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A master's thesis regarding ravens, grouse and land use in western Wyoming.

Bui 2009 Raven Thesis.pdf

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The Effects of Nest and Brood Predation by Common Ravens (*Corvus corax*) on Greater Sage-grouse (*Centrocercus urophasianus*) in Relation to Land Use in Western Wyoming

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Introduction

The western United States is a land in transition. In only two centuries, a sparsely inhabited wilderness that first supplied minerals, food, and timber for an eastern population is now increasingly settled by the populus it helped grow (Hansen *et al*. 2002). One explanation for the migration of people and businesses to the West is the availability of abundant "natural amenities," including scenery, wilderness, outdoor recreation, and wildlife (Johnson and Rasker 1995). As more people move to the West, and as human populations in this region continue to expand, ecosystem processes and biodiversity are increasingly altered because of where people choose to live and recreate (Theobald 2000). People who are attracted to the lands surrounding reserves may be altering the ecosystems within them. As a consequence of this development and activity, anthropogenic influences increasingly affect western ecosystems (Leu et al. 2008). Urban sprawl and other human activity change the quantity and quality of habitat for native wildlife (Robinson *et al*. 2005).

Most bird species respond to these human-induced changes to the landscape through population increases or decreases (Rodriguez-Estrella 2007). The expansion of urban land cover is predicted to eventually reduce total avian biodiversity within a region, with losses primarily in native specialists whose suitable habitat is decreased or degraded (Hepinstall *et al.* 2008; Marzluff *et al.* 2007). In contrast, anthropogenic changes in the landscape can favor generalist species adapted to human conditions through the provision of new resources, such as food, water, nesting structures, and protection from adverse weather or predators (Boarman *et al*. 2006). Human subsidies help fuel the expansion of these synanthropic species into habitats where they are normally found at much lower densities or not at all (Restani *et al*. 2001, Kristan and Boarman 2003). In landscapes where resource levels are naturally low, the inflation of predator

densities caused by anthropogenic resources can be significant (Webb *et al*. 2004). Increased densities of synanthropic predators can then negatively impact prey species through increased predation pressure, as subsidies insulate predator populations from the effects of declines in prey densities (Sinclair *et al*. 1998).

The Common Raven (*Corvus corax*) benefits from human activity and has been implicated as an important predator on other native species. Anthropogenic food sources increase raven populations in lightly settled areas (Marzluff and Neatherlin 2006). As human populations increase and natural resources decline, human settlements become increasingly important food sources for ravens. Groups of ravens composed mainly of juveniles and subadults congregate at concentrated food sources (Restani *et al.* 2001). In some arid environments, where resource levels are naturally low, food and water are important subsidies for ravens, particularly at landfills and sewage ponds, and are responsible for recent regional increases in raven abundance (Boarman *et al*. 2007). Development of the landscape by humans can also provide ravens with artificial nesting and roosting structures, such as trees, poles, and buildings, thereby increasing local breeding density and reproductive rates (Kristan and Boarman 2007; Webb *et al*. 2004). Roads, in particular, allow ravens to scavenge food that they would otherwise need to hunt, and make available prey that would otherwise be too big for them to kill (Knight and Kawashima 1993; Boarman and Heinrich 1999). Furthermore, juvenile movement patterns from the nest may reflect areas of anthropogenic activity, such as livestock operations in the Mojave Desert, which provide abundant, concentrated, and continually replenished food and water in an otherwise resource-poor environment (Webb *et al.* 2007). However, raven distribution is not restricted to high-quality habitat near areas of high anthropogenic activity; ravens travel from residential areas to natural vegetation where they may prey upon the nests of other bird species (Hansen *et* al. 2002). Younger, less dominant birds that are excluded from

higher quality habitat may also be forced to breed in territories further away from human subsidies of food and water (Kristan and Boarman 2007), where they can pose a threat to prey populations (Kristan and Boarman 2003).

Jackson Hole and the Upper Green River Valley in western Wyoming are experiencing accelerated rates of human development. These areas encompass sagebrush steppe and grassland habitats surrounded by the Wind River, Wyoming, and Gros Ventre mountain ranges. Until recently, these areas supported only light human settlement and wide-ranging cattle ranching. However, today human settlements are expanding from tourism in Jackson Hole and natural gas development in the Upper Green River Valley. Jackson's local economy is largely dependent on year-round tourism, as it is a major gateway for millions of tourists visiting nearby Grand Teton National Park, Yellowstone National Park, and the National Elk Refuge in the summer and the Jackson Hole Ski Area in the winter. Oil and gas production in the Valley has grown rapidly as pressure to develop domestic energy supplies continue to escalate. Over 8,500 well sites have already been drilled in this region, and another 10,000 to 15,000 are forecast over the next decade (Berger 2004). The overall density of linear features, such as roads and pipelines, in the Upper Green River Valley are well above that of national forests (Thomson *et al.* 2005). Although the physical footprint of oil and gas infrastructure comprises only a small portion of the valley, research has shown that the effect of this infrastructure on native wildlife species can be extensive (Weller *et al.* 2002). In particular, the reduction in patch size and diversity of sagebrush habitat as well as the construction of fences, powerlines, and other infrastructure are likely to subsidize the Common Raven (Braun 2002).

Subsidizing Common Ravens in Jackson Hole and the Upper Green River Valley may come at a price to sensitive sagebrush specialists, notably the Greater Sage-grouse (*Centrocercus urophasianus*). These areas support some of

the largest remaining populations of sage-grouse (Bureau of Land Management 2000; Braun 1998), a species that is declining in most portions of its range (Connelly *et al.* 2004). Declines are mostly due to degradation of sagebrush habitat brought on by increases in human activity and nest failure due to predation (Connelly *et al.* 2000; Schroeder and Baydack 2001). Sage-grouse strongly avoid nesting near developed areas (Lyon and Anderson 2003), where the risk of local extirpation is highest (Aldridge *et al.* 2008). Adequate buffers between developed areas and sagebrush used by grouse are necessary to maintain long-term persistence of the species throughout North America (Aldridge *et al.* 2008). Conserving areas of undeveloped sagebrush surrounding grouse leks are particularly important, as these locations encompass the majority of sage-grouse nests and increased nest densities due to a reduction in availability of suitable habitat can negatively influence nesting success (Holloran and Anderson 2005). Increasing development in Jackson Hole and the Upper Green River Valley may maintain raven densities at inflated levels through the provisioning of food, water, and nest-site subsidies. Raven numbers can then remain high when prey populations decline, and local populations can continue to depredate prey species, such as sage-grouse, that are at very low densities (Sinclair *et al.* 1998). Limiting raven access to anthropogenic subsidies could potentially lessen predation pressure by ravens on sage-grouse.

We investigated landscape-level patterns in raven behavior and distribution and their potential effects on sage-grouse reproduction in western Wyoming. Using point-count data from 2007 and 2008, we related raven occurrence and density to land cover, landscape pattern, and human activity. We predicted raven populations to concentrate near areas of frequent human activity, such as cities and oil fields, with gradual decreases in raven density with increasing distance from anthropogenic structures. We also expected raven abundance would positively correlate with human population size, so that large

towns, such as Jackson, Wyoming, would have the greatest raven densities. Because raven abundance can be related to predation risk posed to sage-grouse nests, we examined raven density and occupancy at sage-grouse lek locations and determined whether ravens were attracted to areas of sage-grouse nesting and brood-rearing. We hypothesized both raven occurrence and density would be greater near sage-grouse nests and broods than at control locations.

Finally, we investigated the effect of raven activity on the fate of individual sage-grouse nests and broods. We expected greater raven abundance and more predatory behavior by ravens at sage-grouse nests and broods that eventually failed than at those that survived throughout the entire reproductive season. We synthesized our findings to provide management recommendations for those interested in reducing potential negative effects of ravens on sage-grouse.

METHODS

Study Area

We measured raven response to land cover and raven activity near sage-grouse nests and broods in two separate areas of western Wyoming (Fig. 1). The "Pinedale" study area covered approximately 6,000 square kilometers and encircled the area from approximately Pinedale (2007 population= 2,043; U.S. Census Bureau) in the north, Big Piney (2007 population= 476; U.S. Census Bureau) in the south, and Boulder (2000 population= 30) in the east. The study area is characterized by sagebrush, riparian and surrounding agricultural land, oil fields, and human settlement. Areas dominated by sagebrush were dispersed among private property and land parcels governed by the Bureau of Land Management; most riparian and all agricultural lands were privately owned. All oil fields were publicly owned. The "Jackson" study area encompassed the city of Jackson (2007 population=9,631; U.S. Census Bureau) and the National Elk Refuge to the south, the towns of Moose (2000 population=1,439; U.S. Census Bureau) and Kelly (population=242), and extended northwards into Grand Teton National Park. The study area was characterized by sagebrush, riparian and abandoned agricultural land, and human settlements. All lands, except for a small neighborhood and homes, were publicly owned.

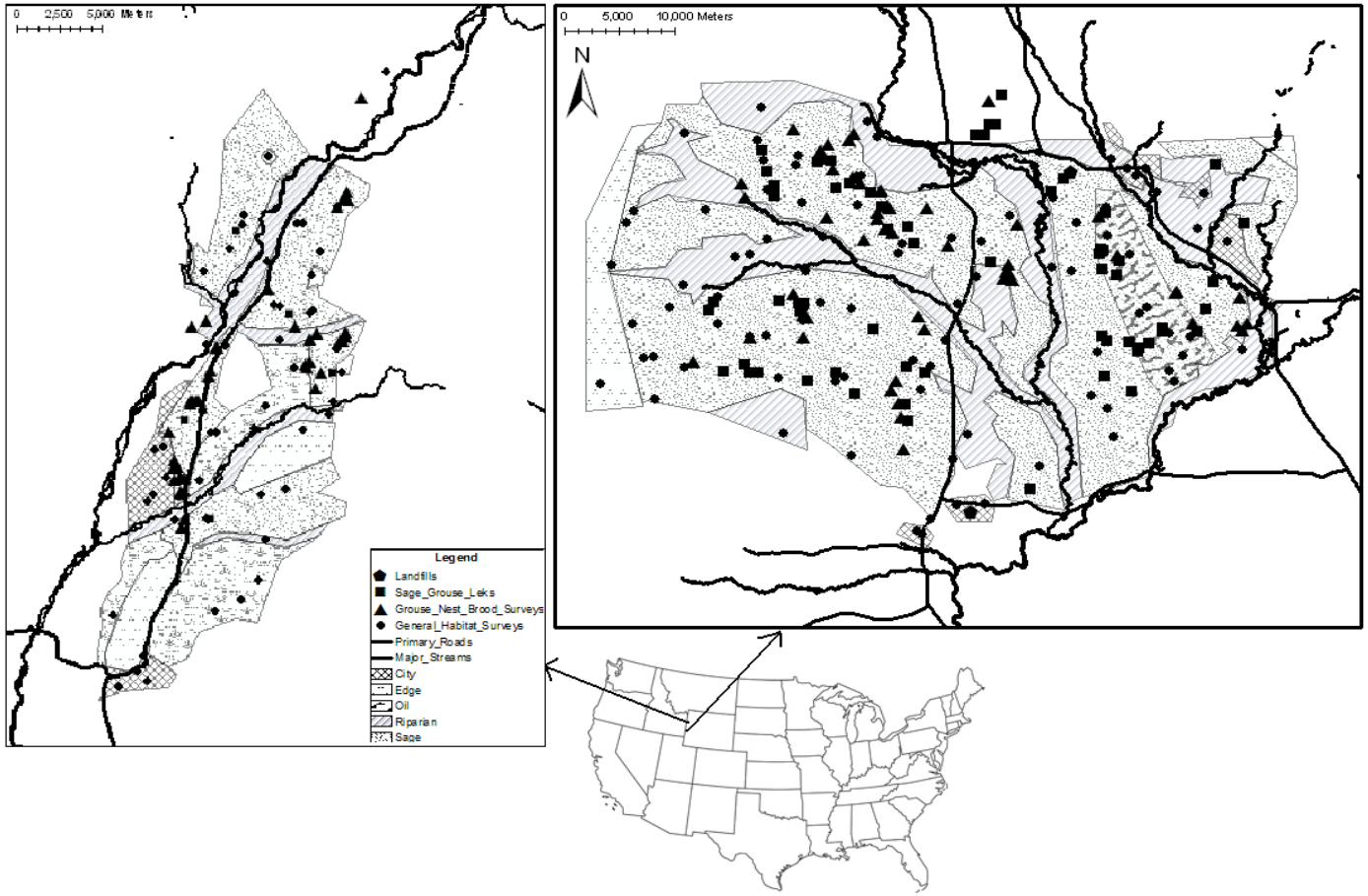

Figure 1. Map of United States (bottom) depicting locations of study areas in Wyoming, with magnified views of Pinedale (upper right) and Jackson study area (left) showing locations of raven survey points, sage-grouse leks, main roads, major streams, and land cover (sage, riparian, oil, edge, city, hayfield).

Sampling

To assess the correlation between raven abundance and land cover, we used stratified random sampling to select 166 raven survey points representing land covers within each study area (sage, riparian, oil, edge, city, road, and hayfield; Fig. 1). A minimum distance of approximately 1km separated survey points. In 2007, we conducted surveys at 74 locations in the Pinedale area and at 45 locations in the Jackson area. In 2008, we surveyed at 28 and at 19 locations in the respective study areas; these surveys were randomly located in those sections of the study area not surveyed during the previous year. We performed two surveys at each location from June 3 to August 1, 2007 and from May 16 to July 2, 2008.

To assess the activity of ravens near sage-grouse nests and broods, we conducted 249 surveys in the vicinity of known sage-grouse hens and their young (Fig. 1). These survey locations were determined by tracking radiocollared sage-grouse hens and their young throughout the reproductive season, and included grouse nests and broods of varying ages. The majority of surveys near sage-grouse nests and broods were in areas dominated by sagebrush, but some also contained riparian or oil field habitat. In the two study areas, combined, we conducted 111 surveys around grouse in 2007 (May 3 to July 25) and 138 surveys in 2008 (May 6 to July 23). Survey effort varied due to breeding success and activity. We conducted between one and five surveys at each grouse nests and between one and four surveys at each grouse brood. We surveyed around 91 radiocollared sage-grouse hens, for a total of 249 point counts (169 of these were conducted near grouse nests; 80 were conducted near grouse broods).

For each survey, we stood on top of a hill or other vantage point, listened for calls, and scanned with both unaided eyes and binoculars, alternating every

five minutes for a total of 20 minutes (Luginbuhl *et al*. 2001). For surveys near sage-grouse nests and broods, we conducted the surveys with the observer located 200-300m from the nest or brood, so as not to disturb the hen and her young or to attract predators to the nest or brood location. We measured distance to ravens at first detection from the observer using a rangefinder or prominent landscape features of known distance previously measured on aerial photographs.

During surveys, we looked for any potential predators on sage-grouse nests and broods, focusing on ravens but also including raptors and mammals. At each survey, we recorded the following: date, observer initials, start time, end time, observer northing and easting (UTM NAD 83), cloud cover (percent), wind (in mph), temperature (in °F), noise level (on a scale from 0 to 4, 0 being the lowest), habitat within a 400m radius around the observer (by percentage), and any observation of predator activity. For the latter, this included time of observation of predator activity, initial distance of predator from observer, lowest observed height of predator, activity type, habitat under predator, and any necessary comments. We mapped all observed predator activity onto a diagram of the survey point and its vicinity.

Grouse nests were visually examined for survival at least twice weekly; grouse broods were checked at approximately two weeks and at 35 days post-hatch (Schroeder *et al.* 1999, Walker *et al.* 2006). Nests were identified as successful if at least 1 egg hatched (Wallestad and Pyrah 1974); broods were identified as successful if at least 1 chick survived through the entire monitoring period. When possible, we documented cause of nest failure; if nest failure was determined to be due to predation, we attempted to identify predator type (avian or mammal; Sargeant *et al.* 1998). Because we found no remains of broods following failure, all events of brood failure were assumed to be due to predation.

Analysis

We developed a detectability model to predict the probability of observing raven activity across our study areas. Detectability is defined as the probability of observing an organism of interest at a survey location, given the organism is present at that location. Detectability at survey locations can vary by distance from observer, observer ability, and environmental factors, thus creating biases in density estimates (Rosenstock et al. 2002). To examine our data for biases in raven detectability, we tested for effects of land cover, study site, study year, and city/non-city categorization on the probability of detecting ravens at our survey locations. We used DISTANCE v.5.0 (Thomas et al. 2006) to fit detection probability functions to our observed raven detections and to produce estimates of raven density in each land cover type (sage, riparian, oil, edge, city, road, hayfield). Each land cover type constituted a stratum, and each survey point included observations from both rounds of surveys conducted at that location. We assumed survey locations were randomly located with respect to animal distribution.

We used the multiple covariates distance sampling engine, with land cover type, study site, and study year as covariates, to assess the fit of half-normal detection functions (with cosine, simple polynomial, and hermite polynomial series expansions) using Akaike information criteria (AIC) values. The sample size for surveys conducted in edge land cover was too small to conduct a DISTANCE analysis. We omitted surveys conducted in riparian and road habitat from detectability analyses because these land cover types are linear in nature, thus violating the uniform density assumption of DISTANCE analysis. Inclusion of these surveys would have overestimated detectability-converted

raven density and underestimated effective detection radius because the majority of detections at these surveys were located close to the observer.

The null model that detectability was independent of covariates produced the lowest AIC value, when compared with models considering study site, study year, land cover, and city/non-city categorization (Appendix 1: Table 1). Because we found land cover to have no effect on detectability, and detectability-corrected density estimates (Appendix 1: Table 2) were strongly correlated with unadjusted estimates (Appendix 1: Fig. 1), we used observed density estimates instead of detectability-corrected estimates in further analyses. We compared observed densities across land covers using a one-factor (land cover), repeated measures (two rounds of point counts per survey location) ANOVA (SPSS v.11.1).

We developed an occupancy model to predict the probability of raven presence across our study areas. This involved assessing raven presence or absence at each survey location during successive counts and then investigating whether the probability of presence could be modeled as a function of characteristics (land cover, study site, study year, city/noncity categorization) measured at these locations (MacKenzie et al. 2006). We used RMARK (R 2.8.1, White 2008) to assess the relative level of raven use and to estimate occupancy rates for each land-cover type. We considered the following models in our analysis: detectability and occupancy could vary by any combination of land cover, city/noncity, study site, or study year. We expected land covers with high levels of human activity (i.e. city) to have greater occupancy than those with less human use (i.e. noncity). We also hypothesized the Jackson study area would have greater occupancy than the Pinedale study area due to a larger human population. We tested for differences in occupancy rates between the two study years.

We constructed a model to predict raven occurrence across the landscape. Using observed raven occurrence from our survey locations, we conducted a logistic regression analysis that considered the following variables: land cover at the survey point (sage, riparian, oil (in Pinedale only), edge, city, road, hayfield (in Jackson only)), distance to nearest area of high human activity (road, city, landfill (in Pinedale only)), and various landscape pattern metrics (Shannon diversity index, contagion, contrast-weighted edge density, patch richness). We used aerial photos to determine land cover at each survey location and distance to nearest area of high human activity. We calculated landscape pattern metrics within a 1km circle (defined by sampling design to avoid overlap of circles) of each survey point using FRAGSTATS v.3.3 (McGarigal 2002). For contrast-weighted edge density, edges between a land cover with low human activity and another with high human activity received a weight of 1, whereas edges between two land covers with similar levels of human activity received zero weight. Because three of the four landscape pattern metrics (Shannon diversity index, contagion, patch richness) were highly correlated ($r>0.65$, $P<0.01$), we included only contagion and contrast-weighted edge density in our regression model, as these were the least correlated of the landscape pattern metrics ($r<0.47$, $P>0.5$). We used SPSS v.11.1 to produce coefficient estimates for each independent variable in predicting raven occupancy. All coefficient estimates were calculated relative to sage land cover. Using ArcGIS v.9.3 (ESRI 2008), we extrapolated these coefficient estimates from our survey locations to our entire study area to produce a predictive map of raven occurrence across the landscape.

Because our logistic regression model indicated that ravens occur throughout the vast majority of our study area (Figs. 2,3), we also constructed a model to predict variation in raven density. Using observed raven densities from our surveys, we conducted a linear regression analysis that considered the same

independent variables as our logistic regression model. We used the package "ruf.fit" v.1.3 (Handcock 2004) within the statistical software program R v.2.8 (2008) to produce coefficient estimates for each independent variable in predicting raven density. Because predicted raven densities calculated from maximum likelihood estimates accounting for spatial autocorrelation were highly correlated with those calculated from least-squares estimates in the Pinedale study area ($r=0.93$, $n=54,190$, $P<0.001$; maximum likelihood estimates failed to estimate for the Jackson study area), we determined spatial autocorrelation was negligible, supporting our sampling method of separating survey points by at least 1km. Using ArcGIS v.9.3 (ESRI 2008), we extrapolated the unstandardized least-squares coefficient estimate for each independent variable from our survey locations to our entire study area to produce a predictive map of raven abundance across the landscape.

To evaluate attraction of ravens to areas of grouse nesting and brood-rearing, we compared expected raven densities and occupancies, as predicted by our model of raven distribution, to observed values at random locations within contiguous sagebrush habitat (as a control measure) and at locations near grouse nests and broods using paired-t tests (SPSS v.16.0.1). We expected both raven density and occupancy to be greater at locations near grouse nests and broods than at random locations within contiguous sagebrush.

We also developed a multinomial logistic regression model to predict the effects of raven activity on the fate of individual grouse nests and broods. The independent variables considered in our models were: study site, percent sage cover near the grouse nest or brood, distance to nearest city, raven density, raven occupancy, and raven behavior. The dependent variable in our model was grouse fate, which fell into one of three categories: nest failure, brood failure, or survival throughout the entire reproductive season. We hypothesized raven density and occupancy would be greater and more predatory behavior would be

observed near grouse nests and broods that eventually failed than at those that survived. We investigated models considering expected values of raven density and occupancy, as predicted by our model of raven distribution, observed values of raven density, occupancy, and behavior averaged over all surveys conducted near a particular grouse nest or brood throughout the reproductive season, and observed values of raven density, occupancy, and behavior from the survey conducted latest in the reproductive season near a particular grouse nest or brood. We evaluated model fit by calculating a Pearson goodness-of-fit coefficient for each model. For failed grouse nests or broods, the “last” survey was that which was conducted nearest in time to the event of failure. Raven behavior from each survey was scored such that predatory behavior received a higher score than non-predatory behavior. Either flying at a height of >5m and exhibiting <2 turns or perching further than 50m from a grouse nest or brood received a score of 1, flying at a height of <5m and exhibiting >2 turns received a score of 2, and perching within 50m of a grouse nest or brood received a score of 3.

RESULTS

The abundance of ravens and modeled occupancy rates varied with land cover across both study areas (Table 1; $F_{1,159}$=5.9, P<0.01). City land cover had the highest observed raven density (0.015 ravens/ha) and one of the highest occupancy rates (Table 1). Although raven density was not significantly correlated with human population size within towns (r=0.23, n=6, P=0.33; Appendix 2), the town with the largest human population, Jackson, had the greatest raven density of all towns surveyed. All other land cover types had similarly low estimated raven densities, with hayfield having a slightly higher observed density than the others. Sage and oil land covers both had low observed densities, but at the Pinedale study site, which contained both land covers, the relative occupancy rate in oil habitat (0.93) was higher than in sagebrush (0.25). Riparian and road habitat, the two linearly oriented land cover types in our study, had similarly low observed densities but occupancy was greater in road habitat than in riparian. Edge habitat had the lowest observed density and occupancy rate, but sample size is small for this land cover. With the exception of oil, where the large effective detection radius (EDR) can be explained by a high percentage (56%) of distant detections, the effective detection radii were similar across the various land cover types (Table 1), further supporting our conclusion of equal detectability across land covers (Appendix 1: Table 1).

Table 1. Observed raven density, effective detection radius (EDR), and estimated relative occupancy rate for each land cover type. Occupancy rates are listed separately by study site whereas density estimates are combined across study sites because occupancy, not density, varied significantly between study sites. We used detections within 400m of the observer in our analyses in order to have an area over which to calculate observed densities and because EDRs were approximately 400m. See Appendix 1 for detectability-corrected densities.

Land Cover	No. of Counts	Detections Within 400m: Counts With Detections	Detections Within 400m: No. of Detections	Observed Density (within 400m; ravens/ha)	Effective Detection Radius (m)	Estimated Relative Occupancy Rate: Pinedale	Estimated Relative Occupancy Rate: Jackson
Sage	126	24	36	0.004 (0.001)	317.53 (40.48)	0.25 (0.07)	0.78 (0.11)
Riparian	64	16	26	0.005 (0.001)	N/A	0.57 (0.12)	0.93 (0.53)
Oil	20	6	8	0.005 (0.002)	916.29 (132.89)	0.93 (0.15)	N/A
Edge	12	1	1	0.001 (0.001)	N/A	0.05 (0.06)	0.34 (0.28)
City	56	30	82	0.015 (0.002)	280.87 (13.06)	0.78 (0.15)	0.97 (0.03)
Road	32	9	9	0.004 (0.001)	N/A	0.83 (0.16)	0.98 (0.02)
Hayfield	22	8	15	0.007 (0.002)	363.64 (53.45)	N/A	0.95 (0.14)

Study site, in addition to land cover, influenced occupancy (Table 2). There was some support (ΔAIC<2) for models including varying detectability across land covers, city/noncity area, or study site, but regardless of variability in detecting occupancy, it varied considerably across land covers and study sites. For land cover types found in both study areas, occupancy was greater in Jackson than it was in Pinedale (t_4=4.50; n=5; P=0.01; Table 1), with probability of occupancy almost twice as high in Jackson ($\bar{x}$=0.80, SE=0.12, n=5) as it was in Pinedale ($\bar{x}$=0.50, SE=0.15, n=5). Although average raven density in Jackson ($\bar{x}$=0.005 ravens/ha, SE=0.003, n=5) was about five times as great as in Pinedale ($\bar{x}$=0.001 ravens/ha, SE=0.0003, n=5) in land covers found at both study sites, the difference in densities was not significant (t_4=1.44, n=5, P=0.22).

Table 2. Top ranked models (out of 10 considered) of raven occupancy in relation to land cover, study site, and study year.

Occupancy Model	AIC	ΔAIC	Akaike Weight
Detectability constant; occupancy varies by land cover and study site	403.3	0.0	0.37
Detectability varies by land cover; occupancy varies by land cover and study site	404.5	1.2	0.20
Detectability varies by city/noncity and study site; occupancy varies by land cover and study site	404.8	1.5	0.17
Detectability varies by land cover; occupancy varies by study site	405.4	2.1	0.13
Detectability varies by study site; occupancy varies by land cover and study site	405.5	2.2	0.12

We predicted the greatest levels of raven occupancy in city, oil, and edge land cover but the highest raven densities in cities (Table 3; Figs. 2,3). Land cover was the most indicative of raven occurrence at both study sites, followed by landscape metrics, and finally by distances to areas of high human activity (Table 3). The Jackson raven population appears to be more thinly distributed than the Pinedale raven population, as intermediate to high levels of occupancy are predicted to occur over the majority of the Jackson study site, whereas the Pinedale study site is characterized by generally low levels of raven occurrence, with higher concentrations in cities. Contrast-weighted edge density and land cover were the most indicative of raven density, followed by contagion, and finally by distances to areas of high human activity (Table 3). In the Pinedale study area (Fig. 2), although we predicted oil land cover to have high levels of raven occurrence, we also predicted it to have only low to intermediate raven densities, suggesting constant but low raven activity. In contrast, low raven occupancy and high raven density are predicted in the vicinity of the landfill in the town of Pinedale (Fig. 2), indicating infrequent visits by large groups of ravens to this area. Similar trends were not predicted in the Jackson, as no oil fields or landfills are found in this study area.

Table 3. Coefficients for independent variables in linear and logistic regression analyses for predicting raven density and occupancy, respectively, where density= Intercept + $\Sigma b_i x_i$. and P(occurrence)= $e^z/(1+ e^z)$, and z= intercept + $\Sigma \beta_i x_i$.

	Density Linear Coefficients		Occupancy Logistic Coefficients	
Variable	Pinedale	Jackson	Pinedale	Jackson
Intercept	0.64 (0.67)	0.20 (0.65)	-0.04	1.64
City	1.88 (0.37)	1.64 (0.45)	1.89 (0.87)	2.19 (1.09)
Oil	0.46 (0.41)	N/A	2.33 (0.95)	N/A
Riparian	0.26 (0.30)	0.44 (0.40)	0.29 (0.79)	1.49 (0.98)
Edge	0.04 (0.63)	-0.32 (0.65)	1.22 (1.41)	-1.24 (1.45)
Contrast-Weighted Edge Density	0.05 (0.04)	-0.05 (0.05)	0.03 (0.09)	-0.11 (0.10)
Road	0.01 (0.12)	0.04 (0.50	0.88 (0.90)	1.07 (1.06)
Hayfield	N/A	0.03 (0.39)	N/A	0.52 (0.82)
Contagion	-0.003 (0.006)	0.006 (0.006)	-0.02 (0.01)	-0.02 (0.01)
Distance to Road	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Distance to Landfill	0.00 (0.00)	N/A	0.00 (0.00)	N/A
Distance to City	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)

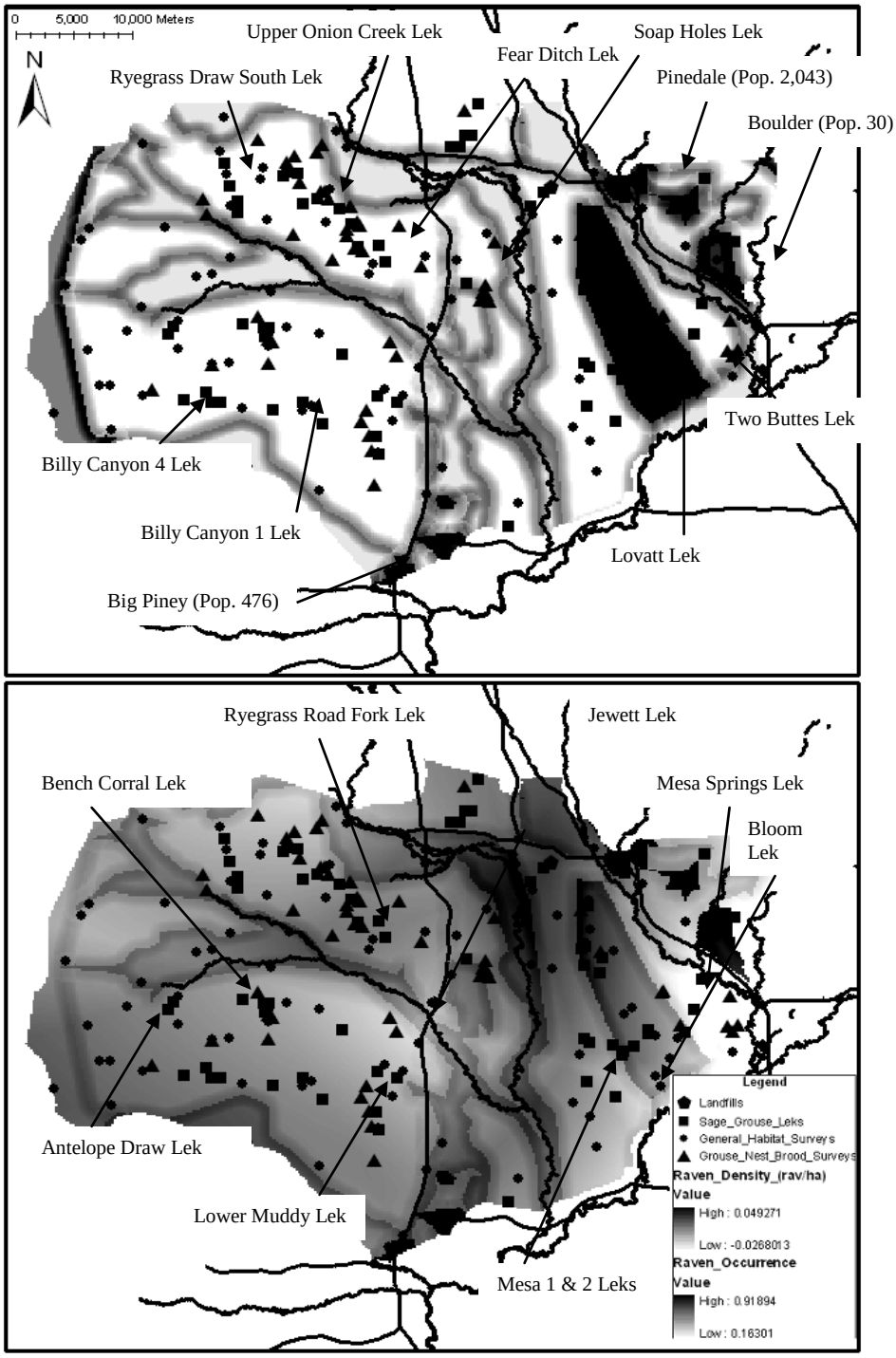

Figure 2. Major cities and landmarks, sage-grouse leks, expected raven occurrence (top), and expected raven density (ravens/ha) (bottom) across the Pinedale study area as predicted by our model.

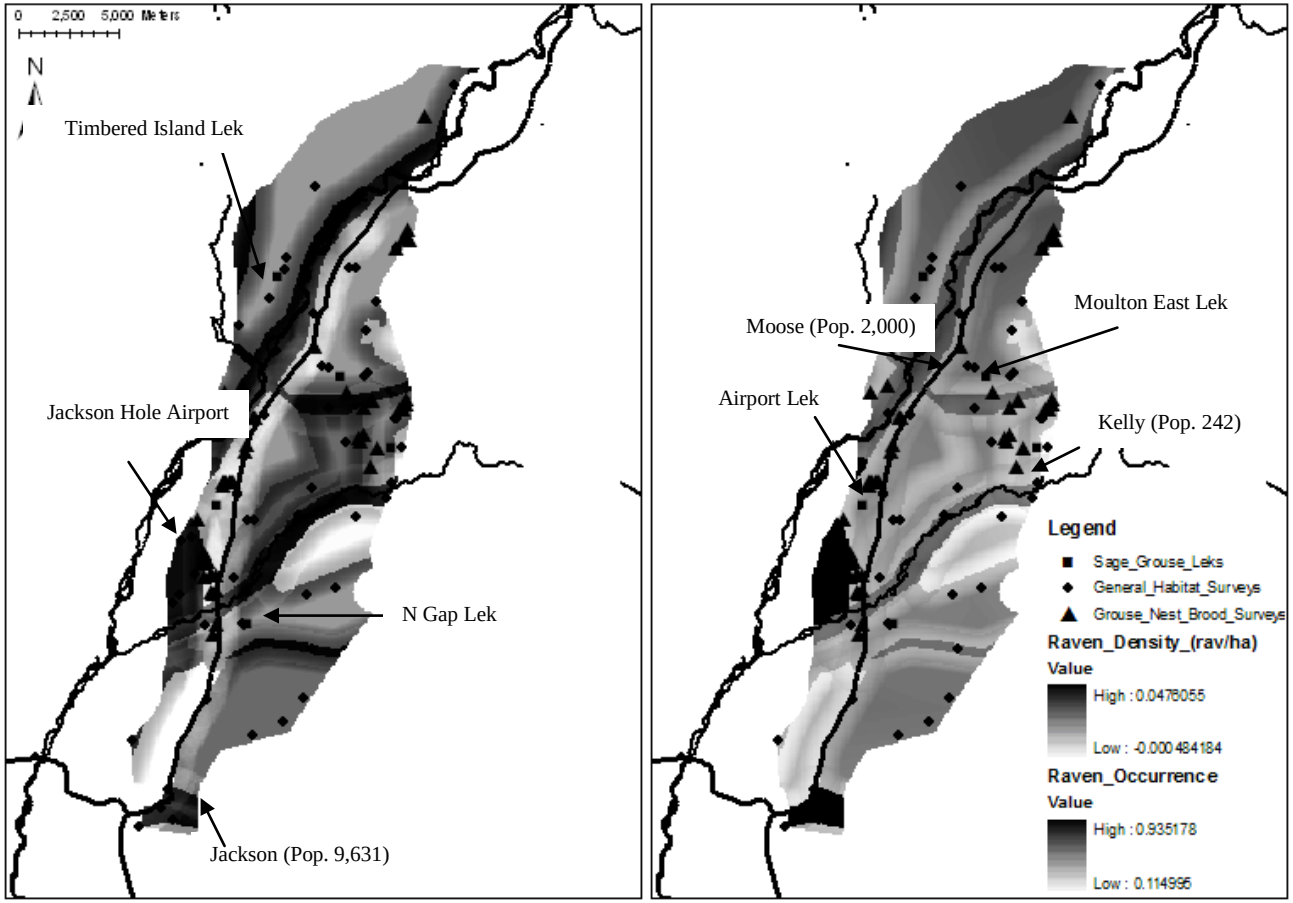

Figure 3. Major cities and landmarks, sage-grouse leks, expected raven occurrence (left), and expected raven density (ravens/ha) (right) across the Jackson study area as predicted by our model.

At both study areas, although cities contained the highest raven densities, density was predicted to sharply decrease at distances beyond approximately 3km from city boundaries, indicating little movement by ravens from cities to adjacent areas of infrequent human activity (i.e. sage). When movement by ravens into undeveloped sage lands did occur, locations of raven nests and incidental sightings of foraging by ravens implicated the role of anthropogenic infrastructure in aiding raven movement. In 2007, we recorded 34 incidental sightings of foraging by ravens throughout the Pinedale study area, of which 18 occurred along roads, 17 in undeveloped sagebrush, and two in agricultural fields. When foraging in the vicinity of roads, ravens were often observed flying along the road network, suggesting raven use of roads in locating food. Ravens also took advantage of available anthropogenic infrastructure throughout the Pinedale study area for nesting, especially in areas of undeveloped sagebrush. Between the two study seasons, we located 27 raven nests, the majority of which (16 out of 27) were located on artificial structures (including oil tanks, windmills, solar panels, and telephone poles; the remaining 11 nests were located in trees).

Predation on sage-grouse nests and broods was frequent during our study but the overall risk to grouse of encountering ravens was low. During our study, 51% of grouse nests failed, 83% of which were determined to be due to predation. Forty-seven percent of grouse broods failed, all of which were assumed to be due to predation. An average of 1.34 and 1.56 juveniles fledged per grouse hen in the Pinedale and Jackson study areas, respectively. We estimated the potential risk of predation by ravens on sage-grouse nests and broods by comparing a particular location within our study area to the predicted raven occupancy and density at that location. At the coarsest spatial scale, the productivity of leks was uncorrelated with expected raven occupancy and abundance. There was no general relationship between nest predation risk and

lek productivity ($r<0.2$, $P>0.3$, Kendall's $T=-0.12$, Spearman's $\rho=0.49$; Table 4). For both study sites, some of the leks with the highest productivity rates were at the lowest risk of nest predation. Furthermore, both predicted raven occupancy ($F_{1,74}=18.2$, $P<0.01$) and density ($F_{1,74}=144.5$, $P<0.01$) differed significantly between grouse leks and cities, with lower mean occupancy ($\bar{x}=0.35$) and density ($\bar{x}=0.004$ ravens/ha) near leks than in cities ($\bar{x}_{occupancy}=0.78$, $\bar{x}_{density}=0.04$ ravens/ha), indicating low expected raven presence near sage-grouse nests in areas of undeveloped sagebrush relative to highly developed areas such as cities.

Table 4. Greater Sage-grouse leks ranked by nest predation risk posed by ravens and grouse nest productivity. We defined risk as predicted raven occurrence and density. Lek productivity was ranked subjectively by researchers familiar with the local grouse populations (M. Holloran and B. Bedrosian, pers. comm.).

Study area	Lek	Rank Risk	Rank Productivity
Pinedale	Lovatt	1	10
Pinedale	Mesa Springs	2	14
Pinedale	Soap Holes	3	13
Pinedale	Mesa 1	4	12
Pinedale	Mesa 2	5	16
Pinedale	Billy Canyon 4	6	6
Pinedale	Antelope Draw	7	8
Pinedale	Jewett	8	4
Pinedale	Ryegrass Road Fork	9	9
Pinedale	Fear Ditch	10	5
Pinedale	Bloom	11	15
Pinedale	Ryegrass Draw South	12	11
Pinedale	Bench Corral	13	2
Pinedale	Billy Canyon 1	14	7
Pinedale	Lower Muddy	15	1
Pinedale	Upper Onion Creek	16	3
Jackson	Timbered Island	1	3
Jackson	Moulton East	2	1
Jackson	N Gap	3	4
Jackson	Airport	4	2

While leks may not be expected to be at high risk of raven predation, ravens appeared to respond numerically to the actual presence of grouse nests and broods. Observed raven density at random locations within contiguous sagebrush ($\bar{x}$=0.007 ravens/ha, SE=0.002) did not differ significantly from model expectations (predicted sagebrush raven density from model in Table 3: $\bar{x}$=0.008 ravens/ha, SE=0.002, t_{73}=0.51, P=0.62), but observed raven occupancy ($\bar{x}$=0.20, SE=0.04) was significantly lower than expected ($\bar{x}$=0.40, SE=0.03,

t_{73}=-5.47, P<0.01; Table 1). Observed raven occupancy ($\bar{x}$=0.29, SE=0.04) was also significantly lower than expected at locations near grouse nests and broods ($\bar{x}$=0.37, SE=0.02, t_{84}=-2.22, P=0.03), but observed raven density ($\bar{x}$ = 0.01 ravens/ha, SE=0.002) was significantly greater than expected at these locations ($\bar{x}$=0.006 ravens/ha, SE=0.001, t_{84}=2.89, P=0.01).

The presence and behavior of ravens were associated with grouse nest and brood fate. Raven occupancy and behavior observed near grouse nests and broods affect grouse fate to a greater degree than raven density (Table 5). Overall, raven density, occupancy, and behavior observed at the "last" surveys affected grouse nest and brood fate more than did values of these variables averaged over all surveys conducted throughout the reproductive season, which, in turn, affected grouse fate to a greater degree than values of raven density and occupancy as predicted by our model of raven distribution. In contrast, neither study site or sage cover near grouse nests and broods significantly affected grouse fate, suggesting nest and brood success rates were similar between Pinedale (27%) and Jackson (29%) and percent sage cover did not differ between grouse fates (98% for failed and successful grouse nests and broods).

Table 5. Multinomial logistic regression models, with AIC, ΔAIC, Akaike weight, degrees of freedom, and Pearson goodness-of-fit coefficient used to test for the effects of raven activity on grouse nest and brood fate.

Model	AIC	Δ AIC	Akaike Weight	df	Pearson	P
Study Site, Sage Cover, Last Observed Raven Occupancy	69.32	0.00	0.95	30	33.09	0.32
Study Site, Sage Cover, Last Observed Raven Behavior	75.64	6.32	0.04	38	35.95	0.57
Study Site, Sage Cover, Last Observed Raven Density	78.15	8.83	0.01	40	46.09	0.23
Study Site, Sage Cover, Average Observed Raven Behavior	101.37	32.05	0.00	62	63.59	0.42
Study Site, Sage Cover, Average Observed Raven Occupancy	107.56	38.24	0.00	70	82.13	0.15
Study Site, Sage Cover, Average Observed Raven Density	116.58	47.26	0.00	76	94.56	0.07
Study Site, Sage Cover, Predicted Raven Occupancy	120.87	51.55	0.00	98	93.11	0.62
Study Site, Sage Cover, Distance to City	153.94	84.62	0.00	128	162.77	0.02
Study Site, Sage Cover, Predicted Raven Density	171.19	101.87	0.00	158	171.43	0.22

There were no significant differences in the mean values of predicted or observed (averaged or "last") raven density, occupancy, or behavior between any of the three categories of grouse fate (nest failure, brood failure, survival). However, for "last" surveys, mean raven density, mean occupancy, and behavior scores were slightly greater at failed grouse nests and broods (n=62, $\bar{x}_{density}$=0.01 ravens/ha, $SE_{density}$=0.004, $\bar{x}_{occupancy}$=0.43, $SE_{occupancy}$=0.11, $\bar{x}_{behavior}$=0.82, $SE_{behavior}$=0.27) than at those that survived throughout the reproductive season (n=24, $\bar{x}_{density}$=0.007 ravens/ha, $SE_{density}$=0.004, $\bar{x}_{occupancy}$=0.26, $SE_{occupancy}$=0.12, behavior=0.25, $SE_{behavior}$=0.11). In addition, we observed more predatory behavior by ravens at failed than at successful grouse nests and broods. The majority (44%) of observed raven behavior at failed grouse nests and broods received a score of 3 (strongly indicative of foraging behavior), 38% received a score of 2, and only 18% received a score of 1 (slightly indicative of foraging behavior). In contrast, the majority (80%) of observed raven behavior at successful grouse nests and broods received a score of 1, 20% received a score of 2, and none received a score of 3. Furthermore, although adding distance to nearest city as a factor in our regression model of grouse fate did not improve model fit (Table 5), failed grouse nests and broods tended to be closer to cities ($\bar{x}$=5,339m, SE=1,236m) than did successful nests and broods ($\bar{x}$=37,608m, SE=20,986m).

DISCUSSION

Recent increases in raven populations have been consistently linked with human activity (Marzluff and Neatherlin 2006; Restani *et al.* 2001; Kristan and Boarman 2007), which provides anthropogenic food, water, and nest sites (Boarman *et al*. 2006), thereby increasing local raven density, productivity, and survival (Webb et al. 2004; Marzluff and Neatherlin 2006). Our results agree with these findings, as we estimated the highest raven density and relative occupancy rate to both occur near cities, the land cover in our study area with the most frequent human activity. Towns in our study areas provide supplemental food, water, and nest sites to ravens, which locally increased density an expected 3km into undeveloped adjacent lands.

We also found high raven occurrence, but low density, in oil fields, which is consistent with presence of a territorial breeding pair. While subsidies provided by oil development may be less than those provided by cities, the encroachment of oil fields upon undeveloped sagebrush can facilitate raven movement into these sage lands, much as campgrounds facilitate crow movements into otherwise rarely visited forests (Neatherlin and Marzluff 2004). Incidental sightings of raven foraging during our study suggest ravens take advantage of road networks associated with oil fields and undeveloped sagebrush (Knight and Kawashima 1993; Knight *et al.* 1995). Furthermore, artificial nesting substrates (i.e. telephone poles, windmills, buildings, and oil storage tanks), both within cities and in undeveloped sagebrush immediately surrounding cities and oil fields allow new breeding pairs to colonize rarely used sage vegetation, which can increase nest predation on sage-grouse (Manzer and Hannon 2005).

Indeed, increased occupancy of areas with minimal human presence (like oil fields) by pairs of ravens rather than increased density associated with flocks

of ravens in human-dominated areas like cities, towns, and landfills, appears to significantly increase the risk of nest predation to sage-grouse. Raven density was greater near sage-grouse nests and broods than at control locations, but it was still relatively low (0.01 ravens/ha), which is consistent with foraging by territorial nesting raven pairs, not large congregations of nonbreeding individuals. Low but consistent raven presence can have a major impact on sage-grouse reproductive behavior. Incubation patterns of grouse, for example may have evolved to avoid visually cued, diurnal predators such as ravens and other corvids (Angelstam 1984; Erikstad 1986). Incubating sage-grouse hens typically briefly leave their nests to forage only during crepuscular periods, when low light conditions are prevalent; longer recesses from the nest that extend nest exposure into high light conditions may increase nest depredation by ravens (Coates and Delehanty 2008). Even with such adaptations, increased occurrence of ravens in sage lands can reduce nesting success. Our model of grouse fate implicated raven behavior and occupancy, rather than density, in determining nesting success.

Local attraction of ravens to nesting hens my be facilitated by the reduction, isolation, and fragmentation of native shrublands that is known to disturb hens and leks, increase exposure of nests to potential predators (Lyon and Anderson 2003), and ultimately lower reproduction (Vander Haegen *et al.* 2002; Aldridge and Boyce 2007). As more suitable grouse habitat is converted to oil fields, agriculture, and other exurban development, grouse nesting and brood-rearing become increasingly spatially restricted. Enhanced prey detection can occur at higher nest concentrations, and increased nest densities could result in increased nest depredation (Schroeder *et al.* 2004), especially when nests are arranged in a clumped spatial configuration (Marzluff and Balda 1992).

Human-mediated, increased occupancy of sage lands by ravens may limit sage-grouse populations. A ratio of 2.25 juveniles/hen through the

reproductive season is needed for a sage-grouse population to be considered stable to increasing (Connelly and Braun 1997). Neither of the sage-grouse populations in our study reached this recommended level of productivity. Because the majority of the grouse nest and brood failures during our study were due to predation, we conclude that long-term persistence of both the Jackson and Pinedale sage-grouse populations is limited, at least in part, by nest and brood predation pressure from several native predator species, including the Common Raven. However, we assumed all brood failure during our study to be due to predation because it was difficult to find brood remains that concluded otherwise. This potentially has the effect of overestimating the impact of predation on grouse reproductive success. For similar reasons, we were unable to quantify partial predation, as grouse nest and brood success were defined as the survival of one or more egg or chick, respectively. Failing to account for partial predation of grouse nests and broods could lead to underestimation of predation pressure on grouse, as some grouse nests or broods categorized as successful in our study may not have actually reached their full reproductive potential. However, this potential underestimation may be negligible because monitoring studies have shown partial predation accounts for a small proportion of predation events by ravens on sage-grouse nests (Coates *et al.* 2008).

Modeling The Risk of Predation

We found it informative to model both raven density and occupancy, although this is rarely done. This allowed us to highlight areas with high occupancy but low density, like oil fields, which provided new nesting sites for pairs but not foraging sites for groups, of ravens. We also were able to identify areas with high density and low occupancy of ravens, such as the immediate area surrounding the Pinedale landfill. This suggests infrequent visits by large foraging groups of ravens, likely consisting mainly of juveniles and sub-adults, to the landfill, a prime location for anthropogenic food subsidies (Kristan and Boarman 2003; Marzluff *et al.* 1996), but not necessarily new nest sites. Although the Pinedale landfill attracts large numbers of ravens, it is important to note that raven occupancy at this location is inconsistent, and therefore, overflow of ravens from the landfill into surrounding sage land is minimal. No comparable locations with high raven density and low occupancy were predicted in the Jackson study area. This is not surprising given this study site contains no landfills or other similar areas of concentrated anthropogenic food subsidies.

Our model of raven distribution overestimated raven occupancy at both control locations (randomly located within contiguous sagebrush) and at locations near sage-grouse nests and broods. This is most likely due to limited observations, especially at control locations, where we conducted only two surveys. Because raven abundance is relatively low in contiguous sagebrush, when compared to other land covers, it is likely that raven presence went undetected at some survey locations. Increasing the number of surveys performed at each location would decrease incidence of undetected ravens, leading observed raven occupancy to approach that predicted by our model. Although our model may not accurately predict absolute rates of raven occupancy, it is still possible that it may show relative differences in occupancy.

Our model of grouse fate implicated raven occupancy and behavior observed near grouse nests and broods later in the reproductive season (i.e. temporally proximal to event of success or failure) as the best predictors of grouse reproductive success, as opposed to raven density, study site, or sage cover near grouse nests or broods. This suggests studies that measure only predator density (for example, Manzer and Hannon 2005) near areas of grouse nesting and brood-rearing may not adequately quantify the effects of predator activity on grouse reproductive success. Observations of predator presence and activity closer to the event of grouse reproductive success or failure are better predictors of grouse fate than observations that are temporally farther from success or failure. This indicates potential predation risk to a particular grouse nest or brood can be gauged temporally throughout the reproductive season by observing nearby predator activity, and a sudden increase in predator occupancy or predatory behavior can be interpreted as an increase in probability of the depredation of a specific grouse nest or brood. Our model of grouse fate also suggested increasing nest and brood predation risk with decreasing distance to areas with frequent human activity. These areas pose high predation risk to sage-grouse by providing abundant food, water, and nest site subsidies to ravens, resulting in higher levels of raven occurrence.

Managing Subsidized Native Predators

Given the potential of subsidized raven populations to limit sensitive species like sage-grouse, how might managers limit raven populations? Direct and indirect controls are available. Direct control involves removal of offending predators, usually through lethal methods such as shooting or poisoning. In contrast, indirect control involves limiting predator populations through nonlethal methods. Researchers have proposed habitat alteration, such as removing perch and denning sites (Jiménez and Conover 2001) and limiting access to anthropogenic subsidies that increase available resources for predators (Boarman 2003; Marzluff and Neatherlin 2006) to reduce predator abundance. Behavioral modification has been employed to reduce predation on native prey species and can be effective in altering raven foraging behavior (Avery *et al*. 1995). In expansive areas of relatively undisturbed habitat where a diversity of native predators may be subsidized by distant human activity, an integrated combination of direct and indirect methods may be effective.

Our results suggest ravens cue in specifically on sage-grouse nests and broods instead of foraging uniformly across sagebrush. Once nesting grouse are found, ravens likely forage in an area-restricted manner (Marzluff and Balda 1992), thereby endangering nearby nests. Therefore, the first line of defense against ravens should be to reduce occupancy of important grouse nesting habitat. This can be at least partially accomplished by removal of anthropogenic subsidies; additional measures of either direct removal of ravens or aversive conditioning of territorial ravens in these sensitive areas can increase the potential of reduction of ravens. Because direct removal of ravens may not be sufficient to benefit sage-grouse populations in the long term (new territorial pairs need simply colonize vacated areas), there may be additional benefits derived from discouraging predation through conditioned taste aversion while

allowing the behaviorally-modified predator to remain on the landscape. Using methiocarb-treated eggs, nest predation at a California least tern colony was completely eliminated, reducing ten-fold the requirement for removal of ravens (Avery *et al.* 1995). This indicates that illness-based aversions are powerful behavior modifiers that can reduce preference for the associated flavor with a single occurrence. Similar techniques could be considered for raven behavior control in the vicinity of sage-grouse nesting grounds. Modifying raven behavior to reduce raven abundance near sage-grouse nests (Coates *et al.* 2007) or raven preference for sage-grouse eggs would result in decreased nest predation while also discouraging activity by non-resident ravens in these areas through territorial behavior by resident breeding pairs.

A second strategy to reduce ravens is to lower the carrying capacity of areas with high raven density. This could be accomplished primarily by limiting the amount and availability of garbage in cities, towns, and landfills to ravens. In addition, access to sewage ponds and roadkill should be reduced. Possible strategies include installation of covers or wires (as deterrents) over dumpsters, incineration of garbage, removal of animal carcasses from roads, and enforcement of regulations concerning waste disposal, as they relate to wildlife (USFWS 2003). Anthropogenic nest sites should be managed to reduce raven use through egg removal, nest destruction, harassment of nesting pairs, retrofitting or installing deterrent fixtures (i.e. strips, netting, screening) on old structures, covering well heads, and modifying future engineering of structures to avoid providing suitable nesting platforms (Leibezeit and George 2000). Education about the effects of feeding wildlife should be widespread; this is especially important at tourist locations, such as in the Jackson study area, where large groups of people congregate. Furthermore, corporations operating within sensitive grouse nesting areas should consider hiring, firing, and fining policies that strongly discourage their employees from purposefully or inadvertently

providing supplemental food to ravens (USFWS 2003). Once subsidies are limited, raven populations may disperse and decline on their own. This reduction in local population may be enhanced by direct control and persecution after subsidies are removed. Reducing the availability of resource subsidies may have great success in controlling raven abundance, but only when similar efforts are coupled on a region-wide basis (Boarman *et al.* 2006).

These strategies must be combined with protection of existing high quality sage lands and restoration of degraded lands. Undeveloped sagebrush should be spared increased oil exploration and development as it enables raven colonization and reduces sage-grouse productivity. Existing sagebrush should be managed at a landscape level to reduce fragmentation, which increased predator foraging efficiency. Because it may be more difficult for predators to locate sage-grouse nests in extensive stands of sagebrush (Vander Haegen *et al.* 2002), restoration of sagebrush ecosystems could be viewed as part of a broad-scale approach towards avoiding extinction of specific sage-grouse populations (Schroeder and Baydack 2001). The Upper Green River Valley is experiencing increasing fragmentation of sagebrush-dominated landscapes due to natural gas development, and the area surrounding Grand Teton National Park, Wyoming, is characterized by high levels of seasonal tourism and recreation. Limiting human activity and restricting further development of sagebrush, especially near areas of grouse nesting and brood-rearing, are necessary to protect the Pinedale and Jackson sage-grouse populations from decline.

Integrated management of native predators is of utmost importance to sage-grouse recovery. It is unlikely that traditional, government sponsored killing of ravens, most of which are not the territorial birds actually responsible for predation, will benefit sensitive nesting species like sage-grouse. Instead, limited removal of offending birds coupled with coordinated, region-wide improvement of sagebrush habitat and removal of anthropogenic subsidies is

needed. Such an integrated approach would reduce predation pressure on grouse locally and regionally, thereby helping to ensure the long-term persistence of vulnerable grouse populations.

Adaptive management such as we suggest would require continued monitoring after implementation of control measures to evaluate raven response to management strategies. Any potential correlations between changes in raven abundance or presence and sage-grouse nest and brood survival should be examined; management strategies should then be adjusted accordingly to improve efficacy of increasing sage-grouse survival.

Future management would also be aided by additional research. Although we measured raven abundance and occupancy both in areas with frequent (i.e. cities) and infrequent (i.e. sagebrush) human activity, it would be useful to compare raven density and presence in areas with towns (such as was done in this study) to those without towns or other locations with concentrated human activity. In addition, we did not investigate raven movement from cities into sagebrush in detail. This could be done in future studies through radio-tracking of ravens to pinpoint individuals most likely responsible for depredation of sage-grouse nests and broods and whose removal would most benefit local sage-grouse populations.

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Appendix 1. Detectability Model Selection

We considered the following models when fitting detectability probability functions to our observed raven detections and to produce estimates of raven density in each land cover type: null (detectability is independent of all covariates considered), study site, study year, study site and year, land cover (sage, riparian, oil, edge, city, road, hayfield), and city/non-city categorization. The null model that detectability is independent of covariates (study site, study year, land cover, city/non-city) had the lowest AIC value of all models considered (Table 1), indicating detectability did not vary among the land covers of interest in our study. Because detectability-corrected density estimates (Table 2) did not vary greatly from observed estimates and were strongly correlated with unadjusted density estimates ($r=0.97$, $n=4$, $P=0.03$), we used observed estimates in our analyses. Observed raven densities within towns were not strongly correlated with human populations of those towns ($r=0.23$, $n=6$, $P=0.33$).

Table 1. AIC value and ΔAIC for each detectability model.

Detectability Model	Covariates Considered	AIC	Δ AIC
Null Model Half-normal Cosine	none	2667.42	0.00
Land cover Half-normal Cosine	land cover	2677.64	10.22
City/Non-city Half-normal Cosine	city	2682.34	14.92
Site Year Half-normal Cosine	study site and year	2693.28	25.86
Site Half-normal Cosine	study site	2695.40	27.98
Year Half-normal Cosine	study year	2701.13	33.71

Table 2. Detectability-corrected density for each land cover using the null model that detectability is independent of covariates.

Land Cover	Detectability-corrected Density (ravens/ha)
Sage	0.037 (0.013)
Riparian	n/a
Oil	0.007 (0.002)
Edge	n/a
City	0.17 (0.035)
Road	n/a
Hayfield	0.064 (0.027)

Appendix 2. Correlation of Density Estimates

Detectability-corrected estimates of raven density by land cover did not vary greatly from observed estimates and were strongly correlated with unadjusted density estimates (Fig. 1), Observed raven densities within towns were not strongly correlated with human populations of those towns (Fig. 2).

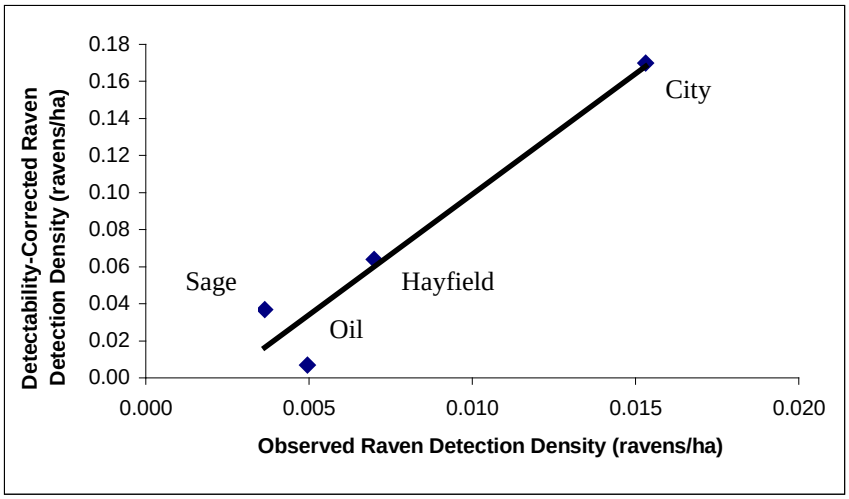

Figure 1. Correlation between detectability-corrected and observed raven densities for land covers (r=0.97, n=4, P=0.03).

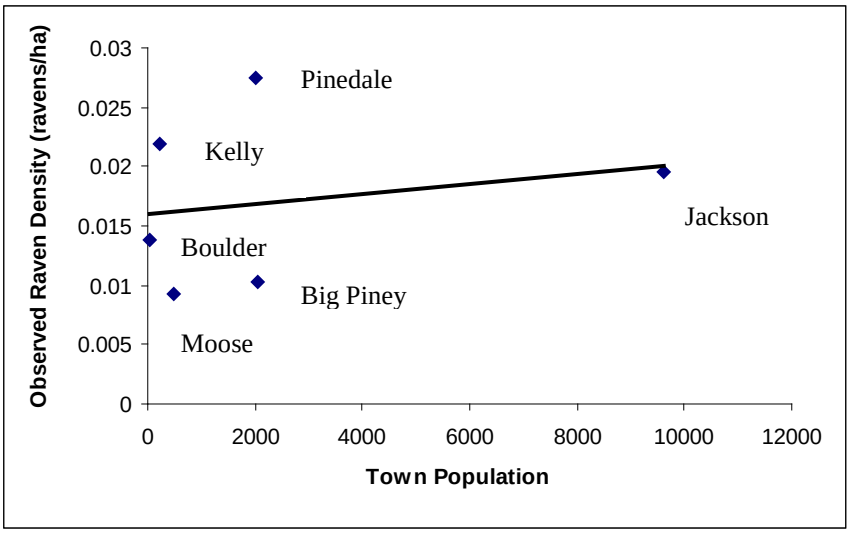

Figure 2. Correlation between observed raven densities and human population of towns surveyed (r=0.23, n=6, P= 0.33).