COMMON RAVEN ACTIVITY IN RELATION TO LAND USE IN WESTERN WYOMING: IMPLICATIONS FOR GREATER SAGE-GROUSE REPRODUCTIVE SUCCESS

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Abstract. Anthropogenic changes in landscapes can favor generalist species adapted to human settlement, such as the Common Raven (*Corvus corax*), by providing new resources. Increased densities of predators can then negatively affect prey, especially rare or sensitive species. Jackson Hole and the upper Green River valley in western Wyoming are experiencing accelerated rates of human development due to tourism and natural gas development, respectively. Increased raven populations in these areas may negatively influence the Greater Sage-Grouse (*Centrocercus urophasianus*), a sensitive sagebrush specialist. We investigated landscape-level patterns in raven behavior and distribution and the correlation of the raven data with the grouse's reproductive success in western Wyoming. In our study areas towns provide ravens with supplemental food, water, and nest sites, leading to locally increased density but with apparently limited (<3 km) movement by ravens from towns to adjacent areas of undeveloped sagebrush. Raven density and occupancy were greatest in land covers with frequent human activity. In sagebrush with little human activity, raven density near incubating and brooding sage-grouse was elevated slightly relative to that expected and observed in sagebrush not known to hold grouse. Raven occupancy near sage-grouse nests and broods was more highly correlated with sage-grouse success than were raven density and behavior, suggesting that the majority of nest predation by ravens is most likely carried out by resident territorial individuals. Integrated region-wide improvement of sagebrush habitat, removal of anthropogenic subsidies, and perhaps removal or aversive conditioning of offending ravens might benefit sage-grouse populations in our study area.

Key words: *anthropogenic subsidies,* Centrocercus urophasianus, *Common Raven,* Corvus corax, *density and occupancy modeling, Greater Sage-Grouse, nest and brood predation.*

Actividad de *Corvus corax* en Relación al Uso del Suelo en el Oeste de Wyoming: Implicancias para el Éxito Reproductivo de *Centrocercus urophasianus*

Resumen. Los cambios en el paisaje de origen antropogénico pueden favorecer especies generalistas adaptadas a asentamientos humanos, como el cuervo *Corvus corax*, al proveer nuevos recursos. Luego, el aumento de la densidad de depredadores puede afectar negativamente a las presas, especialmente a las especies de presas raras o sensibles. Jackson Hole y la parte superior del valle del río Green en el oeste de Wyoming están experimentando tasas aceleradas de desarrollo humano debido a emprendimientos turísticos y de gas natural. El aumento de las poblaciones de *C. corax* en estas áreas puede influenciar de forma negativa a *Centrocercus urophasianus*, una especie sensible y especialista de matorrales de *Artemisia*. Investigamos patrones de comportamiento y distribución de *Corvus corax* a escala de paisaje y la correlación de los cuervos con el éxito reproductivo de *Centrocercus urophasianus* en el oeste de Wyoming. En nuestra área de estudio, las ciudades proveen alimento, agua y sitios de anidación suplementarios a los cuervos. Esto da como resultado el aumento de las densidades reproductivas locales pero con movimientos aparentemente limitados (<3 km) por parte de los cuervos desde las ciudades hacia las áreas no desarrolladas de matorrales de *Artemisia*. La mayor densidad y ocupación de *Corvus corax* fue observada en tipos de coberturas de suelo con actividades humanas frecuentes. En los matorrales de *Artemisia* con poca actividad humana, la densidad de cuervos fue levemente elevada cerca de las áreas de incubación y cría de *Centrocercus urophasianus*, comparada con la densidad esperada y observada en matorrales de *Artemisia* que no presentan individuos de *C. urophasianus*. La ocupación de cuervos en las proximidades de las áreas de cría de *C. urophasianus* tuvo una mejor correlación con el éxito de *C. urophasianus* que la densidad y el comportamiento de los cuervos. Esto sugiere que la mayor parte de la depredación por parte de los cuervos es realizada por individuos territoriales residentes. El mejoramiento integrado de los matorrales de *Artemisia* a nivel regional, la remoción de subsidios antropogénicos y quizás también la remoción o condicionamiento por aversión de los cuervos agresivos podrían beneficiar a las poblaciones de *C. urophasianus* en nuestra área de estudio.

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). As more people move to the West, ecosystem processes and biodiversity are altered (Theobald 2000, Robinson et al. 2005, Leu et al. 2008). Of importance to birds, the process of predation has been greatly modified by western people; large carnivores have been reduced or extirpated (Quammen 2004, Clark et al. 2005), while small generalists have been inadvertently aided by subsidies, enabling population growth and expansion (Restani et al. 2001, Kristan and Boarman 2003, Boarman et al. 2006). In landscapes where resource levels are naturally low, the inflation of densities of generalist predators caused by anthropogenic resources can be significant (Webb et al. 2004) and detrimental to sensitive prey (Sinclair et al. 1998).

The Common Raven (*Corvus corax*) benefits from human activity and has been implicated as a significant predator on other native species. Anthropogenic food sources can increase raven populations in lightly settled areas (Marzluff and Neatherlin 2006). As human populations increase in areas with few natural resources, human settlements become increasingly important for food and water subsidies for ravens and are responsible for recent regional increases in raven abundance (Boarman et al. 2006). 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 (Webb et al. 2004, Kristan and Boarman 2007). Roads, in particular, supplement the diets of ravens by providing a diversity of accessible, road-killed animals (Knight and Kawashima 1993, Boarman and Heinrich 1999). Furthermore, dispersing juveniles tend to concentrate around areas of human activity, which provide abundant, concentrated, and continually replenished food and water in an otherwise resource-poor environment (Webb et al. 2007). However, as ravens saturate high-quality habitat near human activity, they may spread into natural vegetation where they may prey upon the nests of other birds. As populations expand, breeding ravens may begin to colonize more natural habitats surrounding anthropogenic habitats (Kristan and Boarman 2007), where they can pose a threat to populations of prey (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 surrounded by the Wind River, Wyoming, Teton, and Gros Ventre mountain ranges. Until recently, these areas supported only light human settlement and cattle ranching. Today, however, 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 tourism year round, as it is a major gateway for millions of tourists visiting Grand Teton and Yellowstone national parks in the summer and the Jackson Hole ski resorts in the winter. Oil and gas production in the upper Green River valley has grown rapidly as pressure to develop domestic energy supplies continues to escalate. Over 8500 wells 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 is well above that in national forests (Thomson et al. 2005). Although the physical footprint of oil and gas infrastructure covers only a small portion of the valley, Weller et al. (2002) showed that the effects of this infrastructure on native wildlife can be extensive.

Human modification of Jackson Hole and the upper Green River valley may negatively influence sensitive sagebrush specialists, notably the Greater Sage-Grouse (*Centrocercus urophasianus*). These areas support important remaining populations of the sage-grouse (Braun 1998, Bureau of Land Management 2000), a species that is declining over most of its range (Connelly et al. 2004). Declines are due mostly to reduction and degradation of sagebrush habitat brought on by increases in human activity (Connelly et al. 2000, Schroeder and Baydack 2001), including subsidizing of known grouse predators, including the Common Raven (Coates and Delehanty 2008). Insulating traditional leks and nearby breeding areas from encroachment by human development so that the grouse's nesting success remains high is a key to maintaining a viable population (Aldridge et al. 2008). To do so likely will require extensive breeding habitat where nest density (Holloran and Anderson 2005) and predator effects (Coates and Delehanty 2008) are low.

We investigated landscape-level patterns in raven behavior and distribution and their correlation with sage-grouse reproduction in western Wyoming. Using point-count data from 2007 and 2008, we related raven occupancy and density to land cover, landscape pattern, and human activity. We predicted ravens would concentrate near areas of frequent human activity, such as cities and oil fields and that their density should decrease gradually with increasing distance from anthropogenic structures. We also expected raven abundance to be correlated positively with human population size, so that large towns, such as Jackson, Wyoming, should have the greatest raven densities. Because raven abundance may increase the risk of predation of sage-grouse nests (Coates and Delehanty, in press), we examined raven density, occupancy, and behavior at locations of sage-grouse nests and broods to determine if they were correlated with sage-grouse breeding success.

METHODS

STUDY AREA AND SITE SELECTION

We measured raven occupancy, density, and behavior as they relate to land cover and locations of nests and broods of the Greater Sage-Grouse in two separate areas of western Wyoming (Fig. 1). The Pinedale study area covered approximately
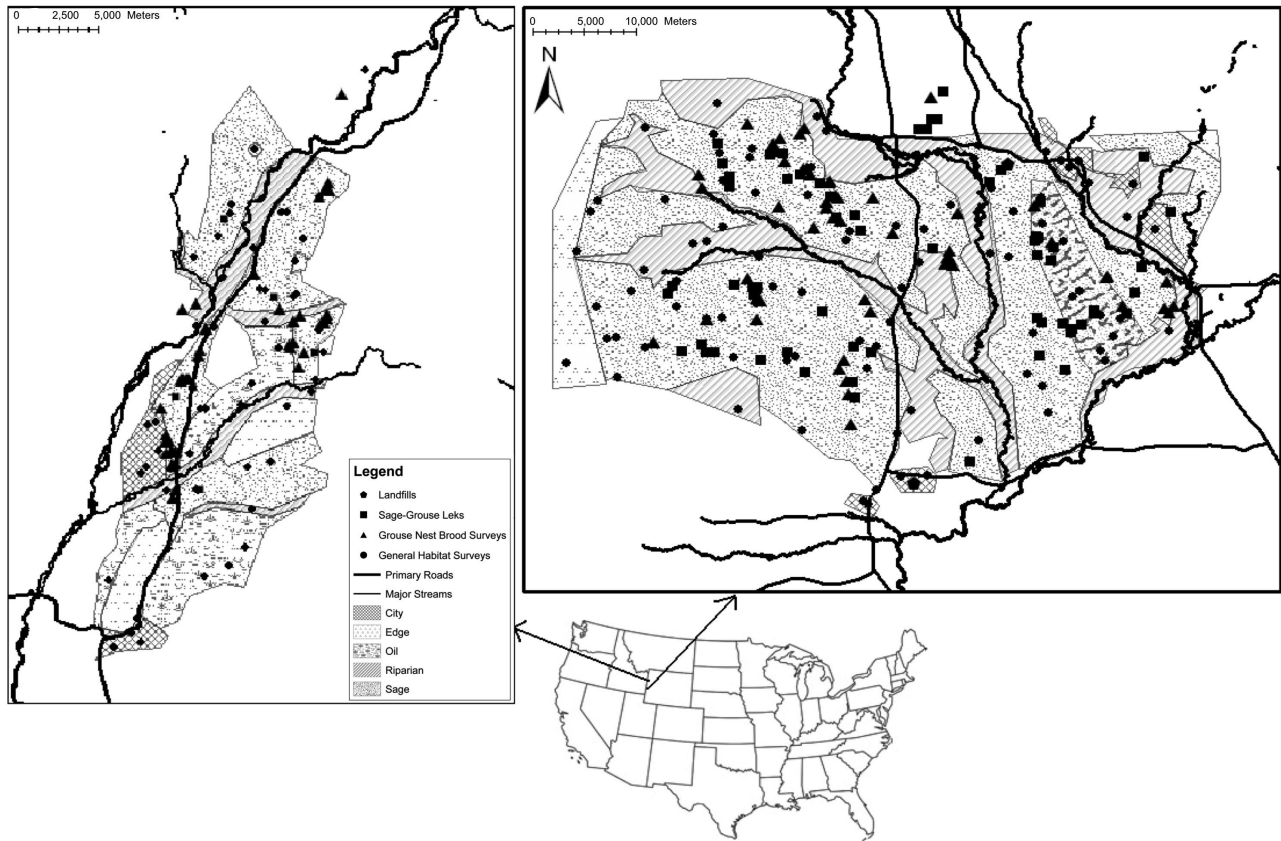
FIGURE 1.   Locations of study areas in Wyoming, with magnified views of Pinedale (upper right) and Jackson study area (left) showing locations of raven survey points, sage-grouse leks, main roads, major streams, and land cover (sagebrush, riparian woodland, oil field, edge, city, hayfield). Filled pentagons represent landfills, filled squares represent sage-grouse leks, filled triangles represent surveys at sage-grouse nests and broods, filled circles represent general habitat surveys, and cross-hatching represents land cover.

6000 km^2 and encircled the area from approximately Pinedale (2007 population 2043; all population figures from U.S. Census Bureau 2009) in the north to Big Piney (2007 population 476) in the south and Boulder (2000 population 30) in the east. The study area was characterized by sagebrush, riparian woodland and surrounding agricultural land, oil fields, and human settlement. Areas dominated by sagebrush were dispersed among private property and 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 9631) and the National Elk Refuge to the south, the towns of Moose (2000 population 1439) and Kelly (population 242), and extended northward into Grand Teton National Park. The study area was characterized by sagebrush, riparian woodland, abandoned agricultural land, and human settlements. All lands, except for a small settlement, were publicly owned.

SAMPLING

To assess the correlation between raven abundance and land cover, we used stratified random sampling to select 166 survey points representing the types of land cover within each study

area (sagebrush, riparian, oil field, edge, city, road, and hayfield; Fig. 1); a minimum distance of 1 km separated survey points. In 2007, we conducted general habitat 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 additional 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 surveyed at each location twice from 3 June to 1 August 2007 and from 16 May to 2 July 2008 to correspond with the sage-grouse's typical nesting and brood-rearing periods in these areas.

To assess the activity of ravens near sage-grouse nests and broods, we conducted 249 surveys in the vicinity of marked incubating or brooding sage-grouse hens (Fig. 1). We selected these survey locations by tracking radio-equipped sage-grouse hens ($n = 91$) throughout the reproductive season and included sage-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 habitats or oil fields. In the two study areas, combined, we conducted 111 surveys around sage-grouse in 2007 (3 May–25 July) and 138 surveys in 2008 (6 May–23 July). Survey effort varied with the sage-grouse's breeding success and activity.

We conducted between one and five surveys at each sage-grouse nest ($n = 169$) and between one and four surveys at each sage-grouse with a brood ($n = 80$).

For each survey, we stood on top of a hill or other vantage point, listened for raven calls, and scanned with both unaided eyes and binoculars, alternating every 5 min for a total of 20 min (Luginbuhl et al. 2001). For surveys near sage-grouse nests and broods, we conducted the surveys with the observer located 200–300 m from the nest or brood, so as not to disturb the hen and her young or to attract predators to the location. Using a rangefinder, we measured the distance to ravens at first detection from the observer or from 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, including raptors and mammals, but report here only our observations of ravens. At each survey point, we recorded the following: date, observer's initials, start time, end time, observer's northing and easting (UTM NAD 83), cloud cover (percent), wind (in miles hr^{-1}), temperature (in °F), noise level (on a scale from 0 to 4, 0 being the lowest), habitat within a 400-m radius of the observer (by percentage), and any observation of predators. For the latter, this included time of observation, initial distance of predator from observer, lowest observed height of predator above ground, predator activity, habitat under predator, and any necessary comments. We mapped all observed predator activity onto a diagram of the survey point and its vicinity.

Sage-grouse nests were checked for survival at least twice weekly; sage-grouse broods were flushed at approximately 2 weeks and at 35 days after hatching (Schroeder et al. 1999, Walker et al. 2006). Nests were identified as successful if at least one egg hatched (Wallestad and Pyrah 1974); broods were identified as successful if at least one chick survived through the entire monitoring period. When possible, we documented the cause of nest failure; if the nest failed because of predation, we attempted to identify the predator as bird or mammal (Sargeant et al. 1998). We found no remains of broods following failure, so could not implicate specific predators in their loss. In our study area, the raven is one of many predators of grouse nests, and we assumed that our statistical analysis revealed the raven's potential contribution to nest and brood failure regardless of which predator actually ate a specific clutch or brood. This assumption overestimates the importance of the raven as a predator to the extent that other species are preying on the grouse simultaneously.

DETECTABILITY ANALYSIS

To estimate raven densities across the landscape, we first developed a detectability model to predict the probability of observing a raven. Detectability (the probability of observing an organism of interest at a survey location, given the organism is present at that location) can vary by distance from observer, observer ability, and environmental factors, creating biases in density estimates (Rosenstock et al. 2002). To examine our data for such bias, we tested for effects of land cover, study site, study year, and city/noncity 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 detections of ravens and to produce estimates of raven density in each land-cover type (sagebrush, riparian, oil field, edge, city, road, hayfield). Each land-cover type constituted a stratum, and each survey point included observations from both rounds of general habitat surveys conducted at that location. We assumed survey sites were located randomly with respect to the raven's 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) with values of Akaike's information criterion (AIC). Surveys conducted in edge category of land cover were too few to allow analysis by DISTANCE. We omitted surveys conducted in riparian habitat and along roads from detectability analyses because these land-cover types are linear, thus violating the assumption in DISTANCE analysis of uniform density. Inclusion of these surveys would have overestimated detectability-converted raven density and underestimated effective detection radius because the majority of detections in these habitats were close to the observer.

The null model that detectability was independent of covariates produced an AIC value lower than that of models considering study site, study year, land cover, and city/noncity categorization (Appendix 1: Table A1). Because we found most land covers to have no effect on the raven's detectability, and detectability-corrected density estimates were strongly correlated with unadjusted estimates (Appendix 1: Table A2), in further analyses we used estimates based on observed density instead of estimates corrected for detectability. We compared observed densities across land covers by using a one-factor (land cover), repeated-measures (two rounds of point counts per survey location) ANOVA (SPSS 2007).

MODELING RAVEN ABUNDANCE AND OCCURRENCE

We developed an occupancy model to predict the probability of raven presence or absence 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 (White 2008) and R for Windows 2.8.1 (R Development Core Team 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 (1) any combination of land cover, (2) a more simplified categorization of land cover as city or noncity, (3) study site, or (4) study year. We expected land covers with high levels of human activity (i.e., city) to have greater occupancy, and perhaps reduced detectability, than those with less human use (i.e., noncity). We also tested for differences in occupancy rates between the two years of the study.

We then constructed a model to predict raven occupancy across the landscape. Using observed raven occupancy from our survey locations, we conducted a logistic regression analysis that considered the following variables: land cover at the survey point (undeveloped sagebrush, riparian, oil field [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 used FRAGSTATS v.3.3 (McGarigal et al. 2002) to calculate landscape-pattern metrics within a 1-km circle (defined by sampling design to avoid overlap of circles) of each survey point. 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 a weight of 0. 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 ($r < 0.47$, $P > 0.5$). In predicting raven occupancy, we used SPSS v.11.1 to estimate coefficients of each independent variable. All coefficient estimates were calculated relative to cover catgory of sagebrush. 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 occupancy across the landscape. Relative differences in predicted occupancy matched expectation, but absolute predicted occupancy was biased high (at 73 sample points in contiguous sagebrush we observed $20 \pm 4\%$ occupancy but predicted $40 \pm 3\%$; $t_{72} = -5.5$, $P < 0.001$).

Because our logistic regression model indicated that ravens occupy 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. In the analysis of the Jackson observations we assumed errors were distributed normally because spatial autocorrelation of residuals was negligible (Moran's $I = -0.21$, $P = 0.62$). However, the residuals from the analysis of the Pinedale observations
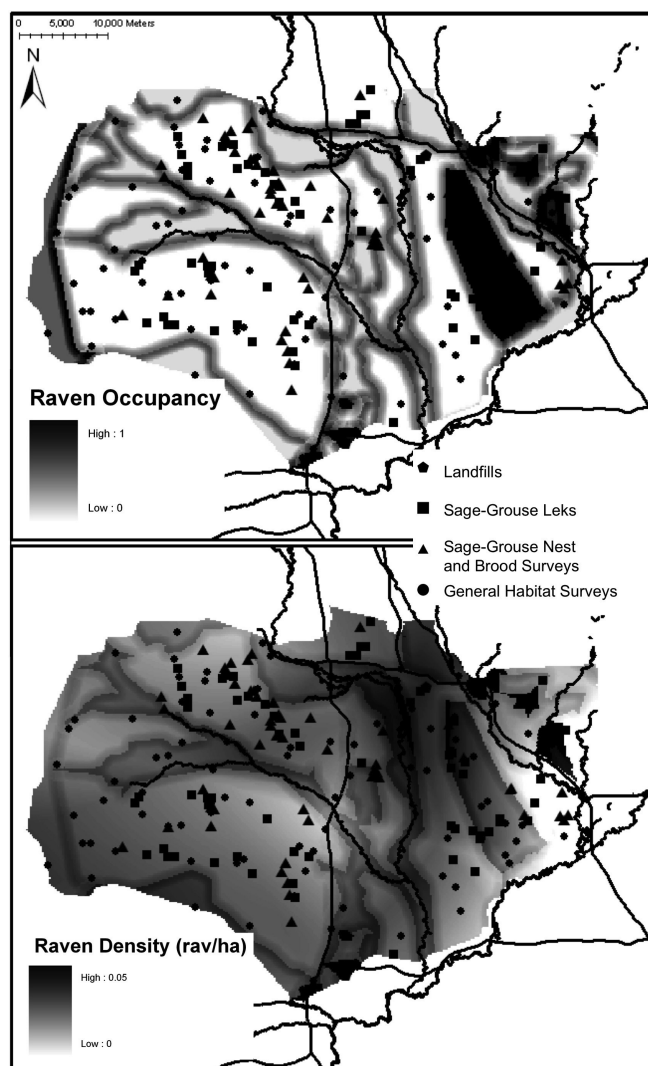

FIGURE 2.   Major cities and landmarks, sage-grouse leks, expected raven occurrence (top), and expected raven density (ravens ha^{-1}) (bottom) in the Pinedale study area as predicted by our model. Filled pentagons represent landfills, filled squares represent sage-grouse leks, filled triangles represent surveys at sage-grouse nests and broods, filled circles represent general habitat surveys, cross-hatching represents land cover, and shading represents raven density and occurrence. Coefficients for occupancy model from Table 3. Coefficients for density model assumed normal error: $0.64 + 1.88$(city) $+ 0.46$(oil) $+ 0.26$(riparian) $+ 0.04$(edge) $+ 0.05$(contrast edge density) $+ 0.01$(road) $- 0.003$(contagion) $+ 0.00006$(distance to road) $- 0.00009$(distance to landfill) $+ 0.00004$(distance to city).

were spatially autocorrelated, especially along the north–south axis (Moran's $I = 0.45$, $P < 0.001$). Therefore, to evaluate the significance and relative importance of model coefficients, for this analysis we assumed a spatially autocorrelated error structure and estimated coefficients and standard errors with a maximum-likelihood estimator. We assumed estimated errors covaried with distance between points and accounted for
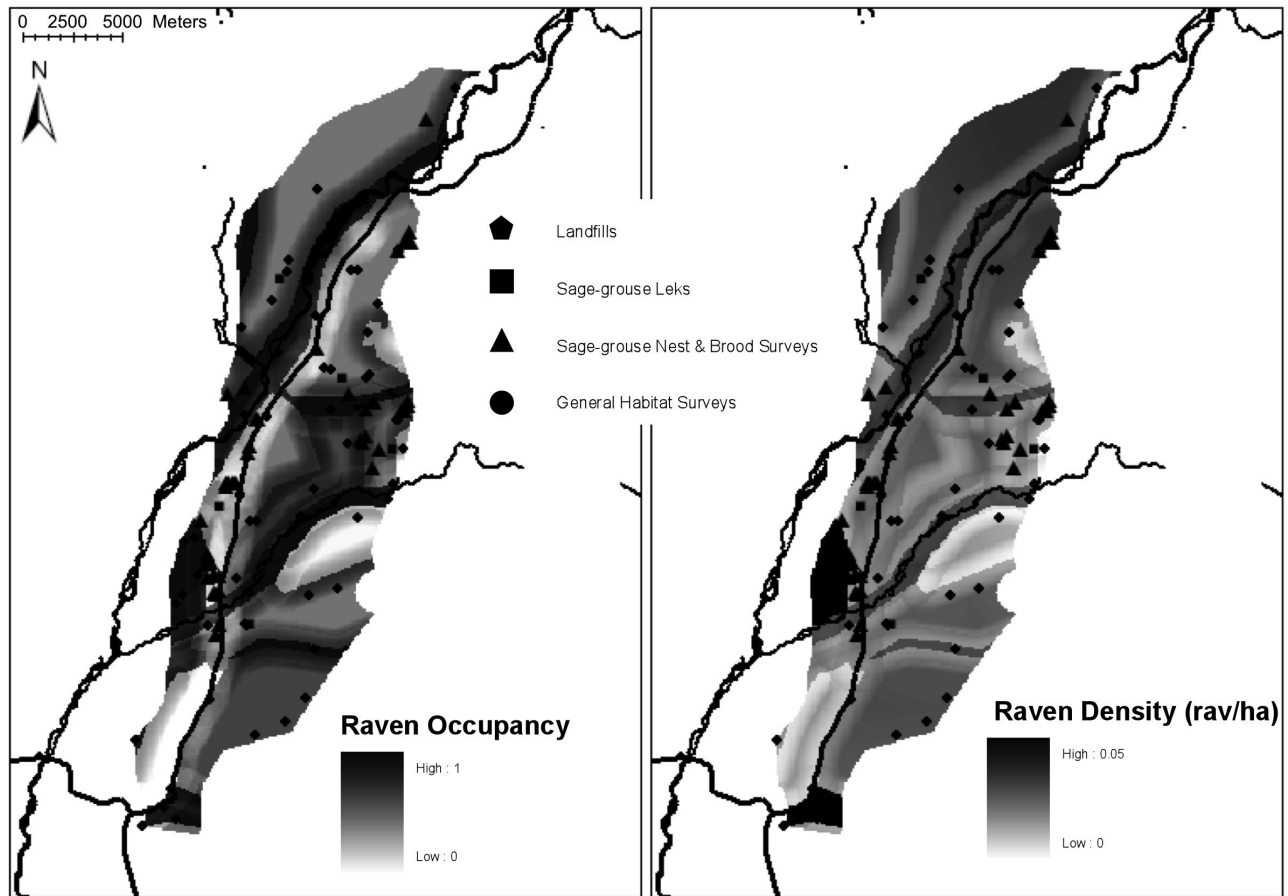
FIGURE 3.   Major cities and landmarks, sage-grouse leks, expected raven occurrence (left), and expected raven density (ravens ha^{-1}; right) across the Jackson study area as predicted by our models (unstandardized coefficients in Table 3). Filled pentagons represent landfills, filled squares represent sage-grouse leks, filled triangles represent surveys at sage-grouse nests and broods, filled circles represent general habitat surveys, cross-hatching represents land cover, and shading represents raven density and occurrence.

this error structure by using maximum-likelihood, rather than least-squares, estimation of regression coefficients, doing this with "ruf.fit" v.1.3 (Handcock 2004) within the statistical software program R v.2.8 (2008). Using ArcGIS v.9.3 (ESRI 2008), we extrapolated the unstandardized regression 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. For consistency we based all predictions on coefficients assuming normal error. As expected (Nielsen et al. 2002, Marzluff et al. 2004), using standard least-squares estimates of coefficients did not influence predictions (raven densities in Pinedale predicted under the assumptions of normal and spatially autocorrelated errors were virtually identical; pixel-by-pixel comparison of model output: $r = 0.93$, $n = 54\,190$, $P < 0.001$). Predicted density also closely matched observation and was not biased (at 73 locations in contiguous sagebrush we observed a raven density of 0.007 ± 0.002 ha^{-1} and predicted 0.008 ± 0.002; $t_{72} = 0.05$, $P < 0.62$). All data are reported as means $\pm$ SE.

CORRELATING RAVEN ACTIVITY AND
SAGE-GROUSE NEST AND BROOD SUCCESS

To evaluate potential attraction of ravens to areas where sage-grouse nest and rear broods, we using paired t-tests (SPSS v.11.1) to compare 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 of sage-grouse nests and broods. We also directly compared observed counts in sagebrush where we did not know sage-grouse to be nesting or rearing broods to counts taken in sagebrush where sage-grouse were actively incubating or brooding.

We also developed a multinomial logistic regression model to assess the correlation of raven activity with the outcome of individual sage-grouse nests and broods. We considered all grouse nests and did not make assumptions about what predator caused each failure. The independent variables considered in our models were study site, percent sagebrush cover near the sage-grouse nest or brood, distance to nearest

city, raven density, raven occupancy, and raven behavior. The dependent variable in our model was sage-grouse success, which fell into one of three categories: nest failure, brood failure, or survival throughout the entire reproductive season. 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 near a particular sage-grouse nest or brood throughout the season, and observed values of raven density, occupancy, and behavior from the survey conducted latest in the reproductive season near a particular sage-grouse nest or brood. We evaluated models' fit by calculating a Pearson goodness-of-fit coefficient for each model. For failed sage-grouse nests or broods, the "last" survey was the one conducted nearest in time to the failure (1 to 11 days, with an average of 5 days, prior to the failure). We scored raven behavior so that foraging received a higher score than nonpredatory behavior. Either flying at a height of >5 m and turning no more than once or perching >50 m from a sage-grouse nest or brood received a score of 1, flying at a height of <5 m and turning more than twice received a score of 2, and perching within 50 m of a sage-grouse nest or brood received a score of 3. It is possible that successful nests might be observed mostly late in the season, and if so this might bias our results if raven abundance were seasonal. Neither potential bias was evident. We observed successful and failed nests throughout the summer (nest failure occurred from 3 May to 23 June, brood failure from 12 to 24 June, and successful nesting from 8 May to 2 July). In each of these intervals raven abundance and occupancy in sagebrush were similar (nest-failure period: $n = 53$, density = 0.006 ± 0.002, occupancy = 0.15 ± 0.05; brood-failure period: $n = 33$, density = 0.004 ± 0.003, occupancy = 0.09 ± 0.05; successful-nesting period: $n = 68$, density = 0.005 ± 0.001, occupancy = 0.13 ± 0.04).

RESULTS

MODELING RAVEN ABUNDANCE AND OCCURRENCE

The density of ravens and modeled occupancy rates varied with land cover across both study areas (Table 1; $F_{1,159} = 5.9$, $P < 0.001$). Among the categories of land cover, city had the highest observed raven density and one of the highest occupancy rates (Table 1). Although raven density was not significantly correlated with the size of a town's human population ($r = 0.23$, $n = 6$, $P = 0.33$), 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 an observed density slightly higher than the others. Observed densities in both sagebrush and oil fields were low, but at the Pinedale study site, which contained both of these land covers, the relative occupancy rate in oil fields was higher than in sagebrush. Riparian habitat and roads, the two linearly oriented land-cover types we studied, had similarly low observed densities but occupancy was greater along roads than in riparian habitat. Edge habitat had the lowest observed density and occupancy rate, but the sample for this land cover was small. With the exception of oil fields, where the large effective detection radius can be explained by a high percentage (56%) of distant detections, the effective detection radii in the various land cover types were similar (Table 1), further supporting our conclusion of equal detectability across land covers (Appendix 1).

Study site, in addition to land cover, influenced occupancy (Table 2). There was some support (ΔAIC < 2) for models including varying detectability across all land covers, categorization as city or noncity, or study site. The four models that implicated detectability differences are different articulations of the influence of physical obstruction (vegetation, buildings, and noise) on our ability to see and hear

TABLE 1. Observed raven density, effective detection radius, 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 400 m of the observer in our analyses in order to have an area over which to calculate observed densities and because effective detection radii were approximately 400 m. See Appendix 1 for detectability-corrected densities.

| | | Detections within 400 m | | Observed density (within 400 m; ravens ha^{-1}) | Effective detection radius (m) | Estimated relative occupancy rate | |
| | No. of counts | Counts with detections | No. of detections | | | Pinedale | Jackson |
Land cover							
Sagebrush	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)

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

Occupancy model	ΔAIC	Akaike weight
Detectability constant; occupancy varies by land cover and study site[a]	0.0	0.37
Detectability varies by land cover; occupancy varies by land cover and study site	1.2	0.20
Detectability varies by city/noncity and study site; occupancy varies by land cover and study site	1.5	0.17
Detectability varies by land cover; occupancy varies by study site	2.1	0.13
Detectability varies by study site; occupancy varies by land cover and study site	2.2	0.12

[a]AIC = 403.3.

ravens. Therefore it is not surprising that each of these similar models was equally consistent with the data. Regardless of variability in detecting occupancy, all of the supported models indicated that occupancy varied considerably across land covers and between study sites. For land-cover types found in both study areas, occupancy was greater in Jackson than it was in Pinedale ($t_4 = 4.5$; $n = 5$ shared land covers; $P = 0.01$; Table 1), with probability of occupancy almost twice as high in Jackson (0.80 ± 0.12, $n = 5$) as it was in Pinedale (0.50 ± 0.15, $n = 5$). Although average raven density in Jackson (0.005 ± 0.003, $n = 5$) was about five times as great as in Pinedale (0.001 ± 0.0003, $n = 5$) in land covers found at both study sites, the difference in densities was not significant ($t_4 = 1.4$, $n = 5$, $P = 0.22$). All supported models indentified study site and land-cover effects, but not detectability, as important to raven occupancy, suggesting that despite differences in obstructions to observing it, the raven is strongly associated with some, and less strongly associated with other, aspects of the landscape.

Our models predicted the greatest levels of raven occupancy in the land covers of city, oil field, and edge but the highest raven densities in cities (Table 3; Figs. 2, 3). At both study sites, land cover was the variable most indicative of raven occupancy, followed by landscape metrics and finally by distance to areas of high human activity (Table 3). The raven population appears to be more uniformly distributed at Jackson than at Pinedale, as intermediate to high levels of occupancy were predicted over the majority of the Jackson study site, whereas the Pinedale study site was characterized by generally low levels of raven occupancy, 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 distance to areas of high human activity (Table 3). In the Pinedale study area (Fig. 2), we predicted oil fields to have high levels of raven occupancy but only low to intermediate raven densities, suggesting constant but low

TABLE 3. Coefficients and SE for independent variables in linear and logistic regression analyses for predicting average raven density within 400 m and raven occupancy, respectively, where density = intercept + $\Sigma\beta_i x_i$, and P(occurrence) = $e^z/(1+e^z)$, and z = intercept + $\Sigma\beta_i x_i$. Analyses assumed a normally distributed error structure, except in the Pinedale density analysis, where errors were adjusted for significant spatial autocorrelation. Standardized coefficients (linear regressions) and odds ratios (logistic regressions) are presented to allow comparison of relative importance of variables.

| | Coefficients (SE) from linear regression on density | | | | Coefficients (SE) from logistic regression on occupancy | | | |
| | Pinedale | | Jackson | | Pinedale | | Jackson | |
Variable	Unstandardized	Standardized	Unstandardized	Standardized	Unstandardized	Odds Ratio	Unstandardized	Odds Ratio
Intercept	0.66 (0.67)	N/A	0.20 (0.65)	N/A	–0.04	N/A	1.64	N/A
City	3.54 (0.36)	1.30	1.64 (0.45)	0.54	1.89 (0.87)	6.6	2.19 (1.09)	8.9
Oil field	0.63 (0.41)	0.18	N/A	N/A	2.33 (0.95)	10.3	N/A	N/A
Riparian	0.52 (0.30)	0.22	0.44 (0.40)	0.13	0.29 (0.79)	1.3	1.49 (0.98)	4.4
Edge	–0.13 (0.63)	–0.02	–0.32 (0.65)	–0.06	1.22 (1.41)	3.4	–1.24 (1.45)	0.29
Contrast-weighted edge density	0.06 (0.04)	0.21	–0.05 (0.05)	–0.17	0.03 (0.09)	1.0	–0.11 (0.10)	0.90
Road	0.12 (0.38)	0.04	0.04 (0.05)	0.01	0.88 (0.90)	2.4	1.07 (1.06)	2.9
Hayfield	N/A	N/A	0.03 (0.39)	0.01	N/A	N/A	0.52 (0.82)	1.7
Contagion	0.003 (0.006)	0.07	0.006 (0.006)	0.11	–0.02 (0.01)	0.98	–0.02 (0.01)	0.98
Distance to road	0.0001 (0.0)	1.00	–0.00002 (0.0)	–0.04	0.000 (0.0)	1.0	0.000 (0.0)	1.0
Distance to landfill	–0.0002 (0.0)	–1.90	N/A	N/A	0.000 (0.0)	1.0	N/A	N/A
Distance to city	0.0001 (0.0)	0.89	0.00002 (0.0)	0.09	0.000 (0.0)	1.0	0.000 (0.0)	1.0

TABLE 4. Multinomial logistic regression models, with ΔAIC, Akaike weight, degrees of freedom, and Pearson goodness-of-fit coefficient, used to test for the effects of raven abundance and behavior on the fate of sage-grouse nests and broods. Fate was classified into one of three states: failure to hatch, failure to survive brood rearing, or success of at least one chick to independence.

Model	ΔAIC	Akaike weight	df	Pearson	P
Study site, sagebrush cover, last observed raven occupancy[a]	0.00	0.95	30	33.09	0.32
Study site, sagebrush cover, last observed raven behavior	6.32	0.04	38	35.95	0.57
Study site, sagebrush cover, last observed raven density	8.83	0.01	40	46.09	0.23
Study site, sagebrush cover, average observed raven behavior	32.05	0.00	62	63.59	0.42
Study site, sagebrush cover, average observed raven occupancy	38.24	0.00	70	82.13	0.15
Study site, sagebrush cover, average observed raven density	47.26	0.00	76	94.56	0.07
Study site, sagebrush cover, predicted raven occupancy	51.55	0.00	98	93.11	0.62
Study site, sagebrush cover, distance to city	84.62	0.00	128	162.77	0.02
Study site, sagebrush cover, predicted raven density	101.87	0.00	158	171.43	0.22

[a] AIC = 69.32.

raven activity. In contrast, we predicted low occupancy and high density around the landfill in the town of Pinedale (Fig. 2), suggesting infrequent visits by large groups of ravens to this area.

We categorized each sampling point by its land cover as well as its distance to cities, roads, and landfills. This resulted in the models' incorporating dual measures of city and roads. These extra variables aided prediction but may confuse interpretation of a variable's relative importance. Ravens were consistently present and abundant in cities and consistently present along roads (Table 3). Including these direct associations in our models reduced the relative importance of the somewhat redundant variables measuring distances to cities and roads (Table 3).

RAVEN MOVEMENT INTO UNDEVELOPED SAGEBRUSH

In the Pinedale study area, although the raven's density was highest in cities, it was predicted to decrease sharply at distances beyond approximately 3 km from city boundaries, suggesting little movement by ravens from cities to adjacent areas of infrequent human activity (i.e., sagebrush). When ravens did move into undeveloped sagebrush, locations of raven nests and incidental sightings of ravens foraging implicated anthropogenic infrastructure in aiding their movement. In 2007, we recorded 34 incidental sightings of foraging by ravens throughout the Pinedale study area; of these, 18 were along roads, 17 in undeveloped sagebrush, and two in agricultural fields. When foraging near roads, ravens were often observed flying along the road network, suggesting they used roads in locating prey. Throughout the Pinedale study area, ravens also took advantage of anthropogenic infrastructure for nesting, especially in areas of undeveloped sagebrush. Between the two study seasons, we located 27 raven nests, 16 of which were on artificial structures including condensation tanks, windmills, solar panels, and telephone poles; the remaining 11 nests were in trees.

CORRELATION BETWEEN RAVEN ACTIVITY AND SAGE-GROUSE REPRODUCTIVE SUCCESS

During our study, predation on sage-grouse nests and broods was frequent; 51% of sage-grouse nests failed, of which 83% were lost to predation. The predators were not identified and certainly included a diversity of mammals and raptors as well as ravens. Forty-seven percent of sage-grouse broods failed, all presumably because of predation. An average of 1.34 and 1.56 juveniles fledged per sage-grouse hen in the Pinedale and Jackson study areas, respectively.

Ravens appeared to respond to the presence of sage-grouse nests and broods. Observed raven density (0.01 ± 0.002 ha^{-1}, $n = 84$) was significantly greater at locations near sage-grouse nests and broods than predicted (Figs. 2, 3) at these same locations (0.006 ± 0.001 ha^{-1}, $t_{83} = 2.89$, $P = 0.01$). This observed density was also marginally greater than the density we observed at other places in contiguous sagebrush where grouse were not known to be nesting (0.007 ± 0.002 ha^{-1}; $F_{1,156} = 2.1$; $P = 0.15$). Observed raven occupancy (0.29 ± 0.04) around grouse nests and broods was marginally greater than observed occupancy at locations within contiguous sagebrush where grouse were not known to be nesting (0.20 ± 0.04; $F_{1,156} = 3.4$, $P = 0.07$). Because of the bias in absolute values of modeled occupancy we did not formally compare observed raven occupancy around grouse to occupancy predicted for the same locations (it was higher).

The presence and behavior of ravens were associated with sage-grouse nest and brood success. Raven occupancy and, to a lesser extent, behavior observed near sage-grouse nests and broods were more highly correlated to sage-grouse fate than was raven density (Table 4). Raven occupancy observed on the "last" surveys was more highly correlated with the fate of sage-grouse nests and broods than was raven occupancy averaged over all surveys over the entire reproductive season, which, in turn, was more highly correlated with sage-grouse fate than were values of raven occupancy as predicted by our model of raven distribution.

There were no significant differences in the mean values of predicted or observed (averaged or "last") raven density, occupancy, or behavior among any of the three categories of sage-grouse nest failure, brood failure, or survival. However, for "last" surveys, mean raven density, mean occupancy, and behavior scores were slightly greater at failed sage-grouse nests and broods ($n = 62$, density = 0.01 ± 0.004, occupancy = 0.43 ± 0.11, behavior = 0.82 ± 0.27) than at those that survived the season ($n = 24$, density = 0.007 ± 0.004, occupancy = 0.26 ± 0.12, behavior = 0.25 ± 0.11). In addition, we observed more foraging behavior by ravens near failed than near successful sage-grouse nests and broods. A plurality (44%) of observations of raven behavior near failed sage-grouse nests and broods received a score of 3 (strongly indicating foraging), 38% received a score of 2, and only 18% received a score of 1 (slightly indicating foraging). In contrast, the majority (80%) of observations of raven behavior near successful sage-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 sage-grouse fate did not improve model fit (Table 4), failed sage-grouse nests and broods tended to be closer to cities (5339 ± 1236 m) than did successful nests and broods (37 608 ± 20 986 m).

DISCUSSION

MODELING THE RISK OF PREDATION

Recent increases in raven populations have been consistently linked with human activity (Restani et al. 2001, Marzluff and Neatherlin 2006, Kristan and Boarman 2007), which provides anthropogenic food, water, and nest sites (Boarman et al. 2006), 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 raven's highest density and relative occupancy rate both to occur near cities, the land cover in our study area with the most frequent human activity. In our study areas, towns provide ravens with supplemental food, water, and nest sites, which may have led to locally increased density 3 km into undeveloped adjacent lands.

In oil fields, the raven's occupancy was high but its density was low, which is consistent with presence of territorial breeding pairs. The encroachment of oil fields upon undeveloped sagebrush appears to facilitate breeding ravens moving into the sagebrush, just as campgrounds facilitate the American Crow (*Corvus brachyrhynchos*) moving into forests it otherwise rarely visits (Neatherlin and Marzluff 2004). Incidental sightings of raven foraging during our study suggest ravens take advantage of the road networks associated with oil fields and undeveloped sagebrush, as found elsewhere (Knight and Kawashima 1993, Knight et al. 1995). Furthermore, artificial nesting substrates (i.e., telephone poles, windmills, buildings, and condensate-storage tanks), both within cities and in undeveloped sagebrush immediately surrounding cities and natural gas fields, may allow new breeding pairs to colonize sagebrush they rarely used previously, which may increase nest predation on sage-grouse (Manzer and Hannon 2005).

By modeling both raven density and occupancy, we were able to highlight areas with high occupancy but low density, like oil fields, which provided ravens with new nesting sites for pairs but not foraging sites for groups. We also were able to identify areas with high density and low occupancy of ravens, such as the area immediately surrounding the Pinedale landfill. This pattern suggested infrequent visits by large foraging groups of ravens, likely consisting mainly of juveniles and subadults, to the landfill, a prime location for anthropogenic food subsidies (Marzluff et al. 1996, Kristan and Boarman 2003) but not necessarily new nest sites. Although the Pinedale landfill attracted large numbers of ravens, their occupancy of this location was notably inconsistent, so overflow of ravens from the landfill into the surrounding sagebrush was minimal. No comparable locations with high raven density and low occupancy were predicted in the Jackson study area, not surprising because this study site contained no landfills or other similar areas of concentrated anthropogenic food subsidies.

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 may affect locally breeding populations of sage-grouse negatively. Raven density was greater near sage-grouse nests and broods than at control locations, but it was still relatively low, which is consistent with foraging by territorial nesting pairs of ravens, not large congregations of nonbreeding individuals. The sage-grouse's patterns of incubation may have evolved to avoid visually cued diurnal predators such as ravens and other corvids (Angelstam 1984, Erikstad 1986; Coates and Delehanty, in press). Incubating sage-grouse hens typically leave their nests briefly to forage only at twilight; longer recesses that expose the nest in bright light may increase nest depredation by ravens (Coates and Delehanty 2008). Even in spite of such adaptations, increased occurrence of ravens in sagebrush can reduce the sage-grouse's nesting success. Our model of the grouse's reproductive fate suggested raven occupancy, rather than density, is important to the grouse's nesting success.

Local attraction of ravens to sage-grouse nesting habitat may be facilitated by the reduction, isolation, and fragmentation of native shrublands that is known to increase exposure of nests to potential predators (Lyon and Anderson 2003; Coates and Delehanty, in press) and ultimately lower reproduction (Vander Haegen et al. 2002, Aldridge and Boyce 2007). As more suitable sage-grouse habitat is converted to oil fields, agriculture, and other exurban development, sage-grouse nesting and brood rearing become increasingly spatially restricted. Where sage-grouse nests are more concentrated they are more

easily detected, and increased nest densities could result in increased nest depredation (Holloran and Anderson 2005), especially when nests are clumped (Marzluff and Balda 1992).

Our model of sage-grouse fate implicated raven occupancy near sage-grouse nests and broods near the time of nest success or failure as the best predictor of the grouse's reproductive success, not raven density near nests or broods. This pattern suggests studies that measure only predator density (e.g., Manzer and Hannon 2005) near areas of sage-grouse nesting and brood rearing may not adequately quantify the potential effects of raven predation on the grouse's reproductive success. We suggest that the risk of predation of a particular sage-grouse nest or brood can be gauged by observing activity of predators nearby; a sudden increase in predator occupancy can be interpreted as an increase in probability of the depredation of the sage-grouse nest or brood. We also suggest that human-mediated increased occupancy of undeveloped sagebrush by ravens may affect sage-grouse populations negatively. This factor may be part of the reason that neither of the sage-grouse populations we studied reached the recommended level of productivity of 2.25 juveniles per hen surviving through the reproductive season to ensure long-term persistence (Connelly and Braun 1997).

There are several sources of potential bias in our methodology and analysis. First, we assumed all failures of sage-grouse broods to be due to predation, but environmental factors (i.e., exposure, starvation) could also contribute to brood mortality. Second, we could not determine how often ravens actually preyed upon sage-grouse eggs and chicks. Our models suggest the potential for raven predation is high, but it does not prove a causal link between raven occurrence and sage-grouse reproductive failure. Third, we likely underestimated successful brood rearing and underestimated absolute predation on eggs and chicks. We assumed all observations of brood failure were complete. Not accounting for the fact that some broods may have partially succeeded has the effect of overestimating the effect of predation on sage-grouse reproductive success. Therefore, our models estimate the maximum potential predation by ravens on sage-grouse broods. This bias may be balanced in part because we defined success as the hatching or rearing of at least one egg or chick. Therefore some sage-grouse nests or broods we categorized as successful may have been reduced by partial predation below their full potential. However, these potential biases may be negligible because monitoring studies have shown only a small proportion of instances of predation by ravens on sage-grouse nests are partial (Coates et al. 2008).

Our model of raven distribution overestimated absolute raven occupancy (but not density). This overestimation is most likely due to limited observations; we conducted only two surveys. Because raven abundance in contiguous sagebrush is lower than in other land covers, it is likely that ravens went undetected at some survey locations. Increasing the number of surveys at each location would decrease the incidence of false negatives and improve the absolute accuracy of resulting models. Although our model may not predict absolute rates of raven occupancy accurately, it clearly captures important relative differences in occupancy, such as those associated with differences in land cover.

MANAGING SUBSIDIZED NATIVE PREDATORS

Restoring viable populations of the Greater Sage-Grouse in increasingly human-dominated western landscapes will require conserving and restoring extensive tracts of sagebrush and, at least in the short-term, managing the factors that limit sage-grouse survival and reproduction within these lands. Humans (through recreational hunting) and a diversity of native species, including the Common Raven, prey upon grouse, limiting their survival and reproduction. Each of these factors—habitat availability and condition, predator populations, and direct harvest by humans—must be considered if the grouse is to be managed effectively. Our results can provide some guidance to managers seeking to minimize the potential and actual influence of expanding raven populations on the sage-grouse. The two species have coexisted for approximately two million years (Omland et al. 2000). Our results suggest that where myriad human factors reduce both grouse and their habitat, while simultaneously increasing generalist predators, this ancient coexistence may become unbalanced.

Managers attempting to reduce the potential effects of ravens on grouse reproduction should first reduce occupancy of important sage-grouse nesting habitat by ravens. This can be at least partially accomplished by education, regulation, and limiting anthropogenic subsidies far from cities and landfills. Anthropogenic nest sites should be managed to reduce raven use through retrofitting or the installation of deterrent fixtures (i.e., strips, netting, screening) on old structures, covering well heads, modifying future engineering of structures to avoid providing suitable nesting platforms, egg removal, nest destruction, and harassment of nesting pairs (Liebezeit and George 2000). Education about the effects of feeding wildlife should be widespread; this is especially important at tourist locations, such as the Jackson study area, where large groups of people congregate, many of whom are naïve to the effects their behavior can have on wildlife. Furthermore, corporations operating within sensitive sage-grouse nesting areas should consider policies of hiring, firing, and fining that strongly discourage their employees from purposefully or inadvertently providing supplemental food to ravens (USFWS 2003). Once subsidies are limited in habitats where sensitive grouse breed, additional measures of either direct removal of ravens or aversive conditioning of territorial ravens may be needed. 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 (Avery et al. 1995). Modifying the raven's behavior to reduce its abundance near sage-grouse nests (Coates et al. 2007) or preference for sage-grouse eggs would result in decreased nest predation while leaving the resident pair of ravens to discourage intrusion by nonresident ravens by their territoriality.

A second strategy to lower the raven's effects on sage-grouse is to reduce the raven-carrying capacity of areas where the raven's density is high. This strategy is of secondary importance because raven density is low where sage-grouse nest. However, ravens may move from areas of high density as new subsidies are provided near sage-grouse or as resident territorial pairs die. Limiting the amount and availability of garbage to ravens in cities, towns, and landfills therefore could be an effective long-term strategy. In addition, access to sewage ponds and road kills should be reduced, perhaps by installing covers or wires (as deterrents) over dumpsters, incinerating garbage, removing animal carcasses from roads and burying them, and enforcing regulations concerning waste disposal, as they relate to wildlife (USFWS 2003). Once subsidies are limited, raven populations may disperse and decline on their own. Reducing the availability of resource subsidies may succeed in controlling raven abundance only when similar efforts are widespread in a region (Boarman 2003, Boarman et al. 2006).

Future management would also be aided by monitoring and additional research. The actual amount of predation by ravens on sage-grouse may vary by site and needs to be quantified. In our study, we assumed that observations of ravens reflected their habitat use; this assumption should be confirmed through utilization-distribution analysis of radio-equipped individuals (Marzluff et al. 2004). Although we measured raven abundance and occupancy in areas with both 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 (as was done in this study) to those in areas 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 through radio-tracking of ravens to pinpoint individuals most likely responsible for depredation of sage-grouse nests and broods. As management is implemented, the response of raven populations and sage-grouse nesting success should be monitored. Failure to do so and adapt management appropriately will help neither sage-grouse nor raven.

ACKNOWLEDGMENTS

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APPENDIX 1. SELECTION OF DETECTABILITY MODEL

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 (sagebrush, riparian, oil, edge, city, road, hayfield), and city/noncity 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 A1), indicating detectability did not vary among the land covers of interest in our study. Because detectability-corrected density estimates (Table A2) 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 A1.   Values of ΔAIC for each detectability model.

Detectability model	Covariates considered	ΔAIC
Null model half-normal cosine[a]	none	0.00
Land cover half-normal cosine	land cover	10.22
City/noncity half-normal cosine	city	14.92
Site year half-normal cosine	study site and year	25.86
Site half-normal cosine	study site	27.98
Year half-normal cosine	study year	33.71

[a]AIC = 2667.42.

TABLE A2.   Detectability-corrected density for each land cover according to the null model that detectability is independent of covariates.

Land cover	Detectability-corrected density (ravens ha^{-1})
Sagebrush	0.037 (0.013)
Riparian	N/A
Oil field	0.007 (0.002)
Edge	N/A
City	0.17 (0.035)
Road	N/A
Hayfield	0.064 (0.027)