. At larger distances, the empirical PCF values were within the simulation significance envelope, which suggested no significant spatial relationship between sage-grouse and building locations.



**Figure 3.** Bivariate pair correlation function,  $\hat{g}_{12}(r)$ , for greater sage-grouse locations and (a) buildings, (b) power transmission lines, (c) minor roads, and (d) major roads. Sage-grouse locations were collected April 2005 to December 2007. The empirical curve (solid line) is plotted against 2 95% significance envelopes: one determined from 1,000 clustered point-pattern simulations (shaded area); and one determined from 1,000 point patterns that were completely spatially random (dotted lines). This study occurred in the west central sage-grouse planning area, Idaho, USA (Washington, Adams, Gem, and Payette Counties).



Sage-grouse showed avoidance of power transmission lines up to distances of 600 m (Fig. 3b) because the PCF values at 150, 300, 450, and 600 m were less than the clustered significance envelope. At all other scales, the empirical PCF values were within the significance envelope, which suggested no significant spatial relationship. The CSR null model again showed that sage-grouse avoided the features at a greater distance of 1.05 km. At larger scales, the empirical curve dipped in and out of the CSR envelope.

Sage-grouse did not appear to avoid minor roads in the study area because the PCF empirical curve landed within the clustered null model significance envelope at all scales (Fig. 3c). The CSR null model showed that sage-grouse avoided minor roads by 450 m. At larger scales (3–4 km), the empirical curve was far above the CSR envelope and nearly left the bounds of the clustered model envelope. This suggests that, at these distances, there were far more sage-grouse near minor roads than was expected.

Sage-grouse also did not appear to avoid major roads in the study area because the PCF empirical curve landed within the clustered null-model significance envelope at all scales (Fig. 3d). There was agreement in the CSR null model up to 600 m, after which the empirical curve was below the envelope at all scales up to 3.9 km, which suggests avoidance at those distances.

## DISCUSSION

This study showed that results from point-pattern simulations could vary greatly between those that incorporate spatial structure and those that employ a CSR method. The CSR null model produced significance envelopes much narrower than the clustered null model, thus setting a much lower standard for significance testing, which may lead to false positive results. This demonstrates the need to explicitly account for spatially dependent data in ecological studies, especially wildlife studies that have presence-only sampling.

Although an improvement over a CSR null model, the homogeneous clustered simulations were not a perfect representation of the observed data. The data appeared to exhibit non-stationary or an inhomogeneous cluster pattern probably caused by differences in seasonal habitat use. Sage-grouse aggregate during the spring lekking season and disperse when breeding has concluded. Analyzing and simulating the data by season and sex may produce improved null models but was not attempted due to small sample size.

Our results support Braun's conjecture (1998; personal communication) that sage-grouse avoid farms and ranch houses. However, he suggested that adult sage-grouse were avoiding occupied farms and ranches by 800 m, while hens with broods might come closer to seek out wet sites. Our study found avoidance up to 150 m, but we did not distinguish between occupied and unoccupied home sites, nor did we consider differences based on sex or season. Sage-grouse may show greater avoidance of occupied houses or farms because of the associated sounds such as human voices or motorized vehicles, or the presence of domestic animals such as cats, dogs, horses, or other livestock.

Our findings on sage-grouse and power transmission lines support other studies suggesting avoidance behavior. Braun (1998) concluded that sage-grouse infrequently use areas within 1 km of a power line, and Hanser et al. (2011) found there was less probability of sage-grouse pellet occurrence within 500 m of power lines. Power lines and transmission structures can serve as perches for avian predators in landscapes with few naturally tall structures (Ellis 1987, Connelly et al. 2004). Sage-grouse may also avoid traditional leks if perches or raptors are visible (Hall and Haney 1997). In California, USA, as distance to overhead power lines decreased, peak male lek attendance also decreased (Hall and Haney 1997). Other studies have found power lines to have a benign effect on sage-grouse. In a 10-year range-wide study, Johnson et al. (2011) found no negative effects of power lines on lek counts, but did report that lek trends were reduced when communication towers were nearby.

Though previous research has shown that sage-grouse may avoid major highways (Hanser et al. 2011), have lower lek attendance (Braun 1986, Johnson et al. 2011), and have lower nest initiation rates near roads (Lyon and Anderson 2003), our results show sage-grouse to be minimally affected by minor and major roads in our study area. There was only one 2-lane highway in the study area and most of the minor roads were composed of dirt or gravel and had infrequent traffic. Anecdotally, some sage-grouse actually lek directly on minor roads in the study area (Gray 2009), and perhaps roads provide an open area in the sagebrush where mating displays can be seen (Connelly et al. 1981, Gates 1985). At some scales for minor roads (3–4 km), more sage-grouse were near roads than was expected to almost a significant level. The reason this occurred is unknown. Sage-grouse may be attracted to riparian areas, agricultural fields, or water developments that are often near farms and ranches. In the summer, sage-grouse have been observed using riparian areas and crop fields, which provide a food source (Dunn and Braun 1986, Schroeder et al. 1999). Topography may be important because leks are often on gentle slopes or in valley bottoms (Rogers 1964), and sage-grouse may simply occupy lands that are popular for human settlements, including locations with roads.

Sage-grouse have been observed being influenced by energy infrastructure at greater distances compared with our results. In Alberta, Canada, sage-grouse avoided energy wells by up to 1.9 km during the winter (Carpenter et al. 2010). In Wyoming, yearling males established themselves less often than expected on leks within 3 km of producing wells and more often on leks farther than 3 km from producing wells (Holloran et al. 2010). Fewer yearling females nested within 950 m of infrastructure than was expected (Holloran et al. 2010). Yearling males and females reared within 1.65 km of a producing well pad or haul road had lower annual survival rates (Holloran et al. 2010). At 5 study sites in Wyoming, lek counts were negatively associated with the presence of producing wells within 800 m, 1.2, 1.6, and 4.8 km at each respective site (Harju et al. 2010). Two other study sites showed no reduced lek counts. In the Powder River Basin of Wyoming and Montana, USA, female sage-grouse in the

winter were more likely to occupy habitats with no natural gas wells within 4 km<sup>2</sup> compared with the legal maximum density of 12.3 wells (Doherty et al. 2008).

Sage-grouse have distinct patterns of habitat use during different times of the year, which will likely affect their tolerance of anthropogenic features (Connelly et al. 2000, 2011). Lumping the seasons and sexes together possibly masked or coarsened the precision of some of the results. For example, during the late brood-rearing period (Jul–Sep), the diet of the chicks changes primarily to forbs and they will choose their habitat based on their availability (Patterson 1952). The hen and chicks may use irrigated crop fields, wet meadows, and riparian areas closer to anthropogenic features (Dunn and Braun 1986, Connelly et al. 1988). During the autumn as the forbs desiccate or are killed by frost, sage-grouse switch their diet back to sagebrush (Patterson 1952, Wallestad et al. 1975). A study in Colorado, USA, found that sage-grouse abandoned irrigated hay fields when the irrigation stopped or after the first frost (Gill and Glover 1965). Had the analysis been separated by season, we might have seen different habitat use between summer and autumn in relation to anthropogenic features.

## MANAGEMENT IMPLICATIONS

Our results can directly inform land managers who are planning infrastructure and other development projects in or near sage-grouse habitat. We revealed a zone of influence around buildings and power lines that affects the occurrence of sage-grouse within their habitat. Our results indicate that anthropogenic features reduce the total amount of habitat available to the species by a factor larger than just the footprints of the features themselves. Planning and zoning commissions, utility companies, and other government entities can use these results to develop building regulations and plan infrastructure routes that are sensitive to sage-grouse populations and habitat. Specific actions that planning entities can take to protect greater sage-grouse populations and habitats in Idaho are to 1) identify goals for species and habitat protection in the county comprehensive plan, 2) incorporate the spatial data from this study and other studies on species of concern into county land use maps, and 3) develop zoning ordinances that encourage the implementation of ‘on-the-ground’ conservation actions by private landowners that minimize or mitigate the zone of influence from anthropogenic features (Haines et al. 2012).

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## **Selection of anthropogenic features and vegetation characteristics by nesting Common Ravens in the sagebrush ecosystem**

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RESEARCH ARTICLE

## Selection of anthropogenic features and vegetation characteristics by nesting Common Ravens in the sagebrush ecosystem

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### ABSTRACT

Common Raven (*Corvus corax*) numbers and distribution are increasing throughout the sagebrush steppe, influencing avian communities in complex ways. Anthropogenic structures are thought to increase raven populations by providing food and nesting subsidies, which is cause for concern because ravens are important nest predators of sensitive species, including Greater Sage-Grouse (*Centrocercus urophasianus*). During 2007–2009, we located raven nests in southeastern Idaho and conducted a resource selection analysis. We measured variables at multiple spatial scales for 72 unique nest locations, including landscape-level vegetation characteristics and anthropogenic structures. Using generalized linear mixed models and an information-theoretic approach, we found a 31% decrease in the odds of nesting by ravens for every 1 km increase in distance away from a transmission line. Furthermore, a 100-m increase in distance away from the edge of two different land cover types decreased the odds of nesting by 20%, and an increase in the amount of edge by 1 km within an area of 102.1 ha centered on the nest increased the odds of nesting by 49%. A post hoc analysis revealed that ravens were most likely to nest near edges of adjoining big sagebrush (*Artemisia tridentata*) and land cover types that were associated with direct human disturbance or fire. These findings contribute to our understanding of raven expansion into rural environments and could be used to make better-informed conservation decisions, especially in the face of increasing renewable energy development.

**Keywords:** anthropogenic features, *Centrocercus urophasianus*, Common Raven, *Corvus corax*, energy development, Greater Sage-Grouse, nest habitat, resource selection function

### Selección de características antropogénicas y vegetacionales por cuervos comunes anidando en el ecosistema de artemisa

### RESUMEN

Los números y la distribución del cuervo común (*Corvus corax*) están aumentando a través de la estepa de artemisa, influyendo comunidades de aves de maneras complejas. Se cree que estructuras antropogénicas aumentan las poblaciones de cuervos al proveer alimento y sitios de nidificación, lo cual es motivo de preocupación porque los cuervos son importantes predadores de especies sensibles, incluyendo el urogallo de las artemisas (*Centrocercus urophasianus*). Durante 2007–2009, ubicamos nidos de cuervo en el sudoeste de Idaho y realizamos un análisis de selección de recursos. Medimos variables a múltiples escalas espaciales para 72 sitios de nidificación únicos, incluyendo características vegetacionales a nivel de paisaje y estructuras antropogénicas. Utilizando modelos lineales generalizados mixtos y una estrategia de información teórica, encontramos una reducción en la probabilidad de anidación por cuervos por cada aumento de un km de distancia desde una línea de transmisión eléctrica. Además, un aumento de 100 m de distancia desde la orilla de dos tipos de cobertura de la tierra redujo la probabilidad de anidación por 20%, y un incremento de 1 km en la cantidad de orilla dentro de un área de 102.1 ha centrada en el nido aumentó la probabilidad de anidación por 49%. Un análisis a posteriori demostró que los cuervos tienen más probabilidad de anidar cerca de las orillas entre artemisa (*Artemisia tridentata*) y tipos de cobertura de la tierra que fueron asociadas con disturbios humanos directos o incendio. Estos resultados contribuyen a nuestro conocimiento de la extensión de cuervos por ambientes rurales y podrían servir para informar políticas de conservación, especialmente ante el creciente desarrollo de energías renovables.

**Palabras clave:** características antropogénicas, *Centrocercus urophasianus*, cuervo común, *Corvus corax*, desarrollo energético, urogallo de las artemisas, hábitat de nidificación, función de selección de recursos

## INTRODUCTION

Common Raven (*Corvus corax*, hereafter raven) populations in the western United States have more than quadrupled over the last 40 years (Sauer et al. 2011). In Idaho, raven numbers have increased 5-fold statewide (Sauer et al. 2011) and 11-fold between 1985 and 2009 within the grounds of the Idaho National Laboratory (D. Halford personal communication). Raven abundance often increases following human alteration of previously natural landscapes (Austin 1971, Knight and Kawashima 1993, Kristan and Boarman 2003). Alteration of the environment is likely responsible for the increase in raven numbers and distribution in the western United States by providing abundant anthropogenic resources that benefit ravens (Boarman 1993). For example, ravens opportunistically feed on a wide range of human-related food sources including road-killed animals (Heinrich 1989), refuse from landfills and trash containers (Harlow et al. 1975, Kristan et al. 2004), gut piles associated with hunting (White 2005, 2006), animal foodstuffs associated with livestock operations (Fuller and Gough 1999), and cereal crops (Engel and Young 1989). Ravens also often use water resources made available through human activity, such as surface water in agricultural fields, stock ponds and troughs, reservoirs, gutters (Fauna West Wildlife Consultants 1989), sewage ponds (Boarman et al. 2006), and water faucets (Hanks et al. 2009).

Importantly, tall structures (e.g., power poles and transmission towers) constructed by humans provide ravens with elevated perches and nesting substrate in areas where natural tall structures (e.g., trees) are rare or nonexistent (Engel et al. 1992, Knight and Kawashima 1993, Steenhof et al. 1993). In these ways, human endeavors subsidize ravens, promoting increases in population size, density, and range by increasing population vital rates and recruitment (Kristan et al. 2004, Webb et al. 2004, Marzluff and Neatherlin 2006).

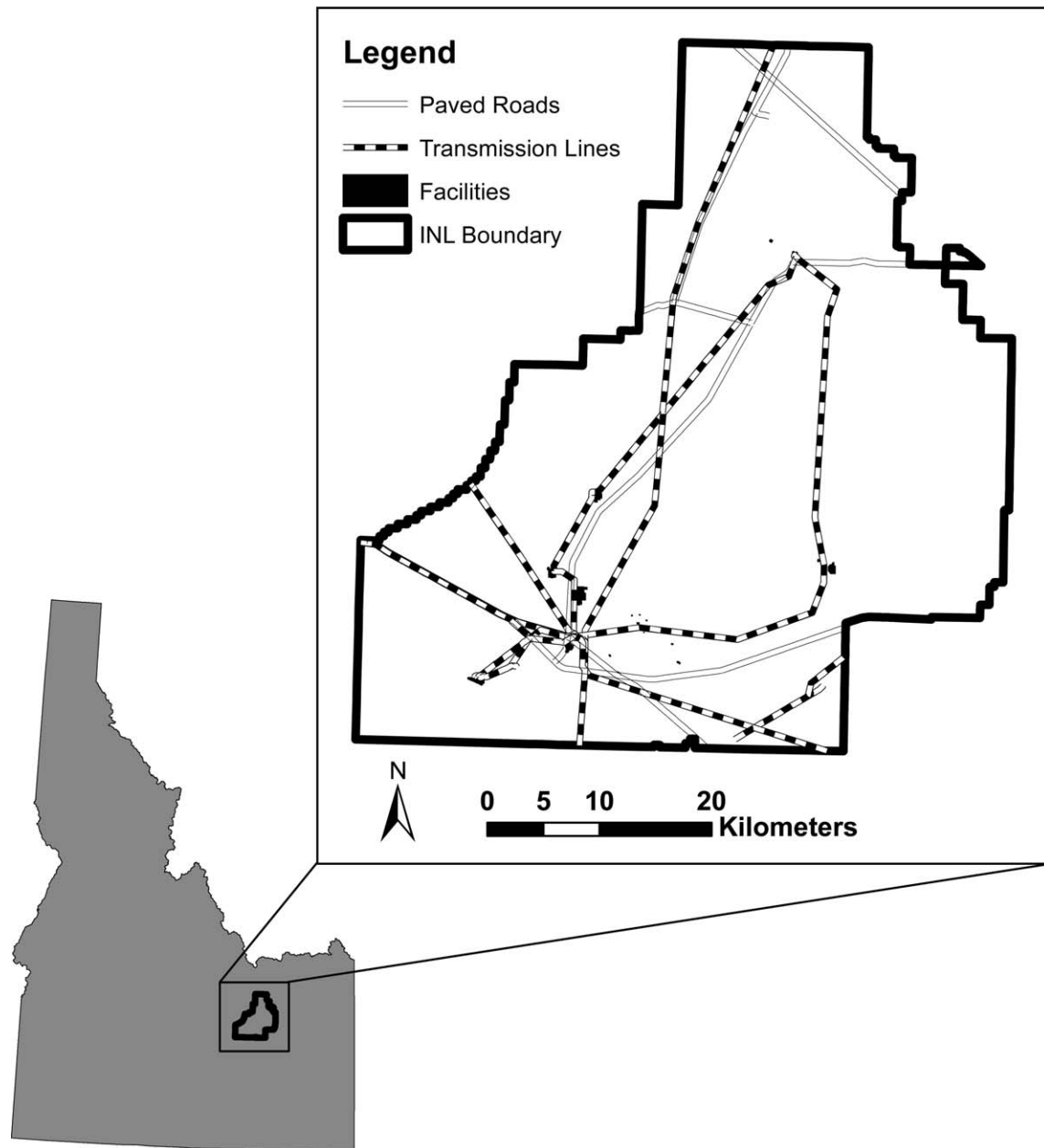
Increased presence of ravens can be deleterious to other species within the geographical range of ravens, a result that can create conservation problems. For example, ravens prey on numerous sensitive species (Belluomini 1991, Boarman 1993), including the federally endangered Desert Tortoise (*Gopherus agassizii*), and the endangered San Clemente Island Loggerhead Shrike (*Lanius ludovicianus mearnsi*) and California Least Tern (*Sterna antillarum browni*). Raven abundance has been positively correlated with predation of eggs or nestlings of other birds breeding within raven range (Andren 1992, Paradis et al. 2000, Luginbuhl et al. 2001), including eggs and nestlings of Greater Sage-Grouse (*Centrocercus urophasianus*, hereafter sage-grouse; Coates et al. 2008, Coates and Delehanty 2010), a species of significant conservation concern.

The daily movement of individual ravens differs by region and breeding status (Boarman and Heinrich 1999), because breeding ravens are territorial and nonbreeding ravens are not. Nonbreeding ravens typically exhibit nomadic movements to follow food supplies (Heinrich 1994). Thus, raven occupancy and raven density can differ spatially and temporally. In Wyoming, sage-grouse nest survival was influenced more by the occupancy of ravens than by raven density near sage-grouse nest sites (Bui et al. 2010), leading Bui et al. (2010) to suggest that resident territorial ravens, rather than nonbreeding transient ravens, were most likely responsible for the majority of sage-grouse nest predation.

A multiscale, comprehensive analysis estimating resource selection by nesting ravens within human-altered sagebrush (*Artemisia* spp.) steppe would be especially useful because of increasing alterations to sagebrush steppe ecosystems through disturbance. Such alterations include the planned development of an energy transmission grid across the western United States (DOE 2008). The frequency of wildfire is also increasing in sagebrush ecosystems, often resulting in the expansion of exotic annual grasses and increased fragmentation (Young and Allen 1987). A better understanding of raven nesting in relation to vegetation characteristics associated with disturbance at a landscape level, coupled with anthropogenic features, is needed to help guide resource management plans.

Our primary objective was to analyze resource selection of nesting ravens within sagebrush steppe ecosystems in relation to anthropogenic structures and landscape-level vegetation characteristics using generalized linear mixed models. We used an information-theoretic approach (Burnham and Anderson 2002) to compare models with different variables of interest, including proportion of dominant vegetation at multiple scales, edge indices, and anthropogenic-related factors. In sagebrush steppe ecosystems, ravens might be more likely to find prey in areas with increased edge habitat because these areas are thought to have less shrub canopy cover. Increased predation rates by corvids in fragmented shrub-steppe environments have been reported elsewhere (Vander Haegen et al. 2002). Thus, we expected that ravens would select sites with more edge habitat and in close proximity to edges. Also, we expected that ravens would select sites with anthropogenic features for nesting based on results from other studies (Engel et al. 1992, Knight and Kawashima 1993, Steenhof et al. 1993). Results from this study will provide land managers with an understanding of the impacts of habitat change on raven breeding opportunities and the subsequent effects of ravens on other species, and are intended to be used when evaluating proposed land use changes such as energy transmission corridors.





**FIGURE 1.** The Idaho National Laboratory in southeastern Idaho, used as the study site for Common Raven resource selection during 2007–2009.

## METHODS

### Study Area

The study area is located in southeastern Idaho, USA (Figure 1) within the grounds of the U.S. Department of Energy Idaho National Laboratory (INL). It encompasses approximately 231,500 ha of cold desert sagebrush steppe, withdrawn from the public domain in 1950 and 1957. The study area is bordered primarily by public lands managed by the Bureau of Land Management (BLM), privately owned croplands, and three towns: Mud Lake (population

297; U.S. Census Bureau 2010) to the north, Atomic City (population 25) to the south, and Howe (population 330) to the west. Approximately 43% of this area has been closed to grazing by domestic livestock since approximately 1957. The study area consists of relatively intact sagebrush steppe interspersed to varying degrees with anthropogenic alterations (e.g., facilities, roads, transmission lines). Less than 1% of the study area is industrialized. Industrialization consists of 8 nuclear research facilities and 19 related structures; however, the facility is not used



for producing power. Approximately 230 km of paved roads and 297 km of transmission and distribution lines intersect the study area. In this study, a distribution line refers to a line that is used to distribute power drawn from high-voltage transmission systems to end-use customers. Distribution line capacity is 12.27 or 13.80 kV. Distribution line poles are wooden posts ranging in height from 15.2 to 16.8 m. Transmission lines are defined as lines used within networks to transmit high-voltage power over long distances. Transmission line capacity at this site is relatively low, ranging from 12.5 to 230.0 kV. Transmission line poles are wooden posts 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.

Average elevation within the study area is 1,500 m (range 1,460–1,620 m). Surface geology has been strongly influenced by volcanic activity, and much of the study site terrain is undulating and broken as a result of geologically recent underlying basalt flows. Annual precipitation averages 208 mm, with most precipitation occurring in the form of snow. Mean annual temperature for the study area is 5.6°C. However, extreme seasonal temperature fluctuations are normal (Anderson and Inouye 2001), meaning that summer is usually relatively hot and dry while winter is relatively cold and wet.

Plant communities within the study area were previously classified into 27 vegetation types in an extensive mapping process (Shive et al. 2011). Of these, 2 are wooded or woodland types, 7 are shrubland types, 4 are shrub herbaceous types, 5 are dwarf shrubland or dwarf-shrub herbaceous types, 6 are herbaceous types, and 3 are seminatural herbaceous types. Seminatural types are generally defined as being dominated by nonnative species. The most dominant overstory species on the study site are Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), basin big sagebrush (*A. t. tridentata*), and their hybrids (Shumar and Anderson 1986). Other common shrubs include three-tip sagebrush (*A. tripartita*), little sagebrush (*A. arbuscula*), black sagebrush (*A. nova*), green rabbitbrush (*Chrysothamnus viscidiflorus*), shadscale saltbush (*Atriplex confertifolia*), spiny hopsage (*Grayia spinosa*), winterfat (*Krascheninnikovia lanata*), granite prickly phlox (*Leptodactylon pungens*), and gray horsebrush (*Tetradymia canescens*). The most abundant understory grass species are bluebunch wheatgrass (*Pseudoroegneria spicata*), Indian ricegrass (*Achnatherum hymenoides*), bottlebrush squirreltail (*Elymus elymoides*), thick-spike wheatgrass (*E. lanceolatus*), and needle-and-thread grass (*Hesperostipa comata*). Woodlands consist of Utah juniper (*Juniperus osteosperma*) stands or juniper stands with a dense shrubland understory.

Several large wildfires since 1994 have influenced the composition of portions of the vegetation communities across the study site. Some postfire communities are

characterized by resprouting shrubs (e.g., green rabbitbrush), native perennial grasses, and forbs. However, some burned areas have been colonized by invasive species, such as cheatgrass (*Bromus tectorum*) and, less commonly, desert alyssum (*Alyssum desertorum*). Additionally, historic military gunnery range bombing scars were seeded with crested wheatgrass (*Agropyron cristatum*) during the 1950s and 1960s (McBride et al. 1978), as were some burned areas, resulting in patches of crested wheatgrass that are spreading into the understory of neighboring shrub communities at a rate of 16 m per year in some areas (R. Blew personal communication). Crested wheatgrass has also been used for “green-stripping,” in which linear medians of crested wheatgrass have been seeded along roads within the study site in an attempt to prevent the spread of any wildfire. These human and natural disturbances have led to some areas with increased vegetation edge (i.e. interface between two cover types). Agriculture did not occur within the INL but was present in adjacent private lands.

### Field Techniques

We located active raven nests within the study area from April to July of 2007–2009. We systematically searched all suitable nesting substrates for raven nests. All anthropogenic structures were examined, which included searching every section of transmission lines, billboards, nest platforms, and facilities. We also conducted foot and vehicle searches at every lone or small group of juniper trees, standing live or dead cottonwood trees, buttes, cliffs and rock-outcrops, lava-tube caves, and landscaped trees. Additionally, we searched all areas of juniper woodland and juniper shrubland. To ensure that raven nests were detected, we supplemented the systematic searches with extensive random point surveys aimed at observing raven territorial behavior and locating nests. Specifically, we generated 1,035 ( $n = 387$ , 2007;  $n = 330$ , 2008;  $n = 328$ , 2009) random points across the study site and conducted a 10-min survey at each random point. When we observed territorial defense or courtship behaviors, we investigated those areas thoroughly for evidence of nesting. Nests were also identified while traveling between survey sites. We made substantial efforts to locate all nests within the study area during each of the three years, and although it is possible that some nests were not detected, we are confident that we located all raven nests during our study years.

We checked all nests by direct observation to determine activity. We visited each potential nest at least twice, if necessary, to confirm nesting activity. A nest was considered active if  $\geq 1$  egg or chick was observed at the nest. If nests were inaccessible, such as those located on transmission poles or facilities, nests were considered active if active nest defense coupled with apparent

incubation or food deliveries were observed over the course of the nesting season.

### Statistical Analysis

**Model covariates.** Our objectives were to study the effects of land cover characteristics and anthropogenic features, such as roads, facilities, and transmission lines, on the probability of raven nesting. Therefore, we carried out multiple mapping techniques to measure landscape-level covariates from high-resolution maps for inclusion in resource selection models. The delineation of land cover types was based on orthorectified digital imagery, as well as 2004 and 2009 National Agricultural Imaging Program (NAIP) imagery, and ancillary data layers described in Shive et al. (2011). Map classification accuracy was 94.2% (Shive et al. 2011). For the model analyses in this study, we condensed the 27 multispecies complexes into 9 landscape-level land cover types based on the dominant overstory cover (when present) and classified them as follows: Sage (Wyoming big sagebrush, basin big sagebrush, and their hybrids); Rab (green rabbitbrush); Grass (grassland dominated by native perennial grasses and native forbs); DSage (low sagebrush or black sagebrush); 3tip (three-tip sagebrush); Salt (saltbrush and shadscale saltbush or sickle saltbush); Exot (exotic plants consisting of nonnative perennial grasses and forbs); Bare (bare ground, gravel pits, and other areas devoid of vegetation); Wood (juniper woodland).

We mapped the location of each raven nest ( $n = 72$  locations) using a geographical information system (GIS; ArcGIS 9.3, ESRI, Redlands, CA) by importing universal transverse Mercator (UTM) coordinates. We evaluated landscape covariates at three spatial extents (scales). The scales were based on the reported average distance that ravens travel from their nest (570 m; Boarman and Heinrich 1999) and home range or territory size for breeding ravens (6.6 km<sup>2</sup>; Smith and Murphy 1973, and 40.5 km<sup>2</sup>; Bruggers 1988). To investigate these spatial extents, we created buffers centered on each nest consisting of 570 m, 1,450 m, and 3,590 m radii to achieve surface areas of 102.1, 660.5, and 4,048.9 ha, respectively. We calculated the area of each land cover type within the different spatial extents.

To estimate the effect of vegetation edges, we developed an edge index and incorporated this value as a covariate in resource selection models. An edge is defined here as the interface between two different land cover types. To develop the index, we first categorized all edge types (e.g., sagebrush interface with grassland) across the study area. We then pooled each edge type and summed the length of edge (Edge) within each spatial area of interest. We also investigated this effect by calculating the shortest straight line, or Euclidean distance (Conner et al. 2003),

between nests and cover type edge (DEdge) using the NEAR tool in ArcGIS 9.3.

We included multiple anthropogenic features in the resource selection models. The rationale for including anthropogenic factors was the reported disproportionately high use by ravens of transmission towers and poles relative to their availability (Knight and Kawashima 1993, Steenhof et al. 1993). We had three specific objectives: (1) to evaluate if raven use of anthropogenic structures also occurred in a sagebrush ecosystem; (2) to calculate a resource selection function (RSF) for each anthropogenic feature; and (3) to evaluate use of transmission poles by ravens while considering relationships with other landscape-level environmental factors. To incorporate the effects of transmission poles and other linear or point features within the landscape, we calculated Euclidean distances (Conner et al. 2003) between the nest and each feature of interest using the NEAR tool in ArcGIS 9.3. This entailed calculating distance to the nearest transmission line (DTrans), paved road (DRoad), and facility (DFacility). Nest locations that fell directly on any distance-based metric received a value of 0. All covariates were standardized to enable comparison across spatial scales.

We used a 2-part approach to investigate habitat selection of nest sites by ravens. First, we calculated RSFs (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006) for each environmental characteristic by contrasting measurements between used points to availability across the study area. For this analysis, we generated a random point for each nest located across the study area and measured the same environmental characteristics (i.e. area of each land cover type and distance variables) as those conducted at used locations (Manly et al. 2002). We followed sampling protocol 'B' of Manly et al. (2002). Therefore, random points were independent of used points. This allowed us to make inferences pertaining to the population. This approach was appropriate for ravens because (1) ravens have large home ranges that often overlap (Bruggers 1988); (2) ravens are capable of long-distance daily movements (Mahringer 1970); and (3) our study questions were specifically related to RSFs within the INL. We also conducted a post hoc analysis to evaluate selection or avoidance for specific edge types (e.g., sagebrush and nonnative vegetation) using a similar technique as described above.

**Model assumptions.** We made several assumptions in interpreting RSFs. First, we assumed that our study site was shaped by similar ecological stressors as those in typical sagebrush ecosystems, such as landscape alterations caused by large-scale wildfires and anthropogenic developments. Second, we assumed that the samples collected in this study provided a reliable representation of raven populations at a relatively large spatial scale. Third, we assumed that individual raven resource selection was

independent of selection by other ravens in the sense that ravens were not copying one another behaviorally. Also, because the analysis was conducted at the population level, we assumed that all individuals had the same available resources across the study area. This assumption was not to deny raven territoriality, but rather to represent the capacity of ravens to make long-distance movements. Ravens have been shown to move up to 320 km from capture locations (Mahringer 1970). Furthermore, potential territoriality likely did not bias our estimates of habitat selection because of relatively low raven densities across a large area. Fourth, we assumed that habitat availability was constant over the study period, an assumption supported by imagery and mapping procedures that were conducted during the same 3 years of our study. Imagery was captured during 2007, sample plots for classification were carried out in 2008, and accuracy was assessed during 2009. Lastly, we assumed that nesting ravens had equal probabilities of detection across the study area. Within sagebrush ecosystems, raven nests are relatively easy to detect regardless of vegetation type, and this assumption likely was met.

**Model development.** We used the design II approach of Manly et al. (2002) for resource selection models, meaning that used resources were assessed at the individual level, but resource availability was assessed at the population level. Each measured resource unit was classified as available or used. Although some nests were reused each year, each unique nest location was represented once to avoid pseudoreplication. We developed generalized linear mixed models (GLMM) and specified the binomial distribution (Zuur et al. 2009). A logistic regression is an effective analytical method to estimate RSF (Manly et al. 2002) and is a function that gives the relative probability of use for each model covariate based on contrasting measurements between used and random locations. We included year as a random effect in the binomial models to account for any variance that may be explained by temporal correlation (Zuur et al. 2009). Without this temporal random intercept, variation associated with year may confound the covariate coefficients that represent RSFs.

The environmental variables in the selection analyses were based on a priori hypotheses (e.g., distance to transmission line), but we used a 2-step exploratory approach to identify the most influential variables based on their additive effects. Also, because spatial scale can influence the selection ratio, we assessed scale by comparing models that employed 3 spatial scales.

In step I, we identified the most parsimonious models within model sets that were grouped by common factors. The 3 groups consisted of (1) distance to features (i.e. transmission lines, roads, facilities, and edge of cover types); (2) length of edge within three spatial scales (102.1

ha, 660.5 ha, and 4,048.9 ha); and (3) area of land cover type at each spatial scale (Table 1). We compared models of covariates between spatial scales and did not allow  $>1$  scale within the same model. For example, all covariates of area included within a model were measured at one scale (e.g., 102.1 ha) while the same covariates measured at a different spatial scale (e.g., 660.5 ha) were included in a separate model. This allowed comparison of evidence for the appropriate spatial scale. Within the first group of distance variables, we developed 10 models, consisting of a single explanatory variable for each of the distance variables, as well as additive models. We did not allow more than 2 covariates in each model. We developed 45 land-cover type models for each scale. These consisted of models for each of the 9 land cover types, as well as additive models using 2 covariates. To evaluate evidence between spatial scales, we compared these models within a set that totaled 135 models. To prevent multicollinearity, which can bias coefficients in predictive models, we planned to exclude correlated variables ( $r \geq |0.65|$ ) using variance inflation factors (VIF; Menard 1995) and biological rationale. However, no variables showed evidence of potential multicollinearity (greatest  $r = 0.58$  and all VIFs were  $<10$ ).

We evaluated evidence of support for models at each scale using Akaike's information criterion with second-order bias correction ( $AIC_c$ ; Anderson 2008). We evaluated uncertainty among models using  $AIC_c$  differences ( $\Delta AIC_c$ ). 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 (intercept and random effects only,  $\alpha = 0.05$ ). We determined the relative importance of each explanatory variable in terms of its contribution by summing the weights across models that included the variable of interest (Burnham and Anderson 2002).

In step II, we developed models using covariates from models that fulfilled two criteria from step I: (1)  $\Delta AIC_c$  was  $\leq 2$ ; and (2) the model fit the data significantly better than the null model. During this step, we developed a new candidate set of models using combinations of covariates that were supported by the data from step I. Although covariates from different groups were allowed to be included in the same model, we did not allow  $>2$  covariates for any given model. We used the information-theoretic approach to evaluate model evidence as described in step I. All model statistical analyses were conducted using Program R version 2.12 ('lme4' package; Bates and Maechler 2010). Standardized model parameter estimates (i.e. coefficients) were averaged using model weights and then back-transformed for meaningful interpretation. We reported values as means  $\pm$  SE.

**TABLE 1.** Models of Common Raven nest location resource selection from data collected in southeastern Idaho, 2007–2009. See Table 2 for model covariate explanations.

Step <sup>a</sup>	Analysis <sup>b</sup>	No.	Model <sup>c</sup>	K	$\Delta AIC_c$	w	Evidence ratio	$\chi^2$ <sup>d</sup>
I	Distance	1	DTrans (–), DEdge (–) <sup>e</sup>	4	0.00	0.98	–	36.4*
		2	DRoad (–), DEdge (–)	4	9.90	0.01	140.5	26.5*
	Edge Area	3	Edge102 (+) <sup>e</sup>	3	0.00	0.99	–	21.5*
		4	Edge660 (+)	3	8.81	0.01	81.9	12.7*
		5	Edge4048 (+)	3	19.91	<0.01	12,771.9	2.6
	Land Cover Area	6	Wood102 (–), Exot102 (+) <sup>e</sup>	4	0.00	0.32	–	11.4*
		7	Wood102 (–)	3	1.85	0.13	2.5	7.5*
		8	Wood102 (–), Rab102	4	3.14	0.07	4.8	8.2*
		9	Wood102 (–), Grass102	4	3.25	0.06	5.1	8.1*
		10	Wood102 (–), Sage102	4	3.54	0.05	5.9	7.8*
		11	Wood102 (–), Dwarf102	4	3.58	0.05	6.0	7.7*
		12	Wood102 (–), 3Tip102	4	3.58	0.05	6.0	7.8*
		13	Wood102 (–), Bare102	4	3.79	0.05	6.7	7.5*
		14	Wood102 (–), Salt102	4	3.85	0.05	6.9	7.5*
II	Combined	15	DTrans (–), DEdge (–) <sup>e</sup>	4	0.00	0.45	–	36.4*
		16	DTrans (–), Edge102 (+)	4	0.21	0.41	1.1	36.2*
		17	DEdge (–), Wood102 (–)	4	3.04	0.10	4.6	33.4*
		18	Edge102 (+), Wood102 (–)	4	6.23	0.02	22.5	30.2*

<sup>a</sup> Step I compared models within each scale (total models,  $n = 135$ ). Covariates of models that met 2 criteria ( $\Delta AIC_c \leq 2$  and fit significantly better than the null model) were included in step II. Step II compared models that were composed of  $\leq 2$  covariates of all combinations of multiple scales (total models,  $n = 15$ ).

<sup>b</sup> Analyses grouped by common predictor variables.

<sup>c</sup> Model statements represent fixed covariates in each binomial model; a random intercept for year was fit to each model. Sign within parentheses indicates the direction of association with the covariate of interest. No sign indicates covariates without evidence of association.

<sup>d</sup>  $\chi^2$  = chi-square statistic to test log ratio model fit relative to the null model. Asterisks (\*) listed in table indicate associations at  $P < 0.05$ .

<sup>e</sup> The  $AIC_c$  values of the best models were: model 1 (DTrans, DEdge) = 171.21; model 3 (Edge102) = 184.17; model 6 (Wood102, Exot102) = 196.30; model 15 (DTrans, DEdge) = 171.21.

**Post hoc edge analysis.** We investigated selection by ravens for different types of edges in an exploratory post hoc analysis. The purpose of this analysis was to evaluate evidence of selection for different types of edges. For example, we hypothesized that edges between shrub and grass land cover types would have more evidence of being selected than edges between two shrub communities. If supported, this finding might explain that ravens select edge habitat because of reduced shrub cover and opening of the shrub canopy. Based on results from our first analysis, we developed 7 models within the 102.1 ha scale (Table 2). We evaluated uncertainty among models using the same procedures described above for the resource selection analysis. The most parsimonious model identified the selected interface between land cover types by nesting ravens.

### Nest Density

We calculated raven nest density within the INL for each study year by dividing the number of nests within the study site by the study site area each year. This simple calculation was sufficient under the assumption that virtually all nests were found within the study area each year. We also calculated the average distance between nests using a

nearest neighbor distance analysis (NND) with the Hawth's Analysis Tool (Beyer 2004) in GIS.

## RESULTS

We located 82 raven nests ( $n = 22$ , 2007;  $n = 26$ , 2008;  $n = 34$ , 2009) in 72 unique locations. Nests were not randomly distributed and were located on multiple types of substrate, with 42 (58%) on transmission poles, 10 (14%) on other human-made towers, 14 (19%) in trees, 4 (6%) on rock ledges, and 2 (3%) on artificial nesting platforms.

### Resource Selection Analysis

Ravens selected nest sites that were simultaneously closer to transmission lines and closer to edges of land cover types than random sites. The most parsimonious of 10 models comprising distance covariates (step I) consisted of distance to transmission line and distance to edge between any two land cover types ( $w_{\text{model 1}} = 0.98$ ; Table 1). Based on the evidence ratio ( $w_{\text{model 1}}/w_{\text{model 2}}$ ), model 1 was 140.5 times more likely to represent resource selection of ravens than the next best model (i.e.  $w_{\text{model 2}} = 0.01$ ; Table 1), a model which included distance to road and distance to edge as covariates. Also, model 1 was 930 times more



**TABLE 2.** Mean  $\pm$  SE of covariates used in model analyses of nest location selection by Common Ravens in southeastern Idaho, 2007–2009.

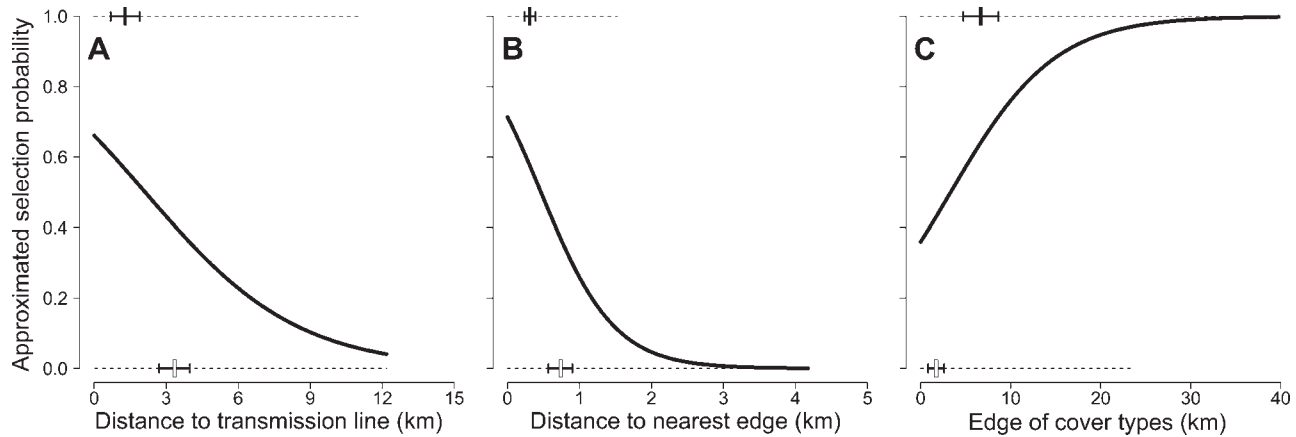
Measure	Type	Abbreviation	Description	Available		Used	
				Mean	SE	Mean	SE
Distance	Point	DRoad	Distance (km) to nearest road	3.67	0.39	2.13	0.34
		DTrans	Distance (km) to nearest transmission line	3.35	0.33	1.29	0.31
		DFacility	Distance (km) to nearest facility	7.14	0.45	6.07	0.52
		DEdge	Distance (km) to nearest edge	0.74	0.09	0.31	0.04
Edge	102.1 ha	Edge102	Length (km) of edge	1.02	0.17	2.48	0.26
	660.5 ha	Edge660	Length (km) of edge	9.02	0.89	14.18	1.14
	4048.9 ha	Edge4048	Length (km) of edge	64.56	4.61	75.46	5.11
Land cover	102.1 ha	Sage102	Area (ha) of big sagebrush species	58.31	5.45	57.45	4.65
		Bare102	Area (ha) of bare ground	0.91	0.70	0.78	0.54
		Grass102	Area (ha) of native grassland	10.52	3.34	8.15	2.36
		Rab102	Area (ha) of rabbitbrush	21.18	4.49	15.95	3.56
		Wood102	Area (ha) of juniper woodland	4.20	2.28	<0.01	<0.01
		DSage02	Area (ha) of dwarf sagebrush species	1.34	1.26	0.68	0.37
		Exot102	Area (ha) of nonnative species	1.98	0.84	6.22	1.91
		Salt102	Area (ha) of saltbush shrubland	1.67	1.13	1.81	0.77
	660.5 ha	3Tip102	Area (ha) of three-tip sagebrush	1.74	1.45	3.18	1.93
		Sage660	Area (ha) of big sagebrush species	377.48	30.76	385.59	23.53
		Bare660	Area (ha) of bare ground	6.94	4.35	5.11	3.10
		Grass660	Area (ha) of native grassland	63.33	17.39	49.75	12.61
		Rab660	Area (ha) of rabbitbrush	135.58	24.92	116.71	20.49
		Wood660	Area (ha) of juniper woodland	21.55	11.37	1.16	0.83
		DSage660	Area (ha) of dwarf sagebrush species	5.37	4.67	3.02	1.66
		Exot660	Area (ha) of nonnative species	18.65	5.98	32.58	8.06
	4048.9 ha	Salt660	Area (ha) of saltbush shrubland	15.59	6.13	17.62	6.14
		3Tip660	Area (ha) of three-tip sagebrush	10.29	6.55	16.23	8.67
		Sage4048	Area (ha) of big sagebrush species	2343.81	135.43	2426.83	116.16
		Bare4048	Area (ha) of bare ground	59.44	27.36	31.02	15.33
		Grass4048	Area (ha) of native grassland	399.99	73.07	309.94	47.83
		Rab4048	Area (ha) of rabbitbrush	757.92	108.47	721.16	106.56
		Wood4048	Area (ha) of juniper woodland	89.33	37.54	25.42	15.22
		DSage4048	Area (ha) of dwarf sagebrush species	25.67	16.01	32.74	20.08
		Exot4048	Area (ha) of nonnative species	127.05	24.90	162.12	28.65
		Salt4048	Area (ha) of saltbush shrubland	98.95	30.16	90.31	26.24
		3tip4048	Area (ha) of three-tip sagebrush	36.10	17.44	50.16	20.90

likely to explain resource selection than a model with a covariate of distance to transmission line only and 228 times more likely to explain resource selection than a model with distance to edge only ( $w < 0.01$  for each single covariate model). The average distance to a transmission line from selected (nest) sites ( $1.29 \pm 0.31$  km; Table 2) was approximately 2.5 times closer than from random sites ( $3.35 \pm 0.33$  km; difference = 2.06 km, 95% CI = 1.17–2.95 km), and distance to land cover edge from used sites ( $0.31 \pm 0.04$  km) was approximately 2.4 times closer than from random sites ( $0.74 \pm 0.09$  km; difference = 0.43 km, 95% CI = 0.24–0.61 km).

Ravens selected areas with increased edge at relatively small spatial scales. For models consisting of covariates of fragmentation (measured as amount of edge) at the three spatial scales (step I), the most parsimonious model was at the 102.1 ha scale ( $w_{\text{model } 3} = 0.99$ ; Table 1). Degree of fragmentation was on average 2.4 times greater at nest

locations ( $2.48 \pm 0.26$  km) than at random locations ( $1.02 \pm 0.17$  km; Table 2), with a 1.46 km (95% CI = 0.86–2.08 km) difference in mean edge length between used and random points at the 102.1 ha spatial scale.

At the 102.1 ha scale, ravens selected areas with nonnative vegetation and avoided areas with junipers. Among step I models of land cover types, the most parsimonious resource selection model for nest location was at the 102.1 ha scale, and consisted of the covariates for nonnative vegetation and juniper woodland ( $w_{\text{model } 6} = 0.32$ ; Table 1). Specifically, we found more nonnative vegetation at nest sites ( $6.22 \pm 1.91$  ha; Table 2) than at random sites ( $1.98 \pm 0.84$  ha; difference = 4.24, 95% CI = 0.09–8.39 ha), and less juniper woodland at nest sites ( $<0.01$  ha) than at random sites ( $4.20 \pm 2.28$  ha; difference = 4.20, 95% CI = –0.35–8.75 ha). However, the 95% CI for the difference in mean juniper woodland between used and random sites overlapped zero, perhaps due to substantial



**FIGURE 2.** Approximated selection probability for Common Raven nest locations in relation to (A) distance to a transmission line, (B) distance to the nearest edge, and (C) length of land cover edge. Vertical black bars represent the mean of resources used by nesting ravens. Vertical white bars represent the mean of resources available. Horizontal solid line represents 95% confidence intervals. Horizontal dashed lines represent the range of used and available resources.

variation in the amount of juniper woodland at random sites, and a model that consisted of only a juniper woodland covariate had only slightly less than half the evidence ( $w_{\text{model } 7} = 0.13$ ; Table 1) than model 6. However, model 6 was approximately 2.5 times more likely to reliably represent resource selection than model 7 using land cover covariates, meaning that the covariate for nonnative vegetation substantially improved the model fit.

Of the 14 models developed from important variables identified in step I, a model consisting of covariates for distance to transmission line and distance to land cover edge was the most parsimonious ( $w_{\text{model } 15} = 0.45$ ; Table 1). The model-averaged parameter estimates indicated a decrease in the odds of nesting by 31% (95% CI = 12–54%; Figure 2) for every 1 km increase in distance away from a transmission line. Furthermore, every 100-m increase in distance away from an edge decreased the odds of nesting by 20% (95% CI = 8.0–33%). The 95% CI for the estimated coefficient of both covariates did not overlap zero. A model that consisted of distance to transmission line and fragmentation indices (102.1 ha scale) was equally competitive ( $w_{\text{model } 16} = 0.41$ ; Table 1) with model 15.

An increase in the amount of edge by 1 km within an area of 102.1 ha across the study area increased the odds of nesting by 49% (95% CI = 19.8–85.4%). The 95% CI for the model coefficient of amount of edge did not overlap zero. Among all models, distance to transmission line, distance to edge, and amount of edge had the greatest relative importance (Table 3).

**Post hoc edge analysis.** For a variety of edge types, ravens disproportionately used nest sites with longer edges relative to availability. The most parsimonious of 7 edge models was a model consisting of 2 edge interfaces, one between big sagebrush (Sage) and native grasslands (Grass) and another between big sagebrush and nonnative (Exot) vegetation ( $w_{\text{edge model } 1} = 0.82$ ; Table 4). Nest sites had a greater amount of these edge types ( $699.95 \pm 132.65$  m; Table 5) than random sites ( $177.49 \pm 52.71$  m; difference = 522.46 m, 95% CI = 239.01–805.91 m). An alternative model consisting of 3 interfaces, between big sagebrush and (1) native grassland; (2) rabbitbrush; and (3) nonnative vegetation, also showed some supporting evidence ( $w_{\text{edge model } 2} = 0.11$ ). Edge model 1 was 7.2 times ( $w_{\text{edge model } 1} / w_{\text{edge model } 2}$ ) more likely to be the best-approximating

**TABLE 3.** Model-averaged parameter estimates and relative importance of explanatory variables used to model resource selection of nesting Common Ravens in southeastern Idaho during 2007–2009.

Explanatory variable	Parameter estimate <sup>a</sup>	SE	Likelihood <sup>b</sup>
Distance to transmission line	−0.80	0.19	0.87
Distance to edge	−1.08	0.34	0.56
Amount of edge (102 ha scale)	0.79	0.18	0.43
Amount of juniper woodland (102 ha scale)	−0.29	0.05	0.13
Amount of nonnative vegetation (102 ha scale)	0.22	0.05	<0.01

<sup>a</sup> Parameter estimates and SE were derived from standardized variables.

<sup>b</sup> The likelihood value represents the relative importance of each explanatory variable and was calculated by summing weights across models that contained the variable of interest.

**TABLE 4.** Resource selection models of land cover edge type ( $n = 7$ ) for nesting Common Ravens in southeastern Idaho, 2007–2009.

Analysis	No.	Model <sup>a</sup>	$K$	$\Delta AIC_c$	$w$	Evidence ratio	$\chi^2$ <sup>b</sup>
Edge type	1	Sage/Grass_Exot (+) <sup>c</sup>	3	0.00	0.82	–	14.4*
	2	Sage/Grass_Rab_Exot (+)	3	3.95	0.11	7.2	10.4*
	3	Sage/Exot	3	5.58	0.05	16.3	8.8*
	4	Sage/Grass (+)	3	9.81	0.01	135.0	4.5*
	5	Sage/Grass_Rab (+)	3	11.68	<0.01	343.8	2.7
	6	Grass/Rab	3	13.86	<0.01	1,022.5	0.5
	7	Sage/Rab	3	14.18	<0.01	1,200.0	0.2

<sup>a</sup> Model statements represent fixed covariates in each binomial model; a random intercept for year was fit to each model. Sign within parentheses indicates the direction of association with the covariate of interest. No sign indicates covariates without evidence of association (95% CI overlapped with 0).

<sup>b</sup>  $\chi^2$  = chi-square statistic to test log ratio model fit relative to the null model. Asterisks (\*) listed indicate an association at  $P < 0.05$ .

<sup>c</sup> The  $AIC_c$  value of the best model was 191.27.

model than edge model 2 in explaining selection for types of edge.

### Nest Density

Raven nest density was calculated to be 0.10, 0.11, and 0.15 nests per 10 km<sup>2</sup> for 2007, 2008, and 2009, respectively, within the boundaries of the INL. Across all three years, average distance between raven nests was  $5.0 \pm 0.4$  km ( $n = 82$ ). Within specific study years, mean nearest neighbor distance between nests was  $5.2 \pm 0.6$  km ( $n = 22$ ) in 2007,  $5.4 \pm 1.0$  km ( $n = 26$ ) in 2008, and  $4.6 \pm 0.5$  km ( $n = 34$ ) in 2009.

### DISCUSSION

We found that 3 important resources were selected by nesting ravens. Ravens selected nest locations that were (1) in close proximity to transmission lines; (2) in close proximity to land cover edges; and (3) within areas that contained abundant edge formed by adjoining land cover types. These findings help to explain recent raven population increases across the western United States,

and will be useful for predicting potential future scenarios related to upcoming disturbances associated with energy grid development. In particular, our findings indicate a high potential for further increases in raven populations within the sagebrush steppe of the western United States following human land use changes.

Among the three spatial scales we examined, we found substantial evidence that the most appropriate spatial scale to represent resource selection by breeding ravens was 102.1 ha. Because we found strong evidence that nesting ravens selected areas with more edge, we conducted an in-depth edge analysis at the 102.1 ha spatial scale and found that ravens nested in close proximity to interfaces between big sagebrush and those land cover types associated with relatively recent disturbance through direct human activity or fire, namely exotic grasses and other invasive plant species. In sagebrush ecosystems, fire frequency has increased with increased exotic annual grass cover (Peters and Bunting 1994), as well as with the increased density of human occupation (Young and Allen 1987), with little indication of forthcoming abatement. Our results coupled with ongoing land use changes suggest there will be

**TABLE 5.** Means  $\pm$  SE of length of land cover edge type used in model analyses of nest location selection of Common Ravens in southeastern Idaho, 2007–2009.

Juxtaposed cover types		Description	Available		Used	
			Mean	SE	Mean	SE
Sage/Grass	Length (m) of edge of adjoining big sagebrush and native grassland		59.81	24.92	226.38	81.23
Sage/Rab	Length (m) of edge of adjoining big sagebrush and rabbitbrush		178.28	69.65	215.15	56.12
Sage/Exot	Length (m) of edge of adjoining big sagebrush and nonnative vegetation		117.67	48.54	473.57	115.66
Sage/Grass_Rab	Length (m) of edge of adjoining big sagebrush and native grassland plus big sagebrush and rabbitbrush		238.10	75.24	441.53	101.92
Grass/Rab	Length (m) of edge of adjoining native grassland and rabbitbrush		121.49	53.13	76.61	36.40
Sage/Grass_Exot	Length (m) of edge of adjoining big sagebrush and native grassland plus big sagebrush and nonnative vegetation		177.49	52.71	699.95	132.65
Sage/Grass_Rab_Exot	Length (m) of edge of adjoining big sagebrush and native grassland plus big sagebrush and rabbitbrush plus big sagebrush and nonnative vegetation		355.77	93.46	915.10	147.72

further increases in raven abundance in sagebrush steppe. Such increases will pose increased threats to sagebrush-steppe species subject to raven depredation, including sage-grouse, of which ravens consume eggs and young (Coates and Delehanty 2010, Lockyer 2012).

Ravens preferred nest sites that were closer to transmission lines than expected based on availability. Transmission poles provide nesting substrates and perches far taller than any other substrate present in our study area. The benefits of nesting on or near transmission poles may include superior hunting advantages due to a greater view of the surrounding landscape for a perched raven, easier take-off, and greater attack speed (Knight and Kawashima 1993). Nesting on transmission poles may also afford greater security from mammalian predators and range fires (Steenhof et al. 1993), and provide protection from heat stress due to increased air flow around elevated perches (Steenhof et al. 1993). Although the presence of large, high-voltage transmission towers has been shown to facilitate raven occupancy in other areas (Knight and Kawashima 1993, Steenhof et al. 1993), the results from this study provide evidence that even smaller, low-voltage transmission lines significantly influence raven populations in sagebrush steppe habitat.

On average, ravens nested within 310 m of land cover edges, and selected areas of increased edge density and multiple edge types at the 102.1 ha scale. Resource selection at this spatial scale is also supported by findings in the Mojave Desert, where breeding ravens hunt live prey an average of  $570 \pm 707.3$  m SD from their nests (Boarman and Heinrich 1999). In addition, results of diet composition studies suggest that ravens forage opportunistically on foods available near their nests (Kristan et al. 2004). Our findings suggest that territorial ravens require the simultaneous availability of multiple land cover types during reproduction, which fits the prevailing concept of a true edge species (Yahner 1988, Matlack and Litvaitis 1999). If the distance to transmission line were related to areas of increased edge, then it may have been possible that ravens incidentally selected increased edge because most nests occurred in relation to transmission lines. However, this is unlikely because the covariates did not show evidence of multicollinearity from our diagnostic examination of the variance inflation factors (VIF was  $<10$ ) and bivariate correlation coefficient ( $r < 0.65$ ; Hensher et al. 2005). Although transmission lines intersected areas of high edge density,  $>50\%$  of the areas intersected by transmission line were not associated with increased edge. Furthermore, we found areas with relatively high amounts of edge in areas far from transmission lines, often caused by wildfire.

Although ravens are capable of foraging over long distances, optimal foraging behavior can affect the absolute distance and frequency of movements (Orians and Pearson

1979). Ravens are less mobile during the nesting period than at any other time of the year (Boarman and Heinrich 1999, Roth et al. 2004) in that they remain near the active nest, and thus are most likely to be affected by spatial variation in vegetation during nesting. Foraging behavior can change over the course of a single season, or even throughout the course of the day, as individuals adjust their behavior in relation to prey availability (Charnov 1976, Parker and Stuart 1976). Birds are described as central place foragers when they collect food from all directions and return to a fixed location such as a nest or cache (Orians and Pearson 1979). Given the generalist diet of ravens (Boarman and Heinrich 1999), nesting in close proximity to multiple habitat types may reduce the physiological and temporal costs of foraging. Individuals within a breeding pair can assess potential prey availability in each of several nearby habitat types and adjust their foraging accordingly. Such foraging behavior likely would aid the provisioning of young while minimizing the energy costs of the parent during travel. Webb et al. (2004) found that ravens that minimized the distance between their nest and food sources (landfill) fledged young at higher rates. Additional research is needed to explore associations between land cover features and raven fitness.

Selection for edge-dominated areas, specifically edges between sagebrush and grasslands and nonnative cover types, suggests that ravens are taking advantage of new habitat conditions caused by a combination of habitat fragmentation and conversion. Fragmentation and patchy habitat conversion of contiguous landscapes affects a suite of physical and biotic parameters, including alterations in fluxes of radiation, wind, and water, and these disturbances can impinge on the remaining native vegetation by altering resource availability and species composition, especially near edges (Saunders et al. 1991). Edge-dominated areas also may provide visually cued predators such as ravens with less visual obstruction than contiguous stands of sagebrush, thereby increasing foraging success, for example through increased depredation of the eggs and young of other bird species. Birds nesting near edges often experience increased rates of nest predation. Vander Haegen et al. (2002) found that fragmentation in shrub-steppe landscapes strongly influenced predation rates for real and artificial nests. Nests in fragmented habitats were approximately 9 times more likely to be depredated as those in continuous habitats, and the majority of nests in fragments were depredated by corvids. Studies in forested landscapes also indicate predation rates of nests are influenced by distance to habitat edge (Gates and Gysel 1978, Wilcove et al. 1986, Andren and Angelstam 1988), and the edge-related increase in predation stabilized at  $\sim 200$ – $500$  m from the forest edge (Wilcove et al. 1986, Andren and Angelstam 1988).



Aside from a strong avoidance of juniper woodlands, and slight evidence of selection for nonnative vegetation near nest sites at the 102.1 ha scale, we did not find evidence for selection of other land cover types. While ravens did select trees as nesting substrate 19% of the time, and some of these nests were in junipers, ravens selected lone trees or areas of 1 or 2 trees and avoided the interior and edges of larger woodland stands. Of those nests located in trees, 21% were located in landscaped trees associated with INL facilities. Avoidance of juniper woodlands for nest sites may be the result of reduced prey visibility, as well as the reduced ability to detect and defend against potential nest predators. Ravens nesting in Jackson Hole, Wyoming, USA, chose open habitats rather than forested areas (Dorn 1972), whereas ravens in Grand Teton National Park, Wyoming, USA, were found to nest in isolated stands of trees or on the edges of larger stands, but seldom used areas of 1 or 2 trees (Dunk et al. 1997).

Facilities within the INL provide food and water resources for ravens (Howe 2012), and raven survey results indicate that the odds of raven presence decrease by 4% for every kilometer increase in distance from facilities (Howe 2012). However, we found no significant difference in distance to a facility between nest and random locations. Although we made the assumption that selection of resources was independent of selection by conspecifics, this assumption may have been violated due to the relatively high territoriality of breeding ravens. For example, raven nests were located on or near a number of the facilities, and perhaps these territorial ravens did not tolerate the presence or nest construction of nearby ravens. It may not be energetically profitable or necessary to defend specific food resources at facilities, whereas defense of nesting territory is beneficial for successful reproduction and likely is persistently and aggressively carried out by breeding ravens.

We also found that, on average, available sites were located farther from roads ( $3.87 \pm 0.39$  km) than sites used by ravens ( $2.13 \pm 0.34$  km). The limited evidence in support of this effect corroborates the hypothesis that ravens prefer hunting areas near roads and highways, perhaps in search of dead animals (Heinrich 1989). Although a distance to road model covariate showed some support from our data, this difference was not strong enough for this variable to be included in the most parsimonious models.

We calculated raven nest density within the study area to be 0.12 nests per 10 km<sup>2</sup> averaged over the 3 years of study. These results are similar to estimates of 0.19 nests per 10 km<sup>2</sup> in Utah (Smith and Murphy 1973) and 0.40–0.46 nests per 10 km<sup>2</sup> in Oregon (Stiehl 1978). The density of raven nests in our study area is lower than some other reported estimates in North America. For example, in Wyoming, USA, Bedrosian (2005) reported an estimated

1.88 nests per 10 km<sup>2</sup>, and 2.13 nests per 10 km<sup>2</sup> has been reported in California, USA (Linz et al. 1992). However, increased raven abundance is a relatively recent occurrence in this study area (D. Halford personal communication), beginning in the mid-1990s, and raven nest density will likely continue to increase in the future, especially in response to expanding anthropogenic disturbances and increased fire frequency at the study site.

The most immediate threat to western shrublands is the loss and concurrent fragmentation of native habitats (Rotenberry 1998). Each of the top explanatory variables identified in these resource selection analyses (distance to transmission line, distance to edge, and density of edge) carried significant importance on its own. However, the additive effect of these covariates indicates that ravens are attracted to multiple features, some of which did not exist prior to anthropogenic developments in contiguous sagebrush steppe. Fragmentation related to anthropogenic activities and wildfire appear to provide benefits to breeding ravens, suggesting that their use of edges and tall structures may be opportunistic rather than obligate. The obvious management implication of these analyses is that ravens will benefit from increasing fragmentation. This could have significant deleterious impacts on native bird species within sagebrush steppe ecosystems exposed to disturbances that promote edges. Ravens interact with other wildlife species that depend on sagebrush, for example sage-grouse (Coates et al. 2008). One recent study in a sagebrush ecosystem indicated that nesting and brood-rearing sage-grouse avoided areas with increased densities of ravens (Dinkins et al. 2012). As fragmentation reduces sagebrush cover, and raven populations increase, there may be a hyperpredation effect, whereby sage-grouse risk of nest depredation is determined by the spatial distribution of breeding ravens throughout developed and undeveloped areas.

The infrastructure associated with energy development within sagebrush ecosystems threatens the contiguous habitats remaining in the western United States. Wind energy is the fastest growing sector of renewable energy in the United States, with 20% of the nation's energy expected to be from wind point sources by 2030 (DOE 2008). The linear right-of-ways associated with wind and other energy developments likely provide anthropogenic nesting subsidies and fragmented landscapes, both of which increase nesting opportunities for ravens. Based on the results of this study, preventing fragmentation by transmission lines, roads, crested wheatgrass plantings, and the invasion of other nonnative vegetation is integral to stemming the increase and range expansion of raven populations. Rehabilitating fragmented landscapes to reduce the amount of edge associated with patches, and reconnecting patches of native habitat, may reduce the benefits that edge-dominated areas provide to ravens.

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Dynamics of Greater Sage-grouse (*Centrocercus urophasianus*)

Populations

in Response to Transmission Lines in Central Nevada

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**ABSTRACT**

We monitored greater sage-grouse (*Centrocercus urophasianus*) associated with 13 breeding leks to characterize demographic processes in a ~6500 km<sup>2</sup> area in Eureka County, Nevada. The long-term goal of this ten-year study is to assess the impact of NV Energy's Falcon-Gondor transmission line on sage grouse population dynamics. We used mark-recapture, lek observations, nest monitoring, and radio telemetry to estimate key demographic parameters, and the relationship between these demographic parameters and an individual's proximity to the Falcon-Gondor transmission line. Support for an effect of distance from the Falcon-Gondor transmission line on sage-grouse demographics varied across our different analyses. We found no support for an effect of distance from the FG line on nest site selection and female nesting propensity, weak support for an effect on male survival, and strong support for an effect on nest survival and female survival. As female survival and nest survival have been supported the demographic parameters most strongly associated with population growth, placement of transmission lines in sage-grouse habitat may negatively influence long-term sage-grouse population dynamics.

## INTRODUCTION

Sage-grouse populations have declined range-wide since the mid 1960's, with some states showing stabilizing trends in the past two decades (Connelly et al. 2004). Sage-grouse are an obligate of sagebrush with both adults and young using this vegetation for food and shelter throughout the year and subsisting solely on it during the winter months (Beck 1977, Dalke et al. 1963, Wallestad et al. 1975). Human disruption of the sagebrush biome has contributed to approximately 530,000 square kilometers of sagebrush steppe habitat loss (Crawford et al. 2004, Connelly et al. 2004, Dalke et al. 1963). Given the amount of sagebrush steppe lost and sage-

grouse dependency on sagebrush, it is believed that the loss and degradation of habitat is an important cause of population decline (Connelly et al. 2000).

Elevated structures, such as utility lines can provide perches for avian predators that are higher than those supplied by local vegetation and topography (Ellis 1984, Braun 1998). The only post-hoc study of the impact of utility lines on sage-grouse suggested general lower lek attendance at leks closer to utility lines, but was unable to account for confounding factors that may have influenced both utility line placement and sage-grouse populations (Hall and Haney 1997). It is hypothesized that avian predators of sage grouse adults (raptors) and nests (corvids) may use utility poles and towers to increase their hunting efficiency, in turn reducing adult survival or nest success and triggering population declines in nearby leks (Hall and Haney 1997, Alstatt 1995). Alternatively, the perceived threat of predation associated with utility lines may cause sage-grouse to avoid utility lines, leading to sage-grouse abandonment leks, nest sites, and brood rearing areas near utility lines (Hall and Haney 1997, Braun 1998).

Recent indirect evidence supports an avoidance hypothesis, in that lek locations have been found to have the least long range visibility in combination with greatest short range visibility that local topography will allow (Aspbury et al. 2004). In short, male sage-grouse may be choosing lek locations that maximize their visibility to female grouse near a lek, while reducing long range visibility to predators (Aspbury et al. 2004).

In fall 2003 Sierra Pacific Power Company (now NV Energy) began construction of a 345 kilovolt transmission line between Falcon and Gondor, Nevada (FG line). Construction of the FG line was completed in the spring of 2004 and was energized in May of that year. The FG line is approximately 290 km long and has 735 towers that vary in height from 23 to 40 m, depending

on topography. The FG line runs through the middle Eureka County's prime sage grouse habitat (M. Podborny, NDOW, personal communication).

## **OBJECTIVES**

The goal of this study is to assess impacts of the FG line on population dynamics of greater sage-grouse in the region. The basic study design calls for estimation of key demographic parameters (male lek attendance over time, movement between leks, adult survival rates, nest success, brood survival, recruitment, and population size) as a function of distance from the line. Under the hypothesis that the line negatively affects local sage-grouse, we expect demographic responses to the line to be greatest for leks and/or individuals nearest the line. Distance from line will be directly incorporated into models of demographic parameters to assess this hypothesis. For parameters in which we hypothesize a time delayed response (e.g., adult survival following an increase in raptors) the appropriate analysis includes a time by distance interaction. Thus, though it may not be immediate, we expect (under the hypothesis of an impact of line) a greater decline in adult survival for leks near the line than for leks distant from the line.

To this end, several leks at varying distances from the FG line were chosen to be monitored for ten years. At each of these leks a regime of capture-mark-recapture and observations throughout the strutting season was initiated. We also radio tagged a sample of hens captured each year and followed these hens throughout the breeding, nesting, and brood-rearing seasons. From 2005-2011, we used a combination of Passive Integrated Transponder (PIT) tags and patagial tags to permanently mark sage grouse chicks. Also in 2005, we began what has become an annual fall trap with Nevada Department of Wildlife (NDOW) to increase number of radio-tagged individuals in the population, hunter band returns and number of radio tagged young.



## STUDY AREA

The study site is located in east central Nevada within Eureka County (Fig. 1). It is bounded by the Cortez and Simpson Park Mountains to the west and the Diamond and Sulphur Spring Mountains to the East. This area includes Denay, Pine, Kobeh, Diamond, Horse Creek, Grass, and Garden valleys. The study area encompasses approximately 6500 km<sup>2</sup> of sagebrush steppe and pinyon-juniper mountain ranges with many ephemeral streams. Sage-grouse utilize two main sagebrush communities in the study area. At low elevations (< ~7000 ft), a Wyoming big sagebrush (*A. tridentata wyomingensis*) community is dominant, with pockets of black sagebrush (*A. nova*) and basin big sagebrush (*A. tridentata tridentata*), as well as rubber rabbitbrush (*Chrysothamnus nauseosus*), greasewood (*Sarcobatus vermiculatus*), and some scattered Utah juniper (*Juniperus osteosperma*). At higher elevations (> ~7000 ft), a mixed mountain big sagebrush (*A. tridentata vaseyana*)/low sagebrush (*Artemisia arbuscula*) community is most prevalent, with some intermixed common snowberry (*Symphoricarpos albus*), western serviceberry (*Amelanchier alnifolia*), and bitterbrush (*Purshia tridentata*). Large expanses of singleleaf pinyon (*Pinus monophylla*)/Utah Juniper forest are also common in the study area and in many cases are found mid-elevation between the two sagebrush communities. Common annual and perennial forbs include phlox (*Phlox* spp.), cateyes (*Cryptantha* spp.), tansy mustard (*Descurainia pinnata*), bur buttercup (*Ceratocephala testiculata*), woollystar (*Eriastrum* spp.), lupine (*Lupinus* spp.), desert parsley (*Lomatium* spp.), and desert buckwheat (*Eriogonum* spp.). Grasses consist of blue grass (*Poa* spp.), cheatgrass (*Bromus tectorum*), crested wheat (*Agropyron cristatum*), indian rice grass (*Achnatherum hymenoides*), and squirrel tail (*Elymus elymoides*). Sage-grouse were generally associated with 2 distinct populations centered on

Roberts Creek Mountain and the Cortez Mountain Range. Movements of sage-grouse between these two populations appear to be relatively infrequent.

The study area includes 120 km of the FG line and focuses on thirteen active leks at various distances from the FG line (Fig. 1). Five of these leks have been monitored by NDOW and Bureau of Land Management (BLM) for the past thirty years. Long term data show male lek attendance at these leks has been declining since the early '70s with some signs of stabilization in the late '90s (Fig. 2).

## **METHODS**

### **Field Methods**

**Mark Recapture** - The predominant trapping method used to capture adult sage grouse was night spotlighting (Giesen et al. 1982). We used a high candlepower spotlight to disorient birds while a dip net was placed over them, with white noise generated throughout to mask researcher movement. Binoculars and eyeshine were used to increase the distance at which birds are detected (Wakkinen et al. 1992). To supply power for the spotlight and white noise we used either an ATV or a portable generator strapped to a backpack frame. Small diameter mesh (Giesen et al. 1982) or rubber netting was used to decrease damage to plumage. Other methods were tried such as ground mounted rocket nets (Giesen et al. 1982) and walk-in traps (Schroeder et al. 1991), but were not as successful.

During the breeding season, we captured individuals on each study lek and surrounding area approximately once a week. During the late summer/early fall trap, known brood rearing areas and ridges were scouted one week before the trap, and then intensively trapped for three nights during the new moon in August or September. Upon capture, birds were aged, sexed, weighed, and a series of morphological measurements were taken (length of 1<sup>st</sup> primary, 5<sup>th</sup> primary, wing

chord, tarsus, foot, and number of tail feathers). Each bird was banded with a National Band and Tag metal band, size 16 for males and 14 for females (Walsh 2002), and all adults and those young that were large enough were banded with a colored plastic band engraved with three character alpha-numeric code for re-sighting during lek observations. All hens captured during the lekking season and a subset of hens captured during the fall trap were fitted with a radio collar. A subset of males were radio tagged in both spring and fall. We used radios from Advanced Telemetry Systems, model number A4060. Each radio weighed approximately 22 g, had a battery life of 383-766 days, and a range of 1-5 miles depending on terrain.

***Lek Observations*** - We monitored ten viable leks in 2003, eleven leks in 2004 & 2005 twelve leks in 2006 & 2007, and 13 leks in 2008-2010, within 20 km of the transmission line. Six leks were within 5 km of the FG line and seven leks were greater than 5 km away. Leks were selected by evaluating previously collected data from BLM and the NDOW. Precise locations of monitored study leks are shown in Figure 1.

Each study lek was observed approximately once a week throughout the breeding season, March through May. Observers arrived on the leks 1/2 hour before first light, and remained until strutting activity ceased or birds disbursed (Walsh 2002). During these periods, researchers monitored leks from mobile blinds with high-powered (15x60) spotting scopes and binoculars. We occasionally included a mobile observation tower to facilitate band reading where terrain permitted and vegetation characteristics required it. In 2011, we placed trail cameras on leks to generate additional band reads. We counted the number of males and females, marked and unmarked, on leks every 30 minutes during each observation period. We also recorded individual band codes (resights) and behavioral interactions with potential predators. For lek

disturbances, bird behavior, time, number of birds affected, and type of predator/disturbance were recorded.

***Radio Telemetry*** - During the nesting season (late March to mid June) each hen was located at least once weekly either visually or by triangulation. Nesting hens were monitored twice weekly, and hens with broods were monitored once a week until 45 days post hatch (Schroeder 1997). Following nest failure hens were returned to the breeding season regime above. If a nest failed after strutting ceased the hen was monitored for survival approximately once a week. After all radio-collared hens had fledged their young or failed, they were monitored approximately once a month using fixed-wing aircraft until the next breeding season. In 2008, 2009, and 2010, all birds were monitored more intensively from August – October to document patterns in fall mortality (further description and results in Blomberg et al. 2010).

***Nest Monitoring & Vegetation Sampling*** - Upon locating a nesting hen, a visual check point at least twenty meters away was marked with a cairn of rocks or local debris and a GPS point recorded. If environmental conditions were favorable (no storm on the horizon and no predators seen nearby) the hen was approached and flushed from the nest. Size of clutch was recorded, eggs were floated to determine stage of incubation, and each egg's length & width was measured. Age of each nest was estimated using egg float data, assuming incubation began with laying of the last egg and one egg was laid every 1.3 days (average laying time per egg [Dalke et al. 1963]). Within 24 hours the nest was checked again from a distance to confirm the hen's return. Nest monitoring followed a twice weekly regime until hatch or failure. A nest was determined successful/hatched if the hen was located nearby with chicks or if at least one egg was present with crown removed and/or the shell membrane was present and detached.

Vegetation was measured at each nest site within 3 days of hatch, or on the predicted hatch date for failed nests. We placed two perpendicular 10 m transects centered at the nest and recorded the percent shrub cover for each meter along the transect (Gregg 1994). In addition, five 20 X 50 cm Daubenmire plots were placed along each transect, where percent cover of grass and forbs was estimated and all plants were measured and identified to species. The same data collected for the Daubenmire plots were also collected for the m<sup>2</sup> area around the nest bowl (Sveum 1998). These same vegetation measurements are also made at 24 random points, located throughout the study area each year.

***Brood Trapping, Monitoring, & Vegetation*** - Within three days of hatch broods were trapped and processed (Gregg 2001). Like Gregg (2001) we found hens to still be brooding their young during the hours before dawn within 2 to 3 days after hatch. Hens were flushed and the young were gathered by hand and placed in a cloth sack, which was then placed inside a researcher's jacket to maintain chick body temperature. Processing involved weighing the individual chicks, measuring their tarsus, foot, and length of bill to back of the head, as well as uniquely marking each individual (Carver et al. 1999, Becker et al. 1997). Once processing was completed, the entire brood was released together and researchers moved away from the brood in the direction opposite where the hen was last heard or seen. Throughout processing the brood the hen's position was periodically determined via radio or visual check, and we remained in the area long enough to confirm reassociation of the hen and chicks.

After capture, broods were checked once a week, hens were flushed and chicks counted to determine fledging and survival rates. In 2008, we modified brood check procedures to increase the precision of our brood count estimates. From initial capture to ~ 30 days of age, each brood was flushed weekly during the early morning while the chicks were still congregated near the

hen. Following 30 days, chicks were counted while roosting at night using a spotlight and binoculars/spotting scope. We continued to collect a daytime location once a week for vegetation monitoring, however lower importance was placed on obtaining a mid-day flush count. Each daytime location was recorded using a GPS and we returned in 3-6 days to measure vegetation. Vegetation measurements were the same as those for 10 m nest transects. In addition to the vegetation measurements, we placed 5 pit traps filled with nontoxic glycerin glycol along one of the transect lines to assess arthropod densities (Gregg 2001).

***Raptor/Corvid Surveys*** - Three transects were located along the FG line in the north, central, and southern portions of the study area. The northern transect had 9 points, the central had 9 points, and the southern had 5 points. We attempted to survey each transect once every 10 days. Starting times (1 hr after sunrise or at 13:00 hrs) and starting direction (north or south) were alternated. Surveys were not conducted if there was precipitation, fog, or if wind speeds exceeded 19 km/hr. Observers spent 10 minutes at each point, identified all raptor and corvid species, number of individuals, activity (perched or flying), location if perched (power line, deterrent, fence, etc), and whether it was within ¼ mile of the line or beyond.

## **Quantitative Analyses**

For 2012 we've conducted demographic analyses in Program MARK (White and Burnham 1999) using data from marked individuals to answer specific research questions regarding various sage-grouse life history stages. We discuss the specific MARK models briefly, and then focus on each individual life stage analysis.

***General modeling approach*** – All demographic analyses were conducted in a general linear modeling framework, and we used an information theoretic approach to model selection (Burnham and Anderson 2002). Covariates were grouped together by type (micro habitat, macro



habitat, environmental, disturbance, individual heterogeneity) and added to a model one covariate at time. Covariates that were correlated with each other (Pearson's  $r > 0.50$ ) were not included in the same models. Although we acknowledge that we were conservative with our cut-off value for correlated variables, we chose a correlation of 0.50 to minimize biased interpretations of spatially-correlated covariates. We evaluated support for explanatory covariates based on their inclusion in competitive models ( $\Delta AIC < 2.0$ ), and their  $\beta$  coefficients and associated estimates standard errors. All covariates were z-standardized (mean = 0.0, standard deviation = 1.0).

***Assessing impacts of the Falcon-Gondor transmission line*** - The underlying hypothesis for each analysis was that a particular demographic rate (i.e., nest success, female survival) was not influenced by an individual's proximity to the FG line. Environmental impact studies often employ a Before-After-Control-Impact (BACI) study design to account for correlations between various temporal or spatial variables and the potential disturbance, which when left unaccounted for may either mask or inflate reported impacts. For this study, a BACI study design was not possible because there was not an adequate period of time to adequately estimate demographic parameters prior to construction of the FG line. Therefore, our modeling approach had to account for potential correlations between an individual's distance from the FG line and other confounding variation. Although modeling interactions between covariates can be an appropriate method for accounting for correlations in models with a few covariates, complex models with numerous parameters and multiple interactions are both difficult to interpret and are sensitive to sparse or outlier data.

Our approach to account for demographic heterogeneity among individuals, while minimizing the number of modeled parameters and interactions between parameters, was to use

the parameter coefficients from the most competitive model structure that did not consider the distance from the FG line covariate. This model was used to develop an estimate of the demographic rate of interest for each individual in each demographic analysis. This estimate represented the predicted demographic probability (e.g., survival) for an individual; given characteristics of the individual and other environmental factors (e.g. habitat characteristics) that individual was exposed to, and in the absence of any transmission line effects. This value was then used as an individual covariate (hereafter demographic weight) in a second analysis where we considered a series of models designed to evaluate whether an individual's proximity to the FG line influenced their demographics, while explicitly accounting for the individuals demographic weight. Support and direction of the effect of distance to the FG line would be inferred from the competitiveness of the models that included distance to the FG line as additive or interactive effects relative to a null (intercept-only) and demographic weight-only models. Lastly, our male capture-mark-recapture data has an inherent spatial structure defined by individual assignment to breeding leks. To evaluate the potential influence of the FG line on male survival, given this spatial structure, we compared models where survival of males assigned to each lek varied independently, with models where survival varied as a function of distance to the FG line. A more detailed description of this approach can be found in the male survival portion of the statistical analyses section.

### ***Description of statistical analyses***

*Female survival:* We used our female telemetry data to estimate 'true' survival ( $S$ ) of breeding-aged female sage-grouse in a known-fate framework in Program MARK. Known-fate models assume that each individual is sampled, or located, during each sampling interval and that their fate (alive or dead) is assigned correctly. As all individuals are detected, estimation of a

detection parameter is not necessary, which allows for more precise estimates of survival.

Additional information on our female survival analyses can be found in Blomberg et al. (2013).

*Female nesting propensity:* We used female telemetry data to conduct a multistate analysis in

Program MARK, which estimated the probability of transitioning to a defined state based on

previous status and explanatory covariates. We developed a novel multistate approach that used repeated observations of individuals in observable states to estimate female breeding propensity,

which we define as the probability that a female initiated a nest during a given nesting season.

We also estimated re-nesting propensity in similar fashion. Multistate models allow estimation of

probability of apparent survival ( $\phi$ ) between sampling periods for individuals within each state,

probability of detection ( $p$ ) of individuals in each state during each sampling interval, and

probability of transitioning ( $\psi$ ) from each state to another state between sampling periods. In this

analysis, states were defined as female located off a nest (A), female located on her first nest (B),

and female located on a second or third nest (C). Therefore,  $\psi_{AB}$  represents the probability an

individual would initiate a nest during an interval,  $\psi_{BA}$  represents the probability an individual

would fail her first nest during an interval,  $\psi_{AC}$  represents the probability an individual would

initiate a second or third nest during an interval, and  $\psi_{CA}$  represents the probability an individual

would fail a second or third nest attempt during an interval.  $\psi_{BC}$  and  $\psi_{CB}$  were fixed to zero

because a female must transition back to a non-nesting state between her first and second nesting

attempts, and transitioning from a second nest attempt to first nest attempt is not possible.

Sampling periods were modeled as 30 consecutive two day intervals, which occurred during the nesting season (April 1<sup>st</sup> - May 31<sup>st</sup>).

The different  $\psi$  parameters can be used to estimate various demographic rates of interest such as interval-specific nest initiation rates and overall nest initiation rates. The interval-specific nest

initiation rate (Equation 1) represents an estimate of nest initiation during a specific interval after accounting for the probability an individual could have initiated a nest earlier in the season.

**Equation 1:**

$$\psi_{Int_n} = \psi_{AB_{j+1}} \times \prod_{i=1}^{j=n-1} \left[ 1 - \psi_{AB_i} \quad 1 - \psi_{AB_{i+1}} \quad \dots \quad 1 - \psi_{AB_j} \right]$$

Overall nest initiation rate represents the probability that an individual would initiate a nest at least once during a nesting season (Equation 2).

**Equation 2:**

$$\psi_{Nest} = 1 - \left[ \prod_{i=1}^{ij} 1 - \psi_{AB_i} \quad 1 - \psi_{AB_{i+1}} \quad \dots \quad 1 - \psi_{AB_j} \right]$$

*Nest survival:* We used our nest monitoring data collected from nesting radio-marked females to estimate nest success with the nest survival module in Program MARK. The nest survival module is a modified known-fate analysis that estimates a probability of daily nest survival ( $S$ ). Unlike apparent nest success (the proportion of nests in a sample that hatch), daily nest survival approaches account for differences in detection between failed and active nests and the fact that nests found further along in incubation are more likely to hatch than nests found earlier in incubation.

*Nest site selection:* We used vegetation and spatial data collected from nest sites (used) and random points (available) to estimate the relative probability that a given location would be selected as a nest site. We used resource selection function models (RSF; Manly et al. 2002) in a generalized linear mixed model framework (Zuur et al. 2009) using the lme4 package in Program

R (Team 2010). We followed methods outlined by Boyce and McDonald (1999) and Hebblewhite and Merrill (2008) to estimate relative probability of use, given the best-fit model.

*Male survival:* We used our capture-mark-recapture dataset of banded male sage-grouse to estimate survival in a robust design framework in Program MARK. Robust design models allows for estimation of state-specific apparent survival ( $\phi$ ), detection ( $p$ ), and re-detection ( $c$ ) parameters, as well as temporary emigration ( $\gamma$ ) parameter, which was equivalent to the probability of a male being absent from a lek during a given breeding season (Blomberg et al. 2013). For this analysis, males were grouped by lek, and  $\phi$ ,  $p$ , and  $c$  were allowed to vary independently among leks. We estimated the proportion of spatial variance in  $\phi$  explained by spatial covariates, such as a lek's distance from the FG line, with an approach originally developed to estimate the proportion of temporal variation explained by climatic covariates ( $R^2_{Dev}$ ; Grosbois et al. 2008):

$$R^2_{Dev} = \frac{Dev(F.) - Dev(F_{cov})}{Dev(F.) - Dev(F_{group})}$$

where  $Dev$  corresponds to the model deviance for the constant ( $F.$ ), group varying ( $F_{group}$ ), and spatial covariate ( $F_{cov}$ ) models. A model that allowed for full group variation on the detection and survival parameters would account for all spatial heterogeneity within those parameters, just as a fully time-varying model would account for all temporal heterogeneity within the parameters. Therefore, use of this approach to estimate the proportion of spatial variance in  $\phi$  explained by spatial covariates is logically sound. Further information regarding our male banding analyses can be found in Blomberg et al. (2012, 2013) and Gibson et al. (2013).

### *Description of covariates*

***Female survival*** - We developed a suite of time-varying spatial covariates for the female survival analyses based on the average values for particular habitat features associated with an individual's locations during a given month. We estimated spatial variables for each month for each female from the Southwest Regional GAP (SWREGAP; USGS National Gap Analysis Program 2004) database, the Climatic Water Deficit Toolbox for ArcGIS 10 (Dilts 2013), a National Elevation Dataset Digital Elevation Model (NED DEM; USGS), the Nevada Department of Wildlife wildfire data layer, and a roads data layer for Eureka County, NV. We used the spatial analyst toolbox in ArcMap 10.0 to estimate the amount of habitat classified as each predictor variable within 1000m for every telemetry location from a female, which were then binned into monthly averages for each female. Covariate values were only generated for the months from March-September for each year (2003-2012) due to scarcity of female location data outside that time period. Covariates included averages of the amount of habitat classified as Wyoming big sagebrush, mountain big sagebrush, all sagebrush, pinion-juniper, and exotic grasslands within 1000m of a female location. We also included a climate water deficit variable represented as a monthly estimate of actual evapotranspiration (AET) within 1000m of a female location, as well as a monthly average elevation for each female. We included binomial covariates that delineated which population (i.e., Cortez or Roberts Mountain) an individual was associated with, which trapping season a female was captured (i.e., spring or fall), and whether or not a female was a successful nester (i.e., hatched or failed). Finally, monthly average minimum distance from a road and monthly average distance from the FG line were also considered to assess the impacts of these anthropogenic features.

***Female nesting propensity*** - We developed a suite of time-varying spatial covariates for the female nesting propensity analyses that represent the average value from all telemetry locations

from a given nesting season (April 1st-May 31st). We estimated spatial variables for each nesting season for each female from the Southwest Regional GAP (SWREGAP; USGS National Gap Analysis Program 2004) database, the Climatic Water Deficit Toolbox for ArcGIS 10 (Dilts 2013), a National Elevation Dataset Digital Elevation Model (NED DEM; USGS), the Nevada Department of Wildlife wildfire data layer, and a roads data layer for Eureka County, NV. We used the spatial analyst toolbox in ArcMap 10.0 to estimate the amount of habitat classified as each predictor variable within 1000m for every telemetry location for a female, which were then binned into nesting season averages for each female. Covariates included averages of the amount of habitat classified as Wyoming big sagebrush, mountain big sagebrush, all sagebrush, pinion-juniper, and exotic grasslands within 1000m of a female location. We also included spatial climate water deficit variables represented as monthly estimates of actual evapotranspiration (AET), potential evapotranspiration (PET), 30-year temperature, and 30-year precipitation within 1000m of a female location, as well as the average elevation of a female during the nesting season. We included binomial covariates that delineated which population (i.e., Cortez or Roberts Mountain) an individual was associated with, and in which trapping season a female was captured (i.e., spring or fall), as well as a minimum hen age covariate. Lastly, we included covariates that represented average road density near a female, average minimum distance from a road, and average distance from the FG line.

***Nest site selection/Nest survival*** - We used a suite of macro habitat characteristics that estimated habitat structure, topography, and disturbance in buffers of three sizes around each point (500m, 1000m, and 2000m radius). Macro habitat predictor variables were generated for every nest location and for each random point. Random points were randomly generated in ArcMap 10.0 (Environmental Systems Research Institute, Redlands, CA) from a data layer



defined by fixing a 1000m buffer around all spring telemetry locations (April 1<sup>st</sup> – June 15<sup>th</sup>) of radio-marked females collected from 2004-2012. The buffered spring telemetry location layer represented a coarse approximation of habitat available to our sample of nesting sage-grouse. We randomly generated approximately one point per km<sup>2</sup> of available habitat which yielded 2200 random points. Each spatially-generated random point was randomly assigned a year and randomly paired with an actual nest point. We extracted geospatial variables for the nest and random points from the Southwest Regional GAP (SWREGAP; USGS National Gap Analysis Program 2004) database, a National Elevation Dataset Digital Elevation Model (NED DEM; USGS), the Nevada Department of Wildlife wildfire data layer, and a roads data layer for Eureka County, NV. We used the spatial analyst toolbox in ArcMap 10.0 to estimate the amount of habitat classified as each predictor variable within buffers of three sizes (radii of 500m, 1000m, and 2000m) centered at each point. In buffers of each size, we measured road density, and the amount of habitat classified as sagebrush, Wyoming big sagebrush, mountain big sagebrush, exotic grasslands, and pinyon-juniper woodlands. Additionally, we estimated slope, elevation, northness ( $\text{northness} = (\cos(\text{aspect}^\circ))$ ), and eastness ( $\text{eastness} = \sin(\text{aspect}^\circ)$ ) of each point, distance from each point to the nearest road, and distance from each point to the FG line. Owing to the conversion of sagebrush habitat to exotic grasslands due to wildfires within our study area during the study, the wildfire data layer was modeled as a time varying covariate for each year at each spatial extent. The amount of habitat classified as exotic grassland for each nest and random point was calculated from the appropriate wildfire data layer for the year the survey was completed. Because random points were randomly assigned a year, they were also attributed the wildfire value for that year.

The nest survival analysis also incorporated micro habitat predictor variables that were generated from the nest vegetation survey data. The ground predictor variables for these analyses included total vegetative cover, forb height, grass height, and shrub height within 1m<sup>2</sup> of the nest, and total cover, forb cover, grass cover, average forb height, average live grass height, average residual grass height, average shrub height, total shrub cover (combined, <40cm, 40-80cm, >80cm), sagebrush cover (combined, <40cm, 40-80cm, >80cm), and non-sagebrush shrub cover within 100m<sup>2</sup> of the nest.

***Male survival*** - As our male database was generated from recaptures and resights of banded individuals, we did not have the ability to assign habitat-based covariates to individual males based on their individual patterns in habitat use. We were able to assess spatial and temporal heterogeneity in survival and detection by grouping individuals captured on the same lek and modeling year and/or lek-level constraints. Additionally, we used time-varying lek-level covariates, in which individuals were assigned a value depending on which lek they were captured or redetected on, to assess which spatial mechanisms influenced male survival. We quantified spatial covariates for each study lek from the Southwest Regional GAP (SWREGAP; USGS National Gap Analysis Program 2004) database, a National Elevation Dataset Digital Elevation Model (NED DEM; USGS), the Nevada Department of Wildlife wildfire data layer, and a roads data layer for Eureka County, NV. We used the spatial analyst toolbox in ArcMap 10.0 to estimate the amount of habitat classified as exotic grasslands and road density within 5km of a lek. We also included lek elevation and the population (i.e., Cortez or Roberts Mountains) each lek was associated with as covariates. Lastly, we included the lek's distance from the FG line as a covariate.

## RESULTS

## Field Results

***Banding*** - During spring trapping we have banded a total of 1116 sage grouse (891 males and 225 females) over nine years of the project (Table 1). During fall trapping, we have banded 264 sage-grouse (155 females, 96 males, and 13 unknown gender chicks) over 7 years. With multiple captures of the same individual within the same year included, we have captured a total of 1785 sage grouse over ten years of this study.

***Lek Observations*** - We conducted 107 total lek observations during the 2012 breeding season. The total number of males observed across all leks continued to show signs of stabilization (Table 2). We observed increased male attendance on 6 leks (Dome House, Lone Mountain, Kobeh, Horse Creek, Pony Express, Quartz Road), and decreased male attendance on 6 leks (Big Pole, Buckhorn, Gable Canyon, Henderson Pass, Modarelli Mine, Pinefield). We observed no males strutting on Camp lek for the third straight year. In 2012, we generated 135 total resights of 402 unique individuals. Total resights of color-banded individuals by year are summarized in Table 1.

***Raptor Surveys*** - In the ten years of the study we conducted 212 raptor surveys for a total of 1620 points. The average number per point for each of the most common raptor species has remained relatively stable over the study (Table 3). The average numbers of common ravens seen per point increased dramatically between 2003 and 2007, declined drastically during 2008 to the second lowest level since the project was initiated, and have again increased over the past 4 years to near 2007 levels (Fig 4). A similar trend in common ravens sightings at sage grouse leks was also observed (Fig. 4).

***Nest monitoring*** – We discovered and monitored 427 nests from 249 unique females from 2003-2012, of which 138 nests from 116 unique females were successful. We classified 355 of the

nests at first nests, 66 as second nests, and 6 as third nest attempts. Adults initiated 312 of the nests, juveniles initiated 96, and 19 nests were from unknown aged females. Additional information regarding annual nesting summary statistics can be found in table 4.

**Brood/Chick Monitoring** - We captured and marked 120, 122, 110, and 97 unique individual chicks from 2009-2012, respectively, and recaptured 14, 26, 27, and 25 of them at approximately 28 days of age. In 2012, we recaptured two adult male sage-grouse that were originally marked with a patagium wing marker at hatch. One male that was recaptured as an adult at the dome house lek was originally marked in 2010 as a chick. His mother was captured at dome house and in 2010 nested approximately 1.5 km from the dome house lek. The other male was recaptured as an adult at Quartz road and was originally marked in 2008 as a chick. His mother was originally captured at horse creek and nested approximately 3.6 km from the Quartz road lek in 2008, and in 2009-2010 she bred at Quartz road.

**Radio Telemetry & Known Fate** - A total of 225 females and 63 males have been radio collared during the spring over the study. During the fall (in collaboration with NDOW) we have radio collared 140 females of which 83 have been adult birds (>1 year old) and 76 have been young of the year (YOY) hens. We have also radioed 16 YOY males during the fall. The number of females monitored per year and breeding rates are summarized in Table 4.

## **Quantitative Results**

**Nest site habitat selection** - Model selection and parameter coefficients from the nest site RSF analysis supported a negative interaction ( $\beta = -0.62$ , 85% C.I.:  $-0.74 - -0.50$ ) between the amount of habitat classified as sagebrush within 1000m ( $\beta = 1.43$ , 85% C.I.:  $1.26 - 1.60$ ) and distance from a lek ( $\beta = -0.64$ , 85% C.I.:  $-0.77 - -0.52$ ), which suggested that females selected for nest sites composed of predominantly sagebrush that were near leks (Table 5). Additionally, there

was strong support for a negative interaction ( $\beta = -0.33$ , 85% C.I.:  $-0.43 - -0.26$ ) between slope ( $\beta = 0.51$ , 85% C.I.:  $0.37 - 0.65$ ) and elevation ( $\beta = 0.60$ , 85% C.I.:  $0.48 - 0.71$ ), which suggested preferential use of areas of moderate elevation with moderate slopes (Table 5).

Model selection and parameter coefficients from the RSF analysis (Table 7) did not support a substantial effect of distance from the transmission line on female nest-site selection, after accounting for other spatial heterogeneity in the study landscape (Fig 1). The lack of support of the distance to FG line suggests that we cannot reject the null hypothesis that distance from the FG line does not influence nest site selection.

***Nest survival*** - Model averaged estimate of daily nest survival was 0.95 (95% C.I.: 0.945-0.957), which was equivalent to an overall probability of nest success (37 day exposure period) of 0.17 (95% C.I.: 0.13 – 0.21). Model selection and parameter coefficients from the nest survival analysis supported a positive interaction ( $\beta = 0.32$ , 85% C.I.: 0.14– 0.49) between non-sagebrush shrub cover ( $\beta = 0.30$ , 85% C.I.: 0.17– 0.42) and forb cover ( $\beta = 0.26$ , 85% C.I.: 0.14– 0.37) within 100m<sup>2</sup> of a nest (Table 7). Additionally, a positive effect of average shrub height within 100m<sup>2</sup> of a nest ( $\beta = 0.12$ , 85% C.I.: 0.03– 0.21) was supported. A negative effect of the amount of habitat classified as exotic grasslands as a result of wildfire within 2000m of a nest ( $\beta = -0.12$ , 85% C.I.:  $-0.21 - -0.02$ ) was also supported. A positive effect of clutch size ( $\beta = 0.21$ , 85% C.I.: 0.12– 0.30) was supported, indicative of a relationship between either overall hen quality or the amount of resources allocated for a nesting attempt and nesting success. Lastly, a negative effect of a female being initially radio-marked in the fall as opposed to the spring was supported ( $\beta = -0.21$ , 85% C.I.:  $-0.30 - -0.13$ ). See appendix A for additional model selection results.

Model selection and parameter coefficients from the demographic-weighted nest survival analysis supported a positive interaction ( $\beta = 0.08$ , 85% C.I.:  $-0.03 - 0.17$ ) between distance from

the FG line ( $\beta = 0.14$ , 85% C.I.: 0.03– 0.24) and the demographic weighting covariate ( $\beta = 0.46$ , 85% C.I.: 0.37– 0.56) (Table 10). This relationship suggested that nests with a higher probability of hatching (e.g., from a higher quality female or located in otherwise more productive nesting habitat) were more likely to hatch when they located further from the FG line. Although nests that were less likely to hatch (e.g., from low quality females or poor nesting habitat) were not influenced by their proximity to the transmission line (Fig 3), their probability of nest success was in general very low regardless of their proximity to the FG line. These results suggest that the probability that a high quality nest hatches improves by 6% for each 5km between the nest and the FG line, however inferences made beyond 20km from the transmission line should be limited. We speculate that the observed relationship between distance from the FG line and nest success could be a result of increased nest predation pressure on nests located closer to the FG line, and that we can only observe the effect on high quality nests because they are able to survive longer under higher levels of predation pressure compared to lesser quality nests.

***Nesting propensity*** - We found support for a strong, but variable effect of the elevation at which a female was located on the probability of nest initiation (Table 9). During the first half of the nesting season, elevation negatively affected the probability of nest initiation ( $\beta = -0.38$ , 85% C.I.: -0.53– -0.24), however in the latter half of the nesting season, elevation was positively associated with nest initiation ( $\beta = 0.45$ , 85% C.I.: 0.33– 0.58). This relationship is most likely related to seasonal variation in snow cover between high and low elevation habitat, where early in the nesting season only low elevation habitats were functionally available, compared to later in the nesting season where higher elevation habitat was available and potentially in better condition. Additionally, we found support for a quadratic relationship ( $\beta = -0.08$ , 85% C.I.: -0.13– -0.03) between a female's age ( $\beta = 0.22$ , 85% C.I.: 0.12– 0.31) and nesting propensity

which suggested that the probability a female would initiate nest increased as she aged until about 4 years of age, and then declined.

Model selection and parameter coefficients from the demographic-weighted nesting propensity analysis (Table 10) did not support a substantial effect of distance from the FG line on nest initiation rates (Fig 6). The lack of support of the distance to FG line suggests that we cannot reject the null hypothesis that distance from the FG line did not affect female nesting propensity.

***Female survival*** - Estimates of monthly survival ranged from a low of 0.92 ( $\pm 0.01$  SE) during the fall (Aug-Oct) to a high of 0.99 ( $< \pm 0.01$  SE) during the winter (Nov-February), which translated into an annual survival of 0.58 ( $\pm 0.02$  SE). Model selection and parameter coefficients from the female survival analysis supported a positive effect of the average amount of habitat classified as Wyoming big sagebrush within 1km of all of a female's locations during spring ( $\beta = 0.18$ , 85% C.I.: -0.01– 0.37) (Table 11). A negative effect of population with which a female was associated ( $\beta = -0.15$ , 85% C.I.: -0.33– 0.02) (i.e., Cortez or Roberts Mountains) was also supported during the spring months, which suggested that females in the Cortez mountains had higher survival during the spring. A negative effect of season the female was captured (spring or the fall;  $\beta = -0.81$ , 85% C.I.: -1.17– -0.44) was supported during the summer months, which suggest spring-captured females were more likely to survive during the summer than females that were originally captured during the fall. A negative effect of nest success ( $\beta = -0.50$ , 85% C.I.: -0.85– -0.16) was supported during the summer months after the nesting season terminated which suggested that females that hatched a nest were more likely to survive the summer than females that were unsuccessful. Lastly, a negative effect of average amount of habitat classified as exotic grasslands across all locations of a female was supported ( $\beta = -0.39$ ,



85% C.I.: -0.68– -0.11), which suggested that females using habitat with greater conversion to exotic grasslands due to wildfire were less likely to survive.

Model selection and parameter coefficients from the demographic-weighted female survival analysis found modest support for a negative interaction ( $\beta = -0.13$ , 85% C.I.: -0.28– 0.00) between a female's monthly average distance from the FG line ( $\beta = -0.18$ , 85% C.I.: -0.03– -0.39) and the weighting covariate ( $\beta = 0.54$ , 85% C.I.: 0.36– 0.73) (Table 12). Also, a model that only considered additive effects of distance to the FG line ( $\beta = 0.26$ , 85% C.I.: 0.06 – 0.45) and weighting covariate ( $\beta = 0.43$ , 85% C.I.: 0.28 – 0.58) performed similarly. Together, these models suggested that the survival of at least a subset of the female population was influenced by their proximity to the FG line (Fig. 4) and that individuals who exhibited behaviors linked with lower survivorship were more affected. As reproductive success, both nest success and brood survival, been associated negatively with female survival (Blomberg et al. 2013), females of higher fitness may be more affected by their proximity to the FG line.

**Male survival** - We found strong support for a positive relationship between annual precipitation ( $\beta = 0.43$ , 85% C.I.: 0.21 – 0.66) and annual male survival, similar to previous results published from this study system (Blomberg et al. 2012) (Table 13). Annual precipitation accounted for the majority of the temporal variation in survival ( $R^2_{Dev} = 0.65$ ) as well as a fair amount of the variation from all sources (i.e., temporal, spatial, unknown) in survival ( $R^2_{Dev} = 0.35$ ) (Table 14). Temporal processes accounted for the majority of variation in the data ( $R^2_{Dev} = 0.54$ ), spatial process accounted for a fair amount of variation ( $R^2_{Dev} = 0.31$ ), which left approximately 15 percent of the variation unaccounted for (e.g., sampling variance). Lek-specific estimates of average annual male survival ranged from a low of 0.39 ( $\pm 0.06$  SE) at the Dome House lek to 0.60 ( $\pm 0.04$  SE) at the Pony Express lek (Table 15). Leks associated with the

Roberts Creek Mountains, which were on average located closer to the FG line than leks associated with the Cortez mountains, showed a positive relationship between distance from the FG line and annual survival (Fig. 5). Leks associated with the Cortez mountains appeared to have the opposite relationship with distance from the FG line (Fig. 5). Additionally, there was very weak support in model selection and parameter estimates for an interaction ( $\beta = 0.31$ , 85% C.I.: -0.11 – 0.50) between population (Cortez or Roberts Creek mountains;  $\beta = 0.11$ , 85% C.I.: -0.01 – 0.24) and a quadratic relationship of distance from the FG line ( $\beta = 0.17$ , 85% C.I.: -0.20 – 0.55) (Fig. 5), which accounted for  $R^2_{Dev} = 0.38$  of the spatial variation, or  $R^2_{Dev} = 0.12$  of all variation in survival. A fair amount of the variation explained by the model was associated with the population covariate, which was partially confounded with other spatial covariates. Therefore, the amount of variation explained in this model should not be interpreted as solely the proportion of variance explained by a lek's distance from the FG line, as there is a slight positive bias. A model that only considered a quadratic relationship ( $\beta = 0.27$ , 85% C.I.: -0.13 – 0.67) between distance from the FG line ( $\beta = -0.05$ , 85% C.I.: -0.52 – 0.41) and survival was also not supported, and accounted for  $R^2_{Dev} = 0.13$  of the spatial variation, or  $R^2_{Dev} = 0.04$  of all variation in survival. It is also possible that there is heterogeneity in survival at the population-level related to a lek's proximity to a transmission line (e.g., existence of a maximum threshold distance for an effect to exist). This would be partially explained by the population covariate, and it is appropriate to assume that the actual proportion of the variation in survival explained by a lek's distance from the FG line falls between 0.04 (FG<sup>2</sup> model) and 0.12 (FG<sup>2</sup> \* Population model).

Together, results from model selection, parameter estimates, and proportion of variation explained by a lek's distance from the FG line, suggest that we can observe a slight positive

relationship between a lek's distance from the FG line and annual male survival; however this relationship is weak and accounted for a relatively small amount of the total variation we observed in annual male survival.

***Management implications*** - Support for an effect of distance from the FG line on sage-grouse demographics was variable across our analyses. Although we found no support for an effect of distance from the FG line on nest site selection (Fig. 4) and female nesting propensity (Fig 6), we found support for a small effect on male survival (Fig 8), and support for substantial effects on nest survival (Fig 5) and female survival (Fig 7). Published results suggest that population growth in sage-grouse is highly sensitive to variation in female survival and nest survival (Taylor et al. 2011); therefore we urge caution when placing transmission lines within sage-grouse habitat. Additionally, placement of the Falcon-Gondor transmission line was selected specifically to minimize the disturbance to sage-grouse (M. Podborny, NDOW, personal communication), therefore our results may underestimate the influence of transmission lines in general on sage-grouse demographic rates, depending on line placement. Current management guidelines for elevated structures within sage-grouse habitat, which were not informed by empirical assessments of transmission lines effects on demographic rates, suggest that no elevated structures should be placed within 5km of a lek (Coates et al. 2013). Our preliminary results suggest that this threshold may need to be increased to minimize demographic responses to transmission lines. Additionally, although there are concerns about the use of a lek-centric methodology for designating a buffer to improve nest survival, results from our nest site selection analysis strongly supported that nesting female sage-grouse selected habitat within a few kilometers from a lek, therefore a lek buffer would encapsulate the majority of nesting

females. Lastly, we must caution limited interpretation from these results as they have not undergone peer review.

***Future analyses*** - We plan to use our male mark-recapture data to assess the influence of the FG line on male lek movement patterns and recruitment using a multistate-robust design and Pradel models, respectively. Additionally, we plan to use our chick monitoring and brood vegetation data to assess the influence of the FG line of chick survival and brood-group habitat selection.

***Current publications from our study***

Gibson, D., E.J. Blomberg, M.T. Atamian, and J.S. Sedinger. *In revision*. High lek fidelity of male greater sage-grouse. *Ibis*. 00:000-000.

Blomberg, E. J., P. L. Wolff, and J. S. Sedinger. *In press*. Geographic variation in liver metal concentrations of greater sage-grouse. *Journal of Fish and Wildlife Management* 00:000-000.

Blomberg, E. J., D. Gibson, J. S. Sedinger, M. L. Casazza, and P. S. Coates. *In press*. Intraseasonal variation in survival and cause-specific mortality of greater sage-grouse. *Wildlife Biology* 00:000-000.

Blomberg, E. J., S. R. Poulson, J. S. Sedinger, and D. Gibson. 2013. Prefledging diet is correlated with individual growth in greater sage-grouse (*Centrocercus urophasianus*). *Auk* 130:715-724.

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Blomberg, E. J., J. S. Sedinger, D. V. Nonne., and M.T. Atamian. 2013. Seasonal reproductive costs contribute to reduced survival of female greater sage-grouse. *Journal of Avian Biology* 44:149-158.

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Table 1. Number of males captured, recaptured, and resighted during spring trapping. Number of unique individuals is shown in parentheses.

<b>Year</b>	<b>New Captures</b>	<b>Recaptures</b>	<b>Resights</b>	<b>Collared Males</b>
2003	146	26(20)	12(11)	7
2004	106	43(36)	41(26)	5
2005	104	55(48)	37(25)	1
2006	134	37(35)	56(35)	1
2007	113	37(30)	34(12)	4
2008	62	30(26)	91(45)	14
2009	46	50(34)	59(23)	9
2010	50	35(31)	109(33)	22
2011	63	44(30)	107(42)	23
2012	68	13(12)	135(40)	8
<b>Total</b>	<b>824</b>	<b>370</b>	<b>681</b>	<b>63*</b>

\* Does not account for unique individuals monitored across study years.



Table 2. Highest single day lek attendance for each lek by sex and year.

**Males**

<b>Lek</b>	<b>2003</b>	<b>2004</b>	<b>2005</b>	<b>2006</b>	<b>2007</b>	<b>2008</b>	<b>2009</b>	<b>2010</b>	<b>2011</b>	<b>2012</b>
Big Pole	13	16	20	19	11	21	22	25	13	2
Buckhorn	23	39	40	48	21	10	11	7	3	1
Camp	8	12	9	9	7	5	4	0	0	0
Dome House	15	17	28	47	22	23	12	17	9	12
Gable Canyon	18	21	30	23	12	19	19	7	12	11
Horse Creek	43	61	40	31	17	15	4	8	8	17
Henderson Pass						27	16	7	8	7
Kobeh	14	10	12	54	6	7	6	9	14	15
Lone Mountain	32	33	50	63	56	34	22	17	30	41
Modarelli Mine	11	9	23	47	17	23	16	19	28	21
Pinefield	36	37	49	67	34	27	22	29	30	25
Pony Express	14	11	15	15	10	6	8	0	11	21
Quartz Road				34	11	22	20	36	27	33
<b>Total</b>	<b>227</b>	<b>266</b>	<b>316</b>	<b>423*</b>	<b>224</b>	<b>212*</b>	<b>182</b>	<b>181</b>	<b>193</b>	<b>206</b>

**Females**

<b>Lek</b>	<b>2003</b>	<b>2004</b>	<b>2005</b>	<b>2006</b>	<b>2007</b>	<b>2008</b>	<b>2009</b>	<b>2010</b>	<b>2011</b>	<b>2012</b>
Big Pole	2	6	2	6	0	5	0	0	4	1
Buckhorn	12	3	5	24	6	7	6	4	2	0
Camp	0	0	1	4	3	2	1	1	0	0
Dome House	1	5	4	5	3	8	5	1	2	2
Gable Canyon	3	6	2	3	1	2	2	1	1	2
Horse Creek	22	28	4	4	1	6	2	1	0	4
Henderson Pass						8	6	3	3	3
Kobeh	5	3	2	4	1	1	2	7	1	4
Lone Mountain	3	7	17	11	14	12	6	2	10	13
Modarelli Mine	1	8	2	2	4	9	3	3	5	5
Pinefield	5	7	13	18	8	8	2	3	3	3
Pony Express	1	1	1	6	3	1	0	0	2	5
Quartz Road				2	2	2	3	8	18	9
<b>Total</b>	<b>55</b>	<b>74</b>	<b>53</b>	<b>87*</b>	<b>46</b>	<b>69*</b>	<b>38</b>	<b>34</b>	<b>51</b>	<b>51</b>

\*Does not include increase associated with the addition of new study lek

Table 3. Average number per point of the most common raptor and corvid species seen across all three transects combined, during the months of March, April, and May.

<b>Species</b>	<b>2003</b>	<b>2004</b>	<b>2005</b>	<b>2006</b>	<b>2007</b>	<b>2008</b>	<b>2009</b>	<b>2010</b>	<b>2011</b>	<b>2012</b>
Common Raven	0.87	0.41	1.03	1.93	2.7	0.79	1.32	1.49	2.52	2.53
American Kestrel	0.1	0.17	0.1	0.19	0.03	0.14	0.21	0.08	0.1	0.09
Golden Eagle	0.12	0.05	0.02	0.07	0.14	0.03	0.07	0.08	0.05	0.1
Ferruginous Hawk	0.05	0.01	0.03	0.05	0.02	0.03	0.07	0	0.03	0.05
Red-tailed Hawk	0.05	0.02	0.04	0.06	0.02	0.08	0.1	0.06	0.18	0.13
Swainson's Hawk	0.04	0	0.01	0.03	0	0.01	0	0	0	0
Northern Harrier	0.03	0.01	0.04	0.03	0	0.01	0.06	0.01	0.05	0.03
Prairie Falcon	0	0	0.01	0.01	0	0.01	0.02	0	0	0
Rough-legged Hawk	0.01	0.01	0	0.01	0.05	0	0.05	0.01	0	0.01
Total Points Surveyed	201	329	144	159	88	185	161	152	110	91

Table 4. Number of radioed females and female reproductive statistics by year.

	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
# of Radioed Hens	15	21	32	61	71	45	66	75	67	73
# of Hens Nested	11	16	30	45	30	32	51	61	51	48
# of Hens Failed 1st	6	9	22	25	21	26	15	46	35	33
# of Hens Renest	1	4	8	1	1	8	17	18	9	5
# Hatch	5	7	12	20	10	7	20	20	18	19
# With Brood at 45 Days			9	11	3	5	9	10	10	6

Table 5: Performance of resource selection models for estimating nest site selection for female sage-grouse in Eureka County, NV.

<b>Disturbance Covariates</b>	<b>No. Par</b>	<b>AIC</b>	<b>Delta AIC</b>
WF500	4	2235.96	0.00
WF1000	4	2238.31	2.35
Distance from Road	4	2239.70	3.74
WF2000	4	2247.18	11.21
Null	3	2252.07	16.11
<b>Topography Covariates</b>	<b>No. Par</b>	<b>AIC</b>	<b>Delta AIC</b>
Slope*Elev	6	2241.96	0.00
Elev	4	2243.10	1.14
Null	3	2252.07	10.11
Northness	4	2253.17	11.21
Eastness	4	2253.85	11.89
Slope	4	2253.88	11.92
<b>Habitat Covariates</b>	<b>No. Par</b>	<b>AIC</b>	<b>Delta AIC</b>
Sagebrush1000	4	2019.45	0.00
Sagebrush2000	4	2033.80	14.35
Sagebrush500	4	2036.90	17.45
PinyonJuniper500	4	2210.37	190.92
MountainSage2000	4	2213.01	193.56
PinyonJuniper1000	4	2213.92	194.48
MountainSage500	4	2220.76	201.32
WyomingSage500	4	2222.52	203.07
MountainSage1000	4	2222.99	203.55
WyomingSage1000	4	2223.70	204.25
PinyonJuniper2000	4	2232.49	213.05
WyomingSage2000	4	2239.38	219.93
Null	3	2252.07	232.62
<b>Lek Covariates</b>	<b>No. Par</b>	<b>AIC</b>	<b>Delta AIC</b>
Distance to Lek	4	2114.95	0.00
Null	3	2252.07	137.12
<b>Final Models</b>	<b>No. Par</b>	<b>AIC</b>	<b>Delta AIC</b>
WF500+Sagebrush1000*DistanceLek+Slope*Elev	10	1770.79	0.00
Sagebrush1000*DistanceLek+Slope*Elev	9	1771.36	0.57
WF500+ALL1000+Slope*Elev+DistanceLek	9	1807.68	36.89
Sagebrush1000+Slope+Elev+DistanceLek	7	1831.80	61.02

<sup>a</sup> Model selection notation follows Burnham and Anderson (2002). WF(500,1000,2000) = the amount of habitat classified as exotic grasslands within 500m,1000m, and 2000m, respectively.

$\text{Sagebrush}(500,1000,2000)$  = the amount of habitat classified as sagebrush within 500m, 1000m, and 2000m, respectively.  $\text{MountainSage}(500,1000,2000)$  = the amount of habitat classified as mountain sagebrush within 500m, 1000m, and 2000m, respectively.  $\text{WyomingSage}(500,1000,2000)$  = the amount of habitat classified as Wyoming sagebrush within 500m, 1000m, and 2000m, respectively.  $\text{PinyonJuniper}(500,1000,2000)$  = the amount of habitat classified as pinyon or juniper within 500m, 1000m, and 2000m, respectively. Slope = slope of the nest or random point. Elev = elevation of nest or random point. Northness and eastness refer to the aspect direction of the nest or random point. Distance from road and distance to lek = the distance from the nearest road or lek. Null denotes the constant or intercept-only model.

Table 6. Performance of resource selection models for assessing the influence of proximity to the Falcon-Gondor on nest site selection for female sage-grouse in Eureka County, NV.

<b>Model</b>	<b>No. Par</b>	<b>AIC</b>	<b>Delta AIC</b>
Distance from Falcon-Gondor <sup>2</sup>	5	895.68	0.00
Weighted Null	3	895.73	0.06
Distance from Falcon-Gondor	4	896.93	1.25

<sup>a</sup> Model selection notation follows Burnham and Anderson (2002). Distance from Falcon-Gondor<sup>2</sup> = a quadratic relationship of distance to the Falcon-Gondor transmission line. Distance from Falcon-Gondor = a linear relationship of distance to the Falcon-Gondor transmission line. Weighted null = intercept-only model. Random points in this analysis were weighted with its relative probability of nest site selection given the most competitive model from Table 5. Nest points were weighted as 1.0.

Table 7. Performance of selected nest survival models for estimating daily nest survival for female sage-grouse in Eureka County, NV.

<b>Weighted Model Development</b>	<b>AIC<sub>c</sub></b>	<b>Delta AIC<sub>c</sub></b>	<b>AIC<sub>c</sub> w<sub>i</sub></b>	<b>No. Par</b>	<b>Dev</b>
Season+CS+NSC*FC+PJ2000+WF2000	1263.10	0.00	0.49	8	1247.08
Season+CS+NSC*FC+PJ2000+WF2000+JD	1264.86	1.76	0.20	9	1246.83
Season+CS+JD <sup>2</sup> +NSC*FC+PJ2000+WF2000	1265.85	2.75	0.12	10	1245.81
Pop+Season+CS+JD <sup>2</sup> +NSC*FC+PJ2000+WF2000	1266.94	3.83	0.07	11	1244.88
Pop+Season+CS+JD <sup>2</sup> +NSC*FC+SH+PJ2000+WF2000	1267.38	4.27	0.06	12	1243.31
NSC*FC+SH	1268.44	5.34	0.03	5	1258.43
Pop+Season+CS+JD <sup>2</sup> +NSC*FC+SH+PJ2000+MT500+WF2000	1269.35	6.25	0.02	13	1243.28
PJ2000+MT500	1275.52	12.41	0.00	3	1269.51
Pop+Season+CS+JD <sup>2</sup>	1277.43	14.32	0.00	6	1265.41
WF2000	1284.64	21.54	0.00	2	1280.64
S(.)	1285.04	21.94	0.00	1	1283.04

<sup>a</sup> Model selection notation follows Burnham and Anderson (2002). Season = time of year of original capture of a female (Spring or Fall). CS = clutch size of nest. NSC = non-sagebrush shrub cover within 100m<sup>2</sup> of a nest. FC = forb cover within 100m<sup>2</sup> of a nest. PJ2000 = amount of habitat classified as either pinyon or juniper within 2000m of a nest. WF2000 = amount of habitat classified as exotic grasslands within 2000m of a nest. JD = Julian date of nest initiation. Pop = population female was associated with (Cortez or Roberts Mountains). SH = average shrub height within 100m<sup>2</sup> of a nest. MT500 = amount of habitat classified as mountain sagebrush within 500m of a nest. (.) denotes constant or intercept-only model. All other models run can be viewed in Appendix A.

Table 8. Performance of weighted nest survival used to assess the influence of proximity to the Falcon-Gondor transmission line on daily nest survival of female sage-grouse in Eureka County, NV.

<b>Model</b>	<b>AIC<sub>c</sub></b>	<b>Delta AIC<sub>c</sub></b>	<b>AIC<sub>c</sub> <math>w_i</math></b>	<b>No. Par</b>	<b>Dev.</b>
Nest Quality * FG	1491.91	0.00	0.39	4	1483.90
Nest Quality + FG	1491.91	0.00	0.39	3	1485.91
Nest Quality	1492.95	1.05	0.23	2	1488.95
S(.)	1541.60	49.70	0.00	1	1539.60
FG	1543.47	51.57	0.00	2	1539.47

<sup>a</sup> Model selection notation follows Burnham and Anderson (2002). FG = distance from nest to the Falcon-Gondor transmission line. Nest Quality = an individual's probability of daily nest survival given the most competitive model from Table 7. (.) denotes constant, or intercept-only model.



Table 9. Performance of multistate models used to estimate female sage-grouse nesting propensity in Eureka County, NV.

Model	AIC <sub>c</sub>	Delta AIC <sub>c</sub>	AIC <sub>c</sub> <i>w<sub>i</sub></i>	No. Par	Dev
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{ElevApril}+\text{ElevMay}+\text{Age}^2)\psi AC(\text{Quad}+\text{Year}+\text{ElevApril}+\text{ElevMay}+\text{Age}^2)\psi BA\sim CA(\text{linear})$	19165.90	0.00	0.72	31	19103.40
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{Elev*Linear}+\text{Age}^2)\psi AC(\text{Quad}+\text{Year}+\text{Elev*linear}+\text{Age}^2)\psi BA\sim CA(\text{linear})$	19169.08	3.18	0.15	31	19106.58
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{Elev*Linear}+\text{Age}^2+\text{FG})\psi AC(\text{Quad}+\text{Year}+\text{Elev*linear}+\text{Age}^2+\text{FG})\psi BA\sim CA(\text{linear})$	19170.14	4.24	0.09	32	19105.60
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{ElevApril})\psi AC(\text{Quad}+\text{Year}+\text{ElevMay})\psi BA\sim CA(\text{linear})$	19172.96	7.06	0.02	29	19114.52
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{April}+\text{May})\psi AC(\text{Quad}+\text{Year}+\text{April}+\text{May})\psi BA\sim CA(\text{linear})$	19174.78	8.88	0.01	29	19116.34
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{ElevApril}+\text{ElevMay*June})\psi AC(\text{Quad}+\text{Year}+\text{ElevApril}+\text{ElevMay*June})\psi BA\sim CA(\text{linear})$	19175.11	9.21	0.01	31	19112.60
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{April}+\text{July})\psi AC(\text{Quad}+\text{Year}+\text{April}+\text{July})\psi BA\sim CA(\text{linear})$	19177.15	11.24	0.00	29	19118.70
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{TempA}+\text{TempM})\psi AC(\text{Quad}+\text{Year}+\text{TempA}+\text{TempM})\psi BA\sim CA(\text{linear})$	19178.90	13.00	0.00	29	19120.46
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{July})\psi AC(\text{Quad}+\text{Year}+\text{July})\psi BA\sim CA(\text{linear})$	19201.89	35.99	0.00	28	19145.48
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{April})\psi AC(\text{Quad}+\text{Year}+\text{April})\psi BA\sim CA(\text{linear})$	19201.96	36.06	0.00	28	19145.55
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{May})\psi AC(\text{Quad}+\text{Year}+\text{May})\psi BA\sim CA(\text{linear})$	19202.02	36.12	0.00	28	19145.60
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{June})\psi AC(\text{Quad}+\text{Year}+\text{June})\psi BA\sim CA(\text{linear})$	19204.56	38.66	0.00	28	19148.15
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{Age})\psi AC(\text{Quad}+\text{Year}+\text{Age})\psi BA\sim CA(\text{linear})$	19205.98	40.07	0.00	28	19149.56
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{PJ})\psi AC(\text{Quad}+\text{Year}+\text{PJ})\psi BA\sim CA(\text{linear})$	19209.41	43.51	0.00	28	19153.00
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year})\psi AC(\text{Quad}+\text{Year})\psi BA\sim CA(\text{linear})$	19209.64	43.74	0.00	27	19155.26
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+30\text{Temp})\psi AC(\text{Quad}+\text{Year}+30\text{Temp})\psi BA\sim CA(\text{linear})$	19209.98	44.08	0.00	28	19153.56
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{Elev})\psi AC(\text{Quad}+\text{Year}+\text{Elev})\psi BA\sim CA(\text{linear})$	19210.07	44.17	0.00	28	19153.66
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{MtSage})\psi AC(\text{Quad}+\text{Year}+\text{MtSage})\psi BA\sim CA(\text{linear})$	19210.31	44.41	0.00	28	19153.89
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{Fire})\psi AC(\text{Quad}+\text{Year}+\text{Fire})\psi BA\sim CA(\text{linear})$	19210.81	44.91	0.00	28	19154.40
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{WySage})\psi AC(\text{Quad}+\text{Year}+\text{WySage})\psi BA\sim CA(\text{linear})$	19211.00	45.09	0.00	28	19154.58
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{Season})\psi AC(\text{Quad}+\text{Year}+\text{Season})\psi BA\sim CA(\text{linear})$	19211.31	45.41	0.00	28	19154.90
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{Pop})\psi AC(\text{Quad}+\text{Year}+\text{Pop})\psi BA\sim CA(\text{linear})$	19211.36	45.46	0.00	28	19154.95
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year}+\text{Allsage})\psi AC(\text{Quad}+\text{Year}+\text{Allsage})\psi BA\sim CA(\text{linear})$	19211.54	45.64	0.00	28	19155.13
$\phi(.)P(\text{Year})\psi AB(\text{Quad}+\text{Year})\psi AC(\text{Quad}+\text{Year})\psi BACA(.)$	19228.07	62.17	0.00	25	19177.74

<sup>a</sup> Model selection notation follows Burnham and Anderson (2002). Parameters estimated are apparent survival ( $\phi$ ), detection (P), and transition probabilities ( $\psi$ ) between a female located off a nest (A), located on her first nest (B), or located on her second or third nest (C). (.) denotes constancy, or intercept-only. Year = full annual variation. Quad = quadratic constraint applied across interval transition probabilities. Elev = average elevation of all locations of a female during the nesting season (April 1<sup>st</sup>-May31<sup>st</sup>). ElevApril = transitions during April constrained with an individual's average elevation. ElevMay = transitions during May constrained with an individual's average elevation. Age and Age<sup>2</sup> = minimum hen age and a quadratic relationship of minimum hen age, respectively. Linear = linear constraint applied across interval transition probabilities. April = average April actual evapotranspiration value across all locations of a female. May = average May actual evapotranspiration value across all locations of a female. June = average June actual evapotranspiration value across all locations of a female. July = average July actual evapotranspiration value across all locations of a female. Temp = average 30 year temperature across all female nesting season locations. PJ = average amount of habitat classified as pinyon or juniper across all nesting season locations. MtSage = average amount of habitat classified as mountain sage across all nesting season locations. WySage = average amount of habitat classified as Wyoming sagebrush across all nesting season locations. Allsage = average amount of habitat classified as sagebrush across all nesting season locations. Fire = average amount of habitat classified as exotic grasslands across all nesting season locations. Season = season of capture (spring or fall). Pop = population female associated with (Cortez or Roberts).

Table 10. Performance of weighted multistate models used to assess the influence of a female sage-grouse's proximity to the Falcon-Gondor transmission line on estimates of nesting propensity in Eureka County, NV.

<b>Model</b>	<b>AIC<sub>c</sub></b>	<b>Delta AIC<sub>c</sub></b>	<b>AIC<sub>c</sub> <math>w_i</math></b>	<b>No. Par</b>	<b>Dev</b>
$\phi(.)P(\text{Year})\psi_{AB}(\text{NP})\psi_{AC}(\text{NP})\psi_{BA\sim CA}(\text{Linear})$	19168.24	0.00	0.57	16	19136.10
$\phi(.)P(\text{Year})\psi_{AB}(\text{FG}+\text{NP})\psi_{AC}(\text{FG}+\text{NP})\psi_{BA\sim CA}(\text{Linear})$	19169.65	1.41	0.28	17	19135.50
$\phi(.)P(\text{Year})\psi_{AB}(\text{FG}*\text{NP})\psi_{AC}(\text{FG}*\text{NP})\psi_{BA\sim CA}(\text{Linear})$	19170.99	2.75	0.14	18	19134.82
$\phi(.)P(\text{Year})\psi_{AB}(\text{FG})\psi_{AC}(\text{FG})\psi_{BA\sim CA}(\text{Linear})$	19309.83	141.59	0.00	16	19277.69
$\phi(.)P(\text{Year})\psi_{AB}(.)\psi_{AC}(.)\psi_{BA\sim CA}(\text{Linear})$	19310.02	141.78	0.00	15	19279.90

<sup>a</sup> Model selection notation follows Burnham and Anderson (2002). Parameters estimated are apparent survival ( $\phi$ ), detection (P), and transition probabilities ( $\psi$ ) between a female located off a nest (A), located on her first nest (B), or located on her second or third nest (C). (.) denotes constancy, or intercept-only. Year = full annual variation. NP = the interval specific probability that an individual would initiate given the most competitive model from Table 9. FG = average nesting season distance from the Falcon-Gondor transmission line. Linear = linear constraint applied across interval transition probabilities.

Table 11. Performance of known fate models used to estimate ‘true’ survival of female sage-grouse in Eureka County, NV.

<b>Model</b>	<b>AIC<sub>c</sub></b>	<b>Delta AIC<sub>c</sub></b>	<b>AIC<sub>c</sub> <i>w<sub>i</sub></i></b>	<b>No. Par</b>	<b>Dev.</b>
S(seasons)+WySage(Sp)+WF(Su)+Nest(Su)+Pop(Sp)+Capture(Su)	1449.61	0.00	0.42	9	1431.56
S(seasons)+WySage(Sp+Su)+WF(Su)+Nest(Su)+Pop(Sp)+Capture(Su)	1450.88	1.26	0.22	10	1430.81
S(seasons)+WySage(Sp+Su)+WF(Su)+Nest(Su)+Pop(Sp)+Capture(Su)+AgeClass	1452.45	2.84	0.10	11	1430.37
S(seasons)+WySage(Sp+Su)+WF(Su)+Nest(Su)+Pop(Sp)+Capture(Su)+PJ(Fa)	1452.60	2.99	0.09	11	1430.51
S(seasons)+WySage(Sp+Su)+WF(Su)+Nest(Su)+Pop(Sp)+Capture(Su)+Elev(Sp)	1452.84	3.23	0.08	11	1430.76
S(seasons)+WySage(Sp+Su)+WF(Su)	1455.70	6.09	0.02	7	1441.66
S(seasons)+WySage(Sp+Su)+WF(Su)+Nest(Su)	1456.32	6.71	0.01	8	1440.28
S(seasons)+Capture(Season)	1457.93	8.32	0.01	8	1441.88
S(seasons)+WySage(Sp+Su)+WF(Su)+PJ(Fa)+Nest(Su)	1458.04	8.43	0.01	9	1439.98
S(seasons)+Nesting(Su)	1459.18	9.57	0.00	5	1449.16
S(seasons)+WySage(season)	1459.19	9.58	0.00	7	1445.16
S(.)	1489.52	39.91	0.00	1	1487.52

<sup>a</sup> Model selection notation follows Burnham and Anderson (2002). SP,SU, and FA refer to the associate covariate only attributed to Spring, Summer, or Fall months. Seasons = seasonal temporal constraints assigning March-May, June-July, Aug-Oct, and Nov-Feb as independent seasons. WySage = time varying covariate for average amount of habitat classified as Wyoming sagebrush across all locations for a female during one month. . WF = time varying covariate for average amount of habitat classified as exotic grasslands across all locations for a female during one month. PJ = time varying covariate for average amount of habitat classified as pinyon or

juniper across all locations for a female during one month. Elev = average elevation over all locations of a female during one month.

Nest = binomial covariate delineating successful nesters (1) from unsuccessful (0). Pop = population female associated with (Cortez or Roberts). Capture = season female was originally captured in (spring or fall). (.) denotes constant, or intercept-only model.

Table 12. Performance of weighted known fate models used to assess the influence of an individual's proximity to the Falcon-Gondor transmission line on estimates of survival of female sage-grouse in Eureka County, NV.

<b>Model</b>	<b>AIC<sub>c</sub></b>	<b>Delta AIC<sub>c</sub></b>	<b>AIC<sub>c</sub> <math>w_i</math></b>	<b>No. Par</b>	<b>Dev.</b>
S(Survivorship * FG)	1462.01	0.00	0.43	5	1451.99
S(Survivorship + FG)	1462.17	0.16	0.40	4	1454.16
S(Survivorship)	1463.86	1.84	0.17	3	1457.85
S(.)	1489.52	27.51	0.00	1	1487.52
S(FG)	1490.59	28.58	0.00	2	1486.58

<sup>a</sup> Model selection notation follows Burnham and Anderson (2002). Survivorship = estimated monthly survival probability for an individual given the most competitive model from Table 11. FG = average distance from the Falcon-Gondor transmission line over all locations in a month. (.) denotes constant or intercept-only model.

Table 13. Performance of robust-design models used to estimate apparent survival of male sage-grouse in Eureka County, NV.

Model	QAIC <sub>c</sub>	Delta QAIC <sub>c</sub>	QAIC <sub>c</sub> w <sub>i</sub>	No. Par	Qdev
$\phi$ (Prec) $\gamma$ (.) $p \sim c$ (Year+Lek+month)	2809.08	0.00	0.92	27	2754.00
$\phi$ (Year) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2817.61	8.54	0.01	34	2747.91
$\phi$ (Pop) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2817.74	8.66	0.01	27	2762.66
$\phi$ (.) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2818.34	9.26	0.01	26	2765.34
$\phi$ (Pop+RoadDen) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2818.79	9.71	0.01	28	2761.63
$\phi$ (Pop+Elev) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2819.25	10.17	0.01	28	2762.09
$\phi$ (FG+Pop) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2819.54	10.47	0.00	28	2762.38
$\phi$ (WF+Pop) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2819.75	10.68	0.00	28	2762.59
$\phi$ (FG) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2820.18	11.10	0.00	27	2765.10
$\phi$ (Pop*RoadDen) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2820.57	11.50	0.00	29	2761.33
$\phi$ (WF*Pop) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2820.59	11.51	0.00	29	2761.34
$\phi$ (FG <sup>2</sup> *Pop) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2820.79	11.71	0.00	29	2761.54
$\phi$ (FG <sup>2</sup> +Pop) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2820.92	11.84	0.00	29	2761.68
$\phi$ (Pop*Elev) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2821.13	12.05	0.00	29	2761.89
$\phi$ (FG <sup>2</sup> ) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2821.20	12.12	0.00	28	2764.04
$\phi$ (FG*Pop) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2821.49	12.41	0.00	29	2762.24
$\phi$ (Lek+Prec) $\gamma$ (.) $p \sim c$ (Year+Lek+Month)	2823.38	14.30	0.00	39	2743.13
$\phi$ (Lek+Year) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2828.37	19.30	0.00	46	2733.24
$\phi$ (Lek) $\gamma$ (.) $p \sim c$ (Lek+Year+Month)	2833.39	24.31	0.00	38	2755.26
$\phi$ (.) $\gamma$ (.) $p \sim c$ (.)	2908.95	99.87	0.00	3	2902.93

<sup>a</sup> Model selection notation follows Burnham and Anderson (2002). Parameters estimated were probabilities of apparent survival ( $\phi$ ), seasonal absence from a breeding lek ( $\gamma$ ), detection ( $p$ ) and re-detection ( $c$ ). Prec = estimate of annual precipitation from August<sub>(year-1)</sub> to July<sub>(year)</sub>. Year = full annual variation. Lek = full variation between lek-groups. Month = full variation between monthly secondary occasions within a primary. ( $\sim$ ) denotes  $p$  and  $c$  parameters were estimated differently by one parameter. Pop = population each lek was associated with (Cortez or Roberts). RoadDen = estimated road density around each lek. FG = lek's distance from Falcon-Gondor

transmission line. WF = amount of habitat classified as exotic grasslands within 5km of each lek.

Elev = elevation at each lek. (.) denotes constant, or intercept-only model.



Table 14. Support for sources of spatial variation in annual survival ( $\phi$ ) of male greater sage-grouse in Eureka County, NV, based on the proportion of deviance explained ( $R^2_{Dev}$ ) and modeled parameter coefficients ( $\beta$ ) with 85% confidence intervals.

Model	$R^2_{Dev}$		$\beta$	85% C.I.
	Spatial Model	Full Model		
Distance from Falcon-Gondor	0.02	0.01	0.12	-0.23-0.46
Distance from Falcon-Gondor <sup>2</sup>	0.13	0.04	0.27	-0.12-0.67
Population	0.27	0.08	0.14	0.02-0.26
Population*Distance from Falcon-Gondor <sup>2</sup>	0.38	0.12		
Amount of habitat classified as exotic grassland	0.06	0.02	-0.11	-.30-0.08
Lek elevation	0.16	0.05	0.24	-0.03-0.51
Road Density	0.24	0.07	0.25	0.02-0.49
Population+Distance from Falcon-Gondor <sup>2</sup>	0.36	0.11		

Table 13. Estimates of apparent survival ( $\phi$ ) and associated variance for male sage-grouse at each study in Eureka County, NV.

Lek	Probability of annual survival	Standard Error	Population
Big Pole	0.50	0.05	Cortez
Buckhorn	0.55	0.07	Cortez
Camp	0.53	0.15	Roberts
Dome House	0.39	0.06	Roberts
Gable Canyon	0.52	0.05	Roberts
Henderson Pass	0.52	0.18	Roberts
Horse Creek	0.40	0.05	Cortez
Kobeh	0.53	0.06	Roberts
Lone Mountain	0.60	0.04	Roberts
Modarelli Mine	0.48	0.06	Cortez
Pinefield	0.39	0.07	Roberts
Pony Express	0.60	0.04	Roberts
Quartz Road	0.49	0.06	Cortez

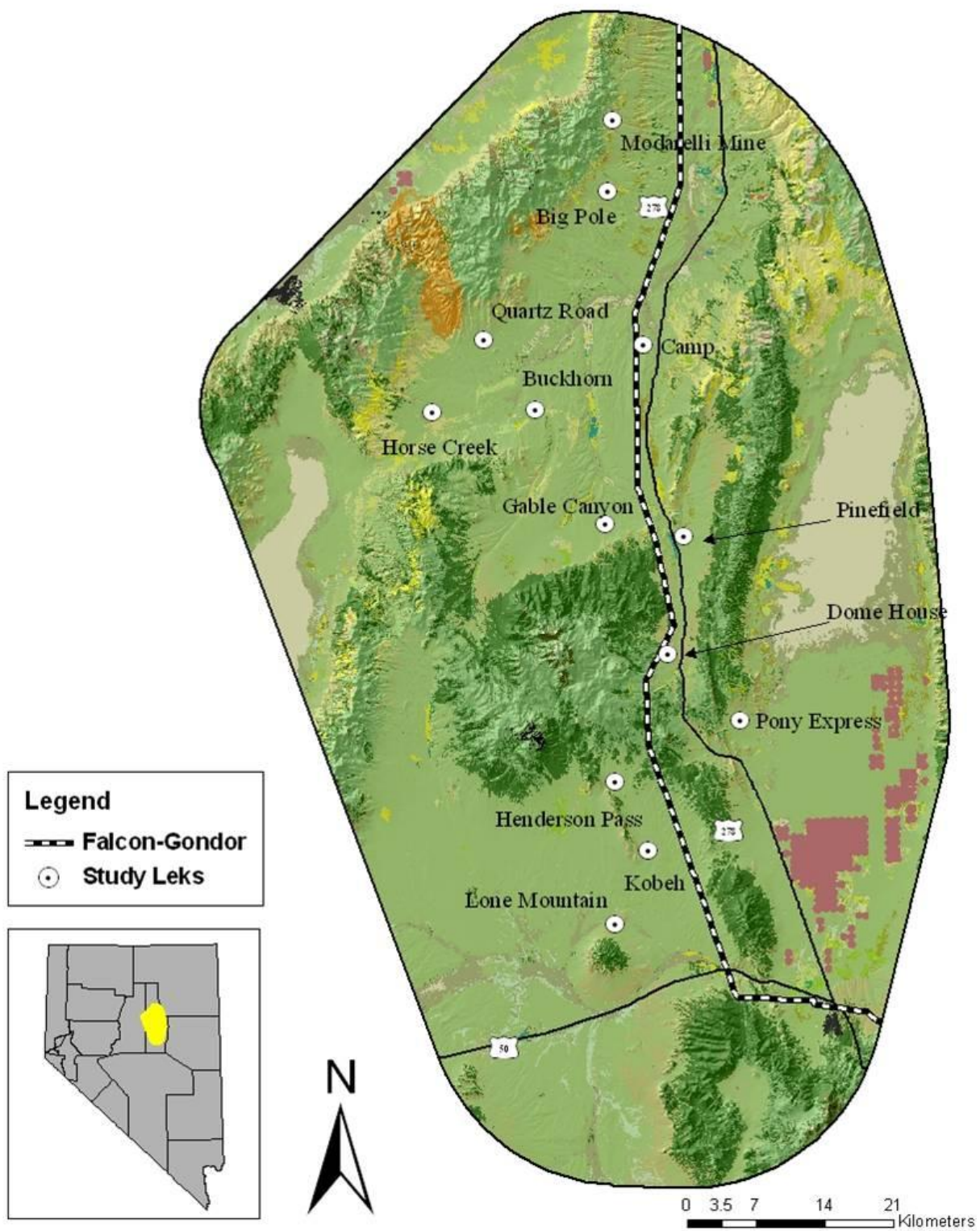


Figure 1. Study lek locations in Eureka County, NV.

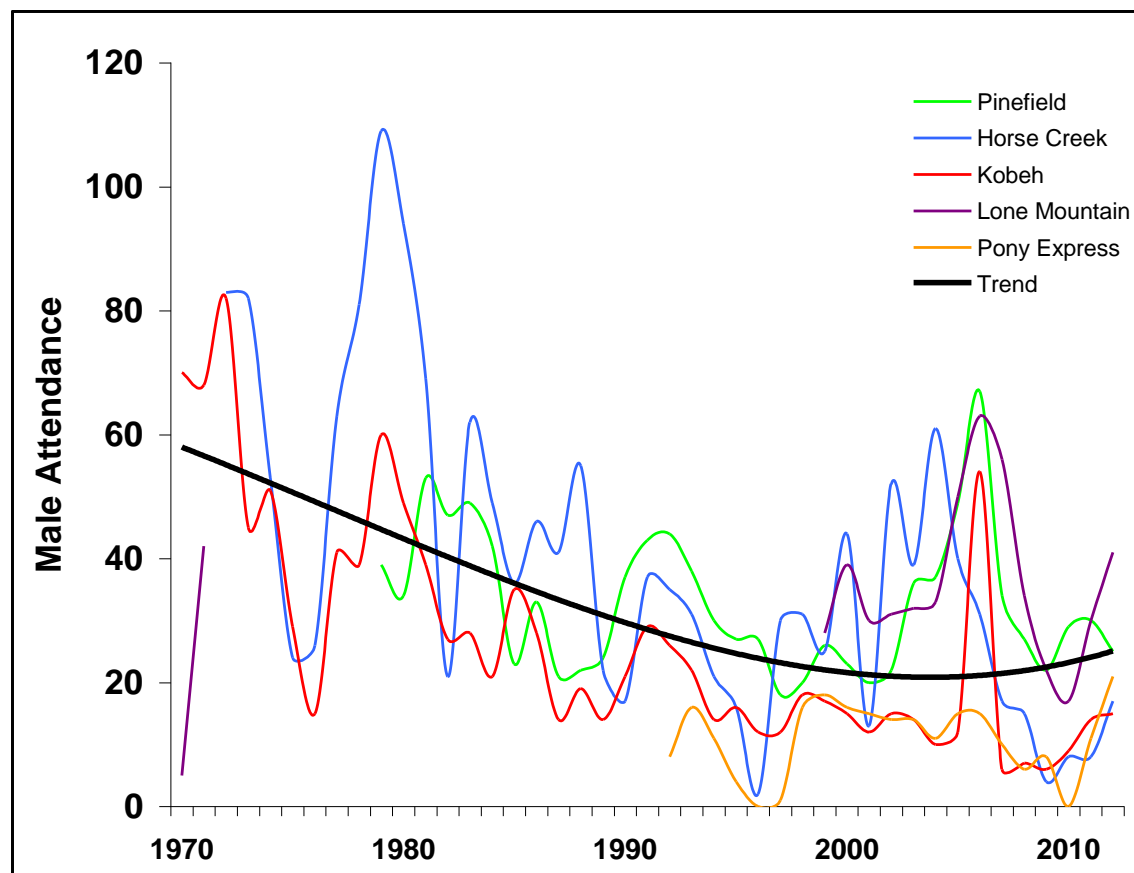


Figure 2. Long term trends in male attendance for 5 NDOW trend leks used in this study.

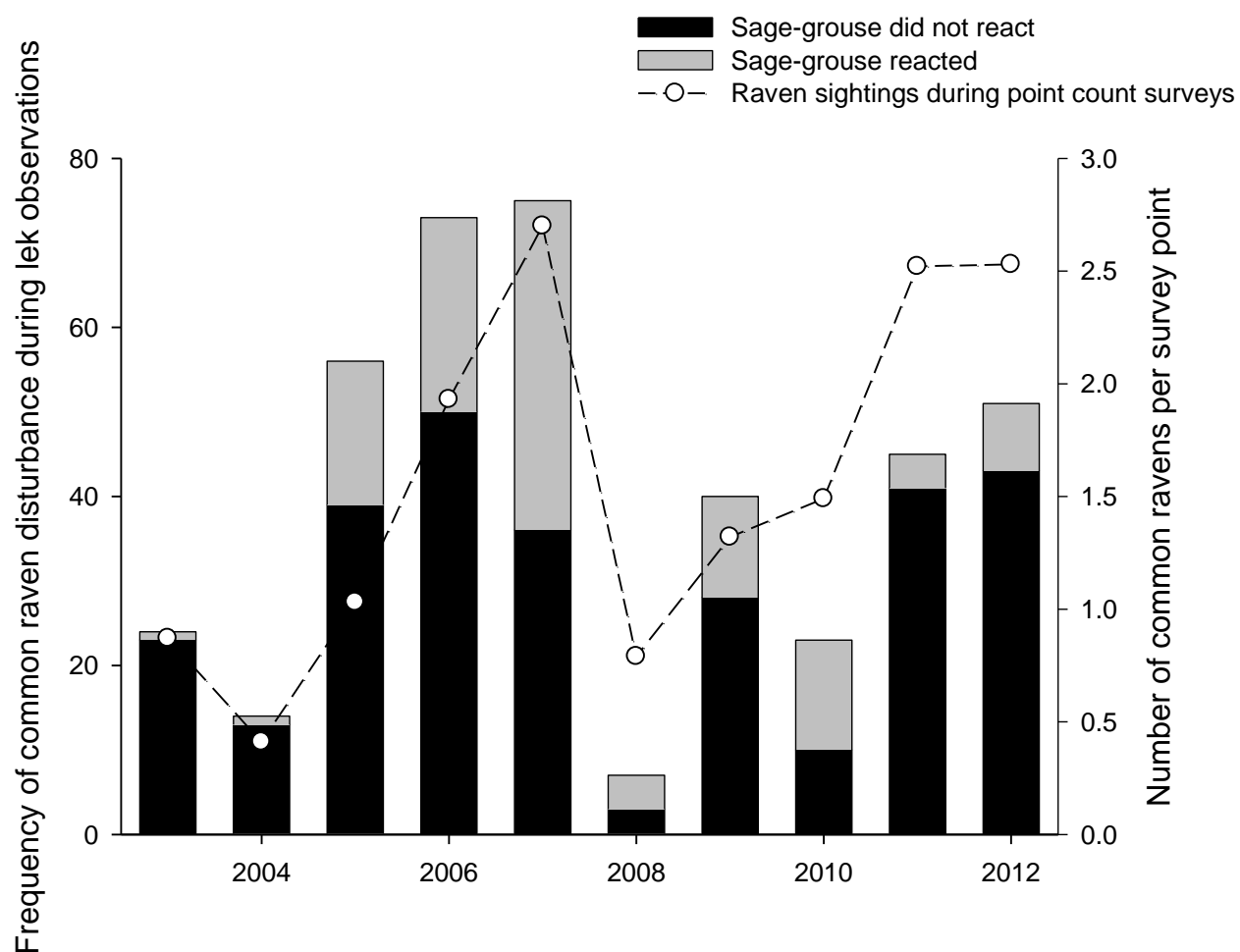


Figure 3. Indices of Common Raven abundance during lek observations and point count surveys in Eureka County, Nevada from 2003-2012. Point count surveys (dashed line with open circles) sightings were recorded along 3 transects. The black and grey bars represent sightings of Common Ravens at Greater Sage-Grouse leks and the apparent reaction to the disturbance. Common Ravens were considered to have elicited a reaction from the sage grouse if any males ceased strutting activities or if any sage grouse (male or female) ducked down, hid, or flushed.

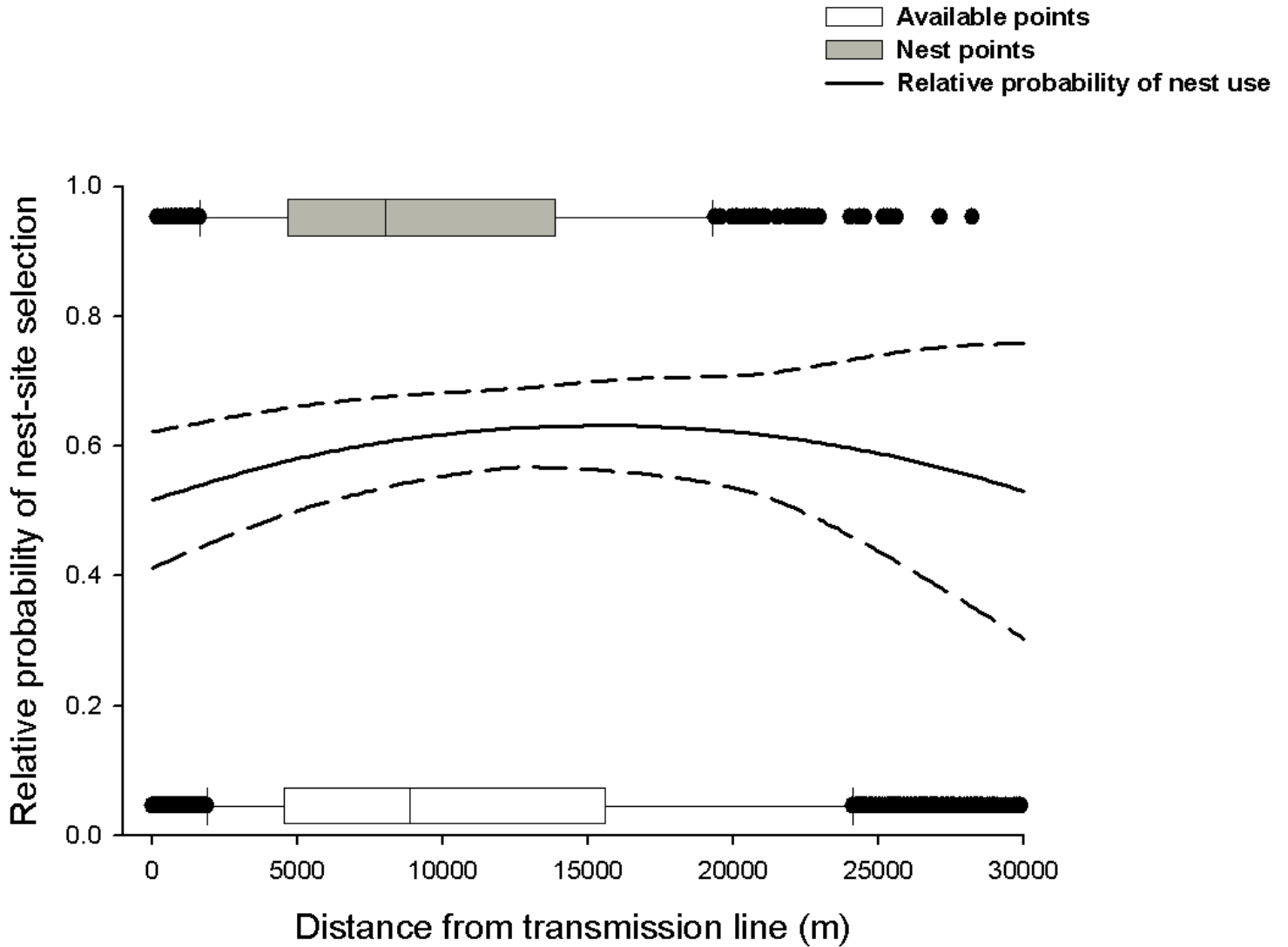


Figure 4. The relationship between the distance from the Falcon-Gondor transmission line and relative probability of nest-site selection after accounting for spatial heterogeneity in habitat characteristics associated with nest site selection (line). Inferences were drawn from comparisons made between nests (gray box plot) and available (white box plot) points. Error lines represent 95% confidence intervals.

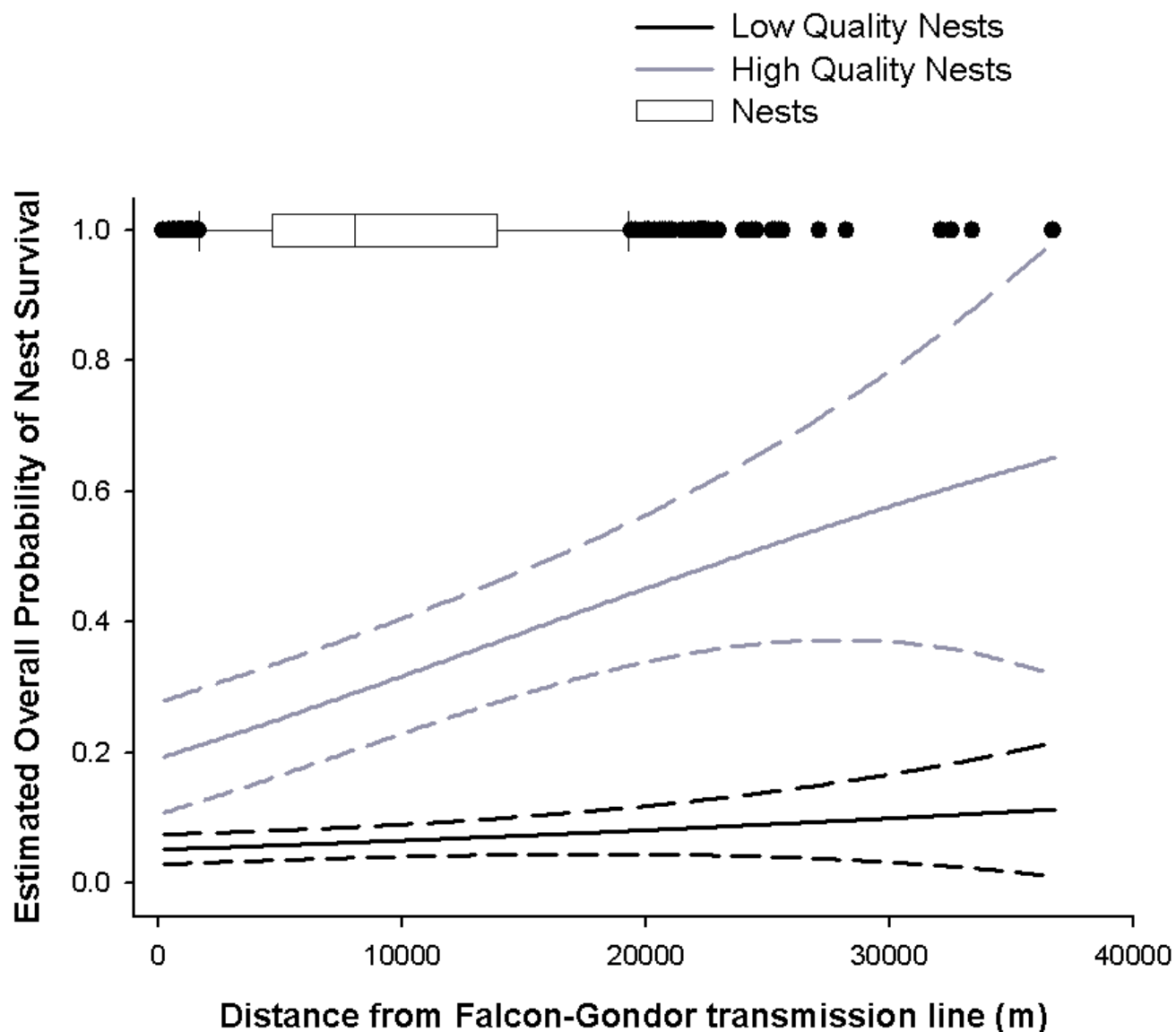


Figure 5. The relationship between the distance a nest was from the Falcon-Gondor transmission line and nest quality (black line = low, gray line = high) on overall nest survival (to 37 days). Nest quality represents the daily nest survival probability for a nest given its habitat and female characteristics that were model supported to influence nest survival. Error lines represent 95% confidence intervals. The range of distances nests were from the Falcon-Gondor transmission line are represented with the white box plot.

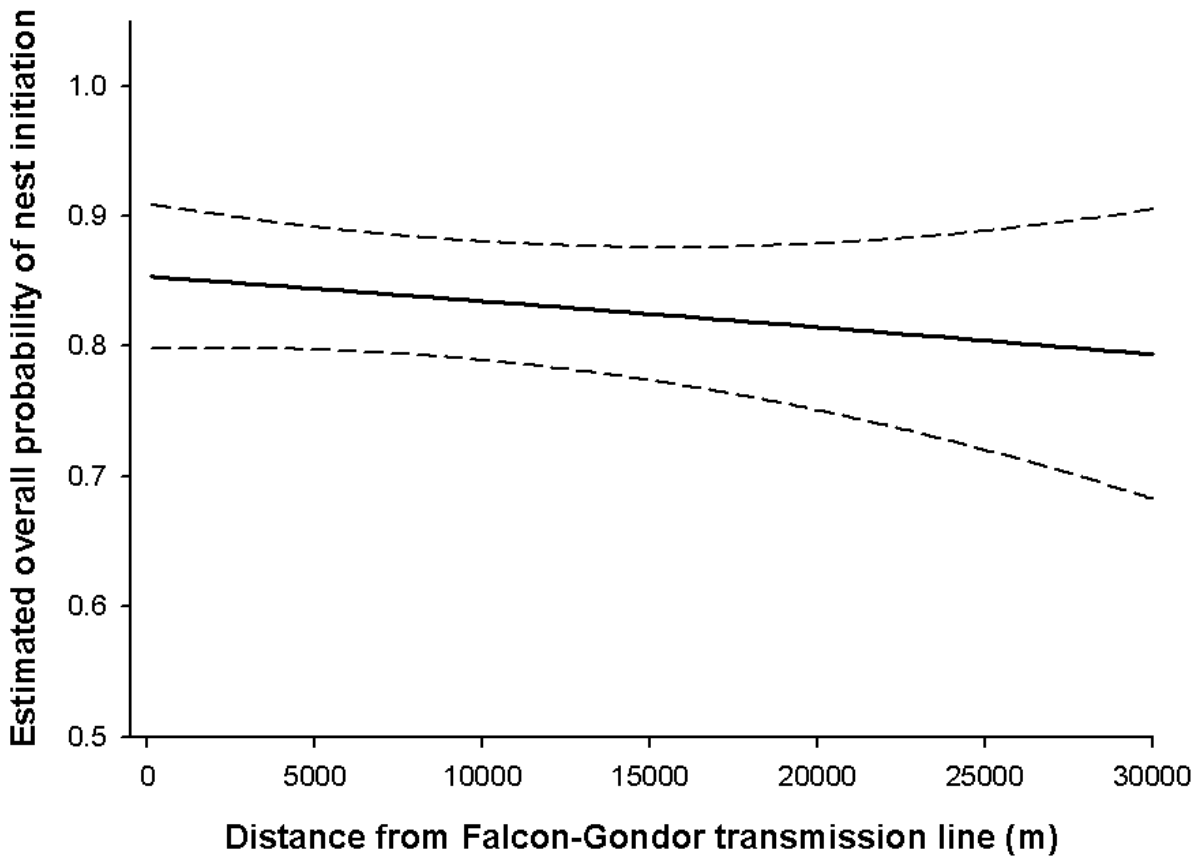


Figure 6. The relationship between a female's average distance from the Falcon-Gondor transmission line during the nesting season (April 1<sup>st</sup>-May 31<sup>st</sup>) and overall probability of nest initiation. Error bars represent 95% confidence intervals.



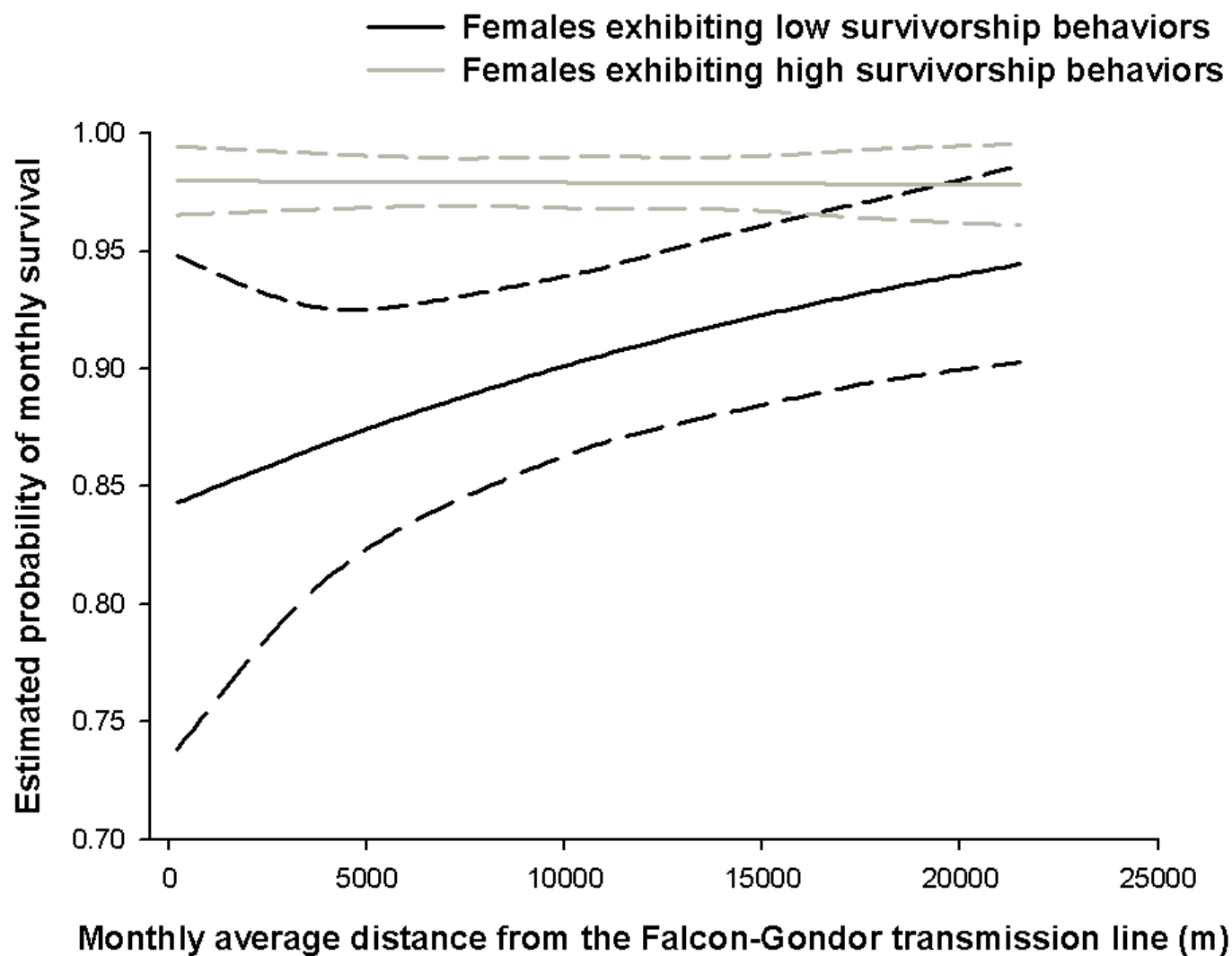


Figure 7. The relationship between the average distance a female was from the Falcon-Gondor transmission line in a given month and her predicted survivorship (black line = low, gray line = high) on monthly estimates of apparent survival. Female survivorship represents monthly survival probability for a female given habitat and behavior characteristics that were model supported to influence apparent survival. Error lines represent 95% confidence intervals.

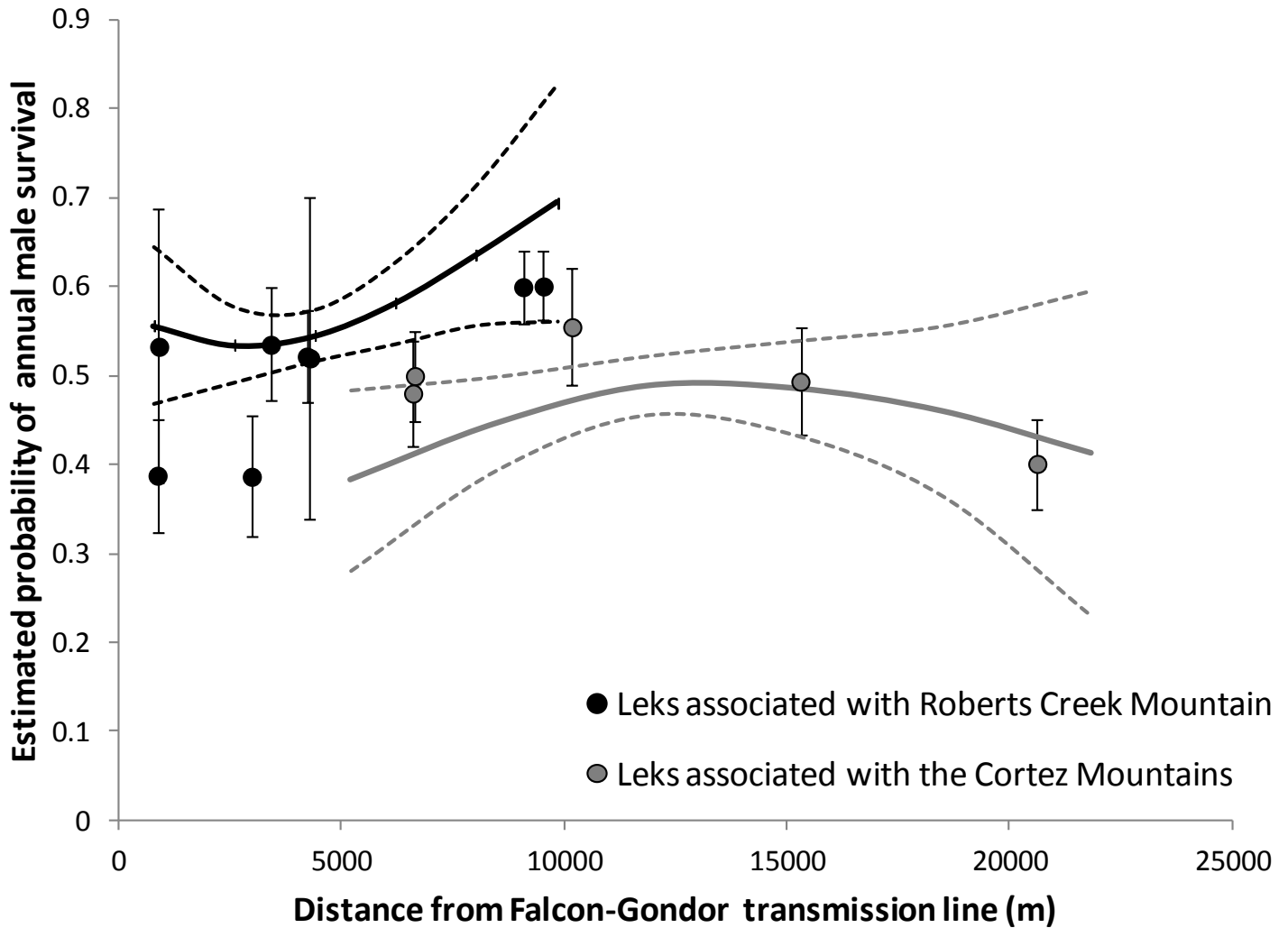


Figure 8. The relationship between sage-grouse population (black line = Roberts Creek Mountain; gray line = Cortez mountains) and lek distance from the Falcon-Gondor transmission line on annual male apparent survival plotted over estimates of annual male apparent survival for each study lek (black dots = leks associated with Roberts Creek Mountain; gray dots associated with Cortez mountains) within Eureka County, NV. Error bars and lines represent 95% confidence intervals.

Appendix A. Performance of all nest survival used to estimate female sage-grouse nest success in Eureka County, NV.

<b>Disturbance</b>	<b>AIC<sub>c</sub></b>	<b>Delta AIC<sub>c</sub></b>	<b>AIC<sub>c</sub> w<sub>i</sub></b>	<b>No. Par</b>	<b>Dev</b>
Wildfire2000	1546.34	0.00	0.18	2	1542.34
(.)	1546.42	0.08	0.18	1	1544.42
Wildfire1000	1546.44	0.10	0.18	2	1542.44
Wildfire500	1547.09	0.75	0.13	2	1543.09
RoadDensity500	1547.48	1.13	0.10	2	1543.47
Road	1547.80	1.46	0.09	2	1543.79
RoadDensity1000	1548.14	1.80	0.08	2	1544.14
RoadDensity2000	1548.41	2.07	0.07	2	1544.41

<b>Individual Traits</b>	<b>AIC<sub>c</sub></b>	<b>Delta AIC<sub>c</sub></b>	<b>AIC<sub>c</sub> w<sub>i</sub></b>	<b>No. Par</b>	<b>Dev</b>
Population+Season+Clutch Size+Julian Date <sup>2</sup>	1527.27	0.00	0.46	6	1515.25
Population+Season+Clutch Size	1528.10	0.83	0.30	4	1520.09
Population+Season+Clutch Size <sup>2</sup> +Julian Date <sup>2</sup>	1528.73	1.46	0.22	7	1514.70
Population+Clutch Size+Julian Date <sup>2</sup>	1535.15	7.88	0.01	5	1525.14
Minimum Age*Clutch Size	1539.52	12.25	0.00	4	1531.51
Population	1541.09	13.82	0.00	2	1537.09
Clutch Size	1541.55	14.28	0.00	2	1537.54
Season	1541.55	14.29	0.00	2	1537.55
Nest Attempt+Clutch Size	1542.87	15.60	0.00	3	1536.86
Clutch Size <sup>2</sup>	1543.21	15.94	0.00	3	1537.21
Minimum Age+Clutch Size	1543.44	16.17	0.00	3	1537.44
Nest Attempt*Clutch Size	1544.18	16.91	0.00	4	1536.17
(.)	1546.42	19.15	0.00	1	1544.42
Julian Date	1548.23	20.96	0.00	2	1544.23
Julian Date <sup>2</sup>	1548.26	20.99	0.00	3	1542.25
Minimum Age	1548.32	21.05	0.00	2	1544.32
Age	1548.39	21.12	0.00	2	1544.39
Nest Attempt	1548.42	21.15	0.00	2	1544.42
Minimum Age+Julian Date	1550.11	22.84	0.00	3	1544.11
Minimum Age <sup>2</sup>	1550.32	23.05	0.00	3	1544.31
Minimum Age+Nest Attempt	1550.32	23.05	0.00	3	1544.32
Minimum Age*Julian Date	1551.85	24.58	0.00	4	1543.84
Minimum Age*Nest Attempt	1551.89	24.62	0.00	4	1543.89

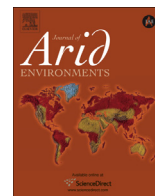
Local Vegetation	AIC <sub>c</sub>	Delta AIC <sub>c</sub>	AIC <sub>c</sub> w <sub>i</sub>	No. Par	Dev
Non-Sagebrush Shrub Cover*Forb Cover+Shrub Height	1524.56	0.00	0.61	5	1514.54
Non-Sagebrush Shrub Cover*Forb Cover	1526.66	2.10	0.21	4	1518.65
Non-Sagebrush Shrub Cover*Forb Cover+Total Plot Cover	1528.18	3.62	0.10	5	1518.17
Non-Sagebrush Shrub Cover+Forb Cover+Shrub Height	1530.57	6.02	0.03	4	1522.56
Non-Sagebrush Shrub Cover+Forb Cover+Shrub Height+Total Plot Cover	1531.83	7.28	0.02	5	1521.82
Non-Sagebrush Shrub Cover+Forb Cover	1532.27	7.71	0.01	3	1526.26
Non-Sagebrush Shrub Cover+Forb Cover+Tall Sagebrush Shrub Cover+Shrub Height+Total Plot Cover	1533.83	9.28	0.01	6	1521.82
Non-Sagebrush Shrub Cover+Forb Cover+Tall Sagebrush Shrub +Nest Cover+Shrub Height+Total Plot Cover	1534.38	9.83	0.00	7	1520.36
Non-Sagebrush Shrub Cover+Forb Cover+Tall Sagebrush Shrub +NC+Shrub Height+Total Plot Cover+Forb Height	1536.32	11.77	0.00	8	1520.30
Non-Sagebrush Shrub Cover+Total Plot Cover	1536.58	12.03	0.00	3	1530.58
Non-Sagebrush Shrub Cover*Sagebrush Shrub Cover	1537.46	12.90	0.00	4	1529.45
Non-Sagebrush Shrub Cover	1537.80	13.24	0.00	2	1533.79
Non-Sagebrush Shrub Cover+Total Shrub Cover	1537.81	13.26	0.00	3	1531.81
Non-Sagebrush Shrub Cover*Total Plot Cover	1537.87	13.31	0.00	4	1529.86
Non-Sagebrush Shrub Cover+Forb Cover+Tall Sagebrush Shrub +Nest Cover+Shrub Height+Total Plot Cover+Forb Height+Nest Shrub Height	1538.23	13.67	0.00	9	1520.19
Non-Sagebrush Shrub Cover+Sagebrush Shrub Cover	1538.39	13.83	0.00	3	1532.39
Non-Sagebrush Shrub Cover*Total Shrub Cover	1539.60	15.04	0.00	4	1531.59
Forb Cover	1539.60	15.05	0.00	2	1535.60
Shrub Height	1540.00	15.44	0.00	2	1536.00
Residual Grass Height*Total Shrub Cover	1540.96	16.40	0.00	4	1532.95
Total Shrub Cover	1541.07	16.51	0.00	2	1537.07
Tall Sagebrush Shrub	1541.64	17.08	0.00	2	1537.63
Nest Cover	1541.93	17.37	0.00	2	1537.93
Residual Grass Height+Total Shrub Cover	1543.02	18.46	0.00	3	1537.01
Total Plot Cover	1543.33	18.78	0.00	2	1539.33
Residual Grass Height+Nest Cover	1543.91	19.35	0.00	3	1537.90
Nest Shrub Height	1544.17	19.61	0.00	2	1540.17
Forb Height	1544.34	19.78	0.00	2	1540.34
Residual Grass Cover * Nest Cover	1545.20	20.64	0.00	4	1537.19
(.)	1546.42	21.86	0.00	1	1544.42
Medium Total Shrub Cover	1546.80	22.25	0.00	2	1542.80
Tall Sagebrush Shrub Cover	1546.93	22.38	0.00	2	1542.93
Nest Grass Height	1547.07	22.51	0.00	2	1543.07
Grass Height	1547.36	22.81	0.00	2	1543.36
Grass Cover	1547.64	23.08	0.00	2	1543.64
Nest Forb Height	1548.00	23.45	0.00	2	1544.00
Low Sagebrush Shrub Cover	1548.12	23.56	0.00	2	1544.12
Sagebrush Shrub Cover	1548.32	23.77	0.00	2	1544.32

Small Total Shrub Cover	1548.35	23.80	0.00	2	1544.35
Medium Sagebrush Shrub Cover	1548.36	23.81	0.00	2	1544.36
Residual Grass Height	1548.40	23.84	0.00	2	1544.39

<b>Spatial</b>	<b>AIC<sub>c</sub></b>	<b>Delta AIC<sub>c</sub></b>	<b>AIC<sub>c</sub> w<sub>i</sub></b>	<b>No. Par</b>	<b>Dev</b>
Pinyon-Juniper2000+Mountain Sagebrush500	1541.70	0.00	0.12	3	1535.70
Pinyon-Juniper2000	1542.40	0.69	0.09	2	1538.40
Pinyon-Juniper2000+Elevation	1542.68	0.97	0.07	3	1536.67
Elevation	1542.79	1.08	0.07	2	1538.79
Pinyon-Juniper2000+Wyoming Sagebrush2000	1542.92	1.22	0.07	3	1536.91
Mountain Sagebrush500	1543.05	1.34	0.06	2	1539.05
Pinyon-Juniper2000+Mountain Sagebrush500+Northness	1543.24	1.54	0.06	4	1535.23
Pinyon-Juniper2000+Mountain Sagebrush500+Slope	1543.31	1.61	0.05	4	1535.31
Wyoming Sagebrush2000	1543.44	1.74	0.05	2	1539.44
Pinyon-Juniper2000+Mountain Sagebrush500+Eastness	1543.70	1.99	0.04	4	1535.69
Wyoming Sagebrush1000	1543.80	2.10	0.04	2	1539.80
Mountain Sagebrush1000	1543.84	2.13	0.04	2	1539.84
Wyoming Sagebrush500	1543.95	2.25	0.04	2	1539.95
Mountain Sagebrush1000+Pinyon-Juniper1000	1544.14	2.43	0.04	3	1538.13
Mountain Sagebrush2000	1544.36	2.66	0.03	2	1540.36
Pinyon-Juniper1000	1544.72	3.02	0.03	2	1540.72
All Sagebrush2000*Elevation	1544.90	3.20	0.02	4	1536.89
Slope*Elevation	1546.25	4.54	0.01	4	1538.24
S(.) PIM	1546.42	4.72	0.01	1	1544.42
Slope	1546.78	5.08	0.01	2	1542.78
All Sagebrush2000	1546.99	5.29	0.01	2	1542.99
Northness	1547.90	6.20	0.01	2	1543.90
Pinyon-Juniper500	1547.94	6.24	0.01	2	1543.94
All Sagebrush1000	1547.97	6.27	0.01	2	1543.97
Eastness	1548.42	6.72	0.00	2	1544.42
All Sagebrush500	1548.42	6.72	0.00	2	1544.42
Northness*Eastness	1551.86	10.16	0.00	4	1543.86

<b>Temporal</b>	<b>AIC<sub>c</sub></b>	<b>Delta AIC<sub>c</sub></b>	<b>AIC<sub>c</sub> w<sub>i</sub></b>	<b>No. Par</b>	<b>Dev</b>
(.)	1546.42	10.11	0.00	1	1544.42
PDSI	1547.77	11.46	0.00	2	1543.77
Snow Pack	1547.94	11.63	0.00	2	1543.94
Raven Indice	1548.13	11.82	0.00	2	1544.13
Spring Precipitation	1548.41	12.09	0.00	2	1544.40
Year	1553.96	17.64	0.00	9	1535.92





# 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

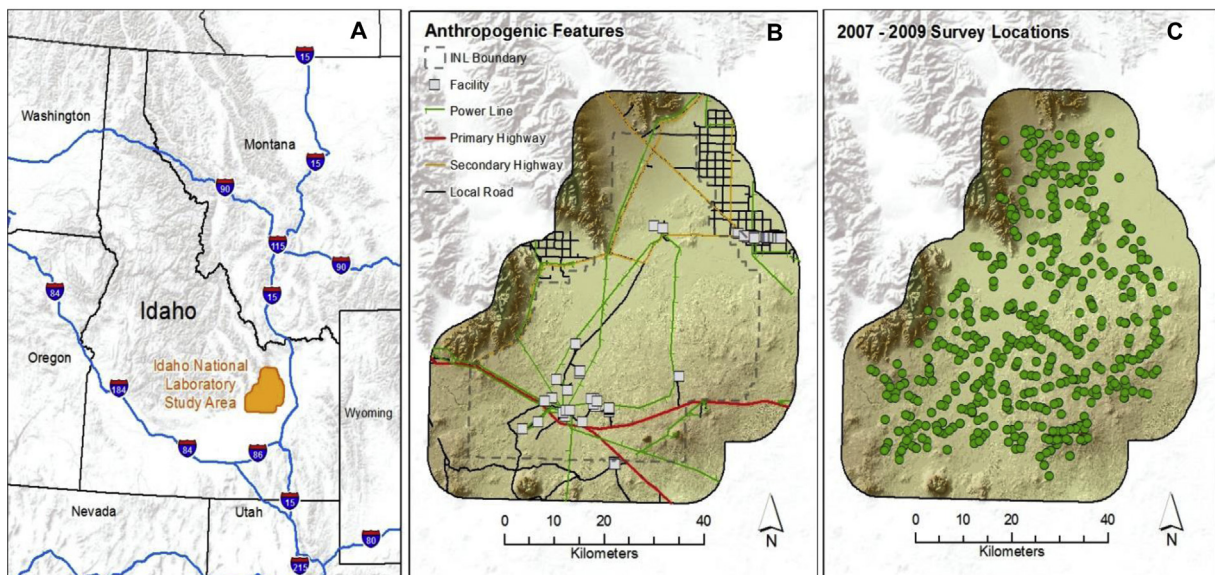
raven occurrence within an altered sagebrush steppe ecosystem. Specifically, we modeled resource selection probability functions for ravens using a combination of covariates that included land cover types at multiple spatial scales, edge (interface between two land cover types) indices, energy infrastructure, 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 alysium (*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  $\alpha$  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 ( $\pm$ 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  $\pm$  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
		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
Land Cover	660.5 ha	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 ( $\Delta$ ) 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 ( $\beta$ s; [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  $\beta$ s 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:

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

Where  $w(x)$  is the probability of use,  $\beta_0$  represents the averaged y-intercept, and  $\beta_1 \dots \beta_k$  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  $\beta$ . Although the surfaces did not directly depict the 85% CI of the predicted value derived from the model-averaged  $\beta$ s, areas that shared similar colors across the three

surfaces illustrated a greater degree of certainty in the predictions of those averaged  $\beta$ s.

## 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  $\pm$  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  $\alpha$ . 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;  $\Delta AIC_c$  = 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](#));  $\chi^2$  = Chi-square statistic from likelihood ratio test to assess model fit relative to null.

Model no.	Description <sup>a</sup>	K	LL	$\Delta AIC_c$	$w$	ER	$\chi^2$ <sup>b</sup>
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

<sup>a</sup> 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.

<sup>b</sup> 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.

## 4. Discussion

The ability of ravens to exploit a broad range of resources made available by human enterprise within sagebrush steppe, and the

**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.

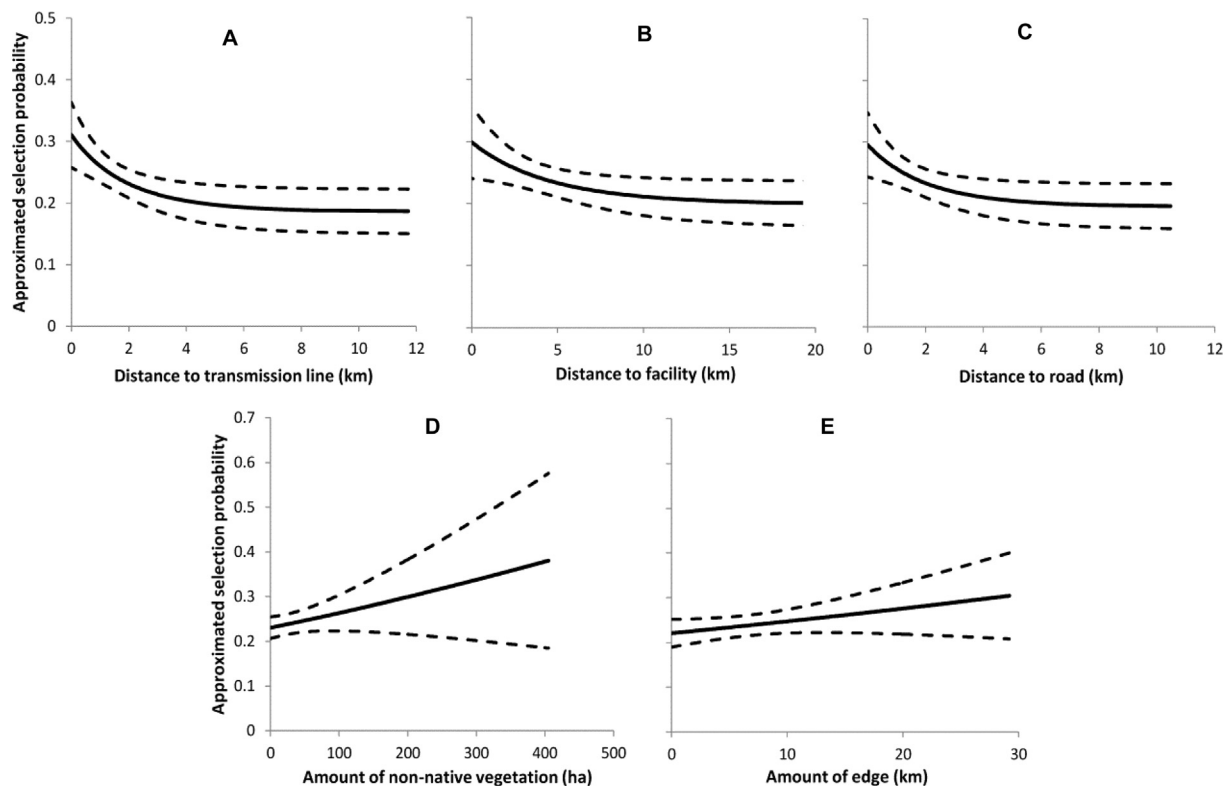
Model covariate <sup>a</sup>	Parameter estimate <sup>b</sup>	Parameter likelihood <sup>c</sup>	Interpretation
DTrans(exp)	0.76**	0.97	Selected transmission lines
DFacility(exp)	0.57**	0.50	Selected facilities
DRoad(exp)	0.48*	0.32	Selected roads
Exot660	0.20*	0.25	Selected areas with non-native vegetation
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	—

<sup>a</sup> 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.

<sup>b</sup> 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).

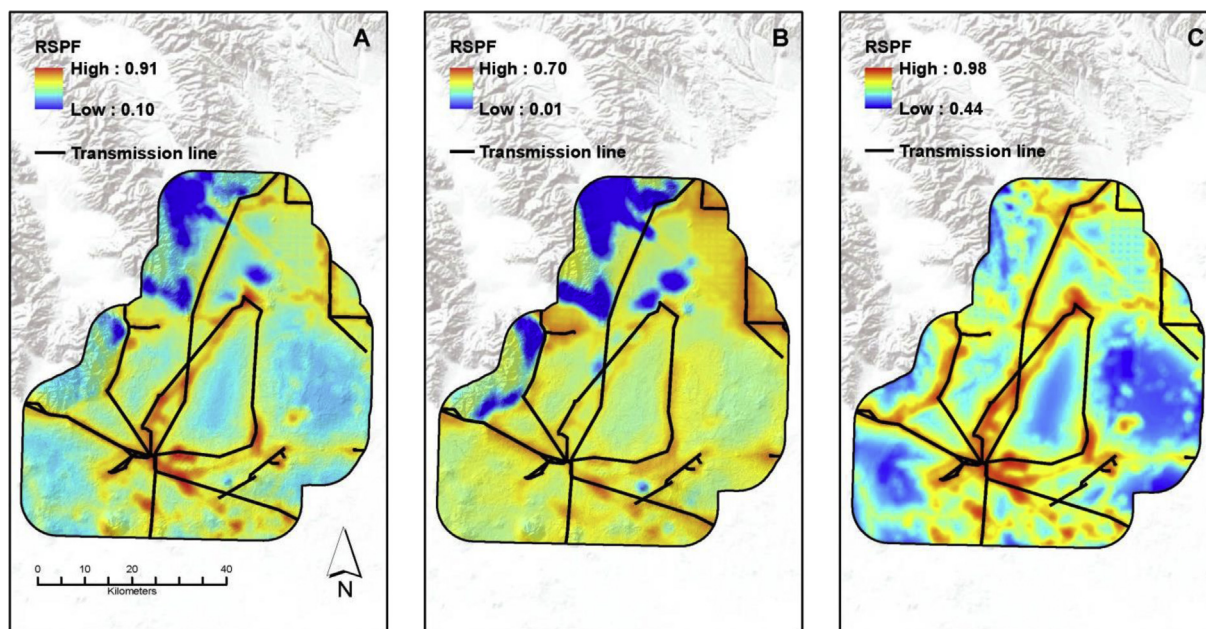
<sup>c</sup> Likelihood value represents the relative importance of explanatory variable (Anderson 2008).

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.

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,

**Table 5**

Resource selection models of land cover edge type ( $n = 20$ ) for common ravens in southeastern Idaho, 2007–2009. LL = log-likelihood;  $\Delta AIC_c$  = 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);  $\chi^2$  = Chi-square statistic for likelihood ratio test (asterisks indicates  $P < 0.05$ ), which compared model fit relative to null (intercept-only model).

Model <sup>a</sup>	LL	$\Delta AIC_c$	$w$	ER	$\chi^2$
Sage/Exot660	-767.44	0.00	0.41	—	8.12*
Sage/Grass_Exot660	-768.41	1.90	0.16	2.59	6.18*
Sage/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

<sup>a</sup> 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.

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 coincidentally 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 ( $\Delta AIC_c$ ) 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)  $\Delta AIC_c$  was  $\leq 4$ ; 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 ( $7.17 \pm 0.39$  km) than at points without raven detection ( $6.01 \pm 0.20$  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 ( $14.32 \pm 0.74$  km) than points without ( $12.25 \pm 0.38$  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 ( $30.66 \pm 3.55$  ha) than at points without ravens ( $19.49 \pm 1.56$  ha; difference = 11.17; 95% CI = 18.79–35.41 ha), and less dwarf sagebrush at points with ravens ( $2.79 \pm 1.50$  ha) than points without ( $7.60 \pm 1.31$  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;  $\Delta AIC_c$  = 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 <sup>a</sup>	No.	Model <sup>b</sup>	$K$	LL	$\Delta AIC_c$	$w$	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 <sup>a</sup>	No.	Model <sup>b</sup>	K	LL	ΔAICc	w	ER	χ <sup>2</sup>
Land Cover 660 ha	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
	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

<sup>a</sup> 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  $\alpha$  was the mean distance of the points where ravens were present) showed substantially greater support than the linear form.

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

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