

Landscape characteristics and livestock presence influence common ravens: relevance to greater sage-grouse conservation

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Abstract. Common raven (*Corvus corax*; hereafter, raven) population abundance in the sagebrush steppe of the American West has increased threefold during the previous four decades, largely as a result of unintended resource subsidies from human land-use practices. This is concerning because ravens frequently depredate nests of species of conservation concern, such as greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse). Grazing by livestock in sagebrush ecosystems is common practice on most public lands, but associations between livestock and ravens are poorly understood. The primary objective of this study was to identify the effects of livestock on raven occurrence while accounting for landscape characteristics within human-altered sagebrush steppe habitat, particularly in areas occupied by breeding sage-grouse. Using data from southeastern Idaho collected during spring and summer across 3 yr, we modeled raven occurrence as a function of the presence of livestock while accounting for multiple landscape covariates, including land cover features, topographical features, and proximity to sage-grouse lek sites (breeding grounds), as well as site-level anthropogenic features. While accounting for landscape characteristics, we found that the odds of raven occurrence increased 45.8% in areas where livestock were present. In addition, ravens selected areas near sage-grouse leks, with the odds of occurrence decreasing 8.9% for every 1-km distance, increase away from the lek. We did not find an association between livestock use and distance to lek. We also found that ravens selected sites with relatively lower elevation containing increased amounts of cropland, wet meadow, and urbanization. Limiting raven access to key anthropogenic subsidies and spatially segregating livestock from sage-grouse breeding areas would likely reduce exposure of predatory ravens to sage-grouse nests and chicks.

Key words: anthropogenic subsidies; cattle; *Centrocercus urophasianus*; *Corvus corax*; lek; sagebrush steppe.

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INTRODUCTION

Common raven (*Corvus corax*; hereafter, raven) abundance in the United States and Canada has tripled from early 1980s to 2010 (Sauer et al. 2008), facilitated by unintended anthropogenic resource subsidies that support raven

reproduction and survival (Boarman 2003). Because ravens are generalist predators and scavengers, human activities provide many food subsidy pathways for ravens such as agricultural wastes, road-killed animals, community dumps, and sewage treatment ponds (Knight and Call 1980, Boarman 1992, Knight and Kawashima

1993, Boarman and Heinrich 1999). These unintentional raven food subsidies have been shown to increase nest fledging rates and juvenile survival (Webb et al. 2004, 2009, Kristan and Boarman 2007). Only a few studies have explored relationships between ravens and livestock (Knight and Call 1980, FaunaWest 1989, Boarman et al. 2006) or other agricultural activities (Engel and Young 1989, 1992) in the American West despite substantial expansion of agriculture in regions where ravens concomitantly have increased in abundance.

However, evidence suggests that livestock operations may provide ravens with a number of direct and indirect resource subsidies. For example, open-air livestock carcass disposal sites may provide abundant carrion for ravens (Engel and Young 1989, Boarman 2003) and ravens have been reported to feed directly on live newborn calves and lambs (Larsen and Dietrich 1970, Engel and Young 1989). Ravens may benefit indirectly from livestock operations by consuming feed grain and dung at feedlots (Engel and Young 1989), as well as consuming invertebrates found in dung and insects disturbed by grazing activity (Knight and Call 1980, Boarman and Heinrich 1999). In addition, stock tanks and water troughs placed across arid landscapes for free-ranging cattle appear to indirectly provide an important source of water for ravens (Knight et al. 1998).

As a generalist predator, increased raven abundance in altered landscapes affects prey species of conservation concern. One species important to conservation in sagebrush ecosystems is the greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse), a species that has declined substantially in distribution and abundance since Euro-American settlement of western North America (Schroeder et al. 2004, Connelly et al. 2011) and for which populations continue to decline within their remaining range (Connelly et al. 2004). Studies indicate that ravens prey on sage-grouse eggs and chicks (Coates et al. 2008, Lockyer et al. 2013) and increased numbers of ravens can lead to increased depredation of sage-grouse nests (Coates and Delehanty 2010, Dinkins 2013). The primary source of sage-grouse nest failure is predation (Moynahan et al. 2007, Coates et al. 2008), and nest survival has been identified as a population vital rate that contributes substantially to recruitment and population

growth rates (Schroeder and Baydack 2001, Taylor et al. 2012). Raven depredation of nests often is higher in fragmented or otherwise human-modified landscapes, at least partially as a result of reduced nest concealment and increased accessibility for ravens (Andr n et al. 1985, Vander Haegen et al. 2002, Coates and Delehanty 2010), as well as outright increases in raven abundance.

Ravens also have been implicated in suppressing reproduction in other species of conservation concern, preying on newly hatched desert tortoises (*Gopherus agassizii*; Boarman 1992) and consuming clutches or young of marbled murrelets (*Brachyramphus marmoratus*; Singer et al. 1991), least terns (*Sterna antillarum*; Avery et al. 1995), and western snowy plovers (*Charadrius alexandrinus nivosus*; Page et al. 2009). Nest predation can reduce prey populations substantially (Garrott et al. 1993, Schneider 2001). Importantly, generalist nest predators such as ravens may continue to depredate nests even at low prey densities (Polis et al. 1997, Sinclair et al. 1998).

The primary objective of this study was to estimate the effects of free-range livestock on the probability of raven occurrence across the landscape within an altered sagebrush steppe ecosystem while accounting for other landscape characteristics that influence raven distribution. In addition, we evaluated this relationship in relation to sage-grouse breeding areas, where ravens likely have access to sage-grouse nests, in order to benefit conservation planning for sage-grouse. Specifically, we sought to measure raven occurrence as a function of: (1) presence of livestock; (2) landscape characteristics (e.g., land cover and topography); (3) proximity to sage-grouse leks (breeding grounds), which are hubs for sage-grouse nesting (Autenrieth 1981, Connelly et al. 2004) and early brood-rearing; and (4) a suite of site-level anthropogenic subsidies. Evaluating raven occurrence as a function of these environmental factors allows managers to assess relationships between ravens, livestock, and breeding sage-grouse within sagebrush steppe ecosystems and provides information to make informed decisions for raven and sage-grouse management plans.

To investigate these relationships, we used generalized linear mixed effect models coupled with Geographical Information Systems (GIS) and site-level characteristics. This approach allowed

us to evaluate the influence of transitory presence of livestock on raven occurrence while simultaneously accounting for landscape-level habitat characteristics. Predictor variables used in these analyses were not necessarily defined based on the resources they provide the ravens, but rather based on distinctions that were important for management purposes. Such analyses help to identify key features within altered sagebrush steppe that influence the occurrence of ravens in areas also occupied by breeding sage-grouse.

METHODS

Study area

The study area (E 357362, N 4678584, NAD 1983, Zone 12) consisted of a 1051 km² area in Oneida and Power Counties in south-central Idaho (Fig. 1), encompassing the Curlew National Grassland, the surrounding public and private rural lands, and the town of Holbrook,

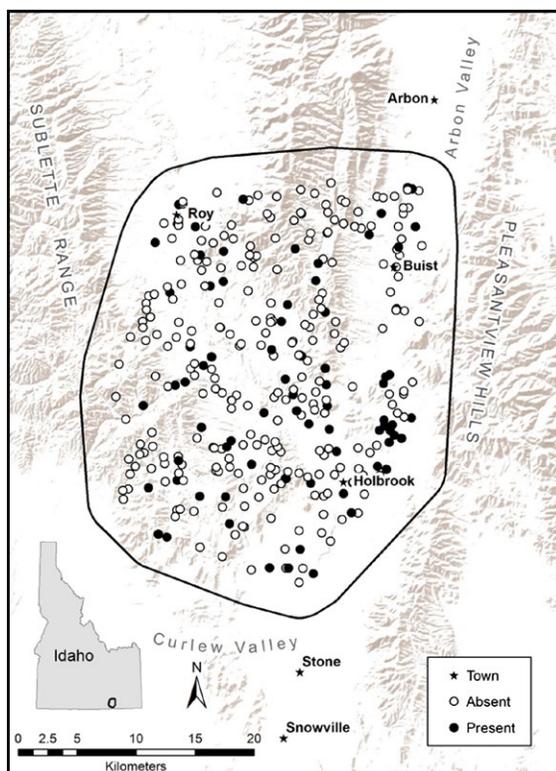


Fig. 1. Map of study area boundaries (black line) and common raven survey points (present = closed circle; absent = open circle) in southeastern Idaho, 2010–2012.

Idaho. The study area was bounded on the south by Stone Reservoir; on the north by the small communities of Roy and Buist, Idaho; on the west by the Sublette Range; and on the east by Pleasantview Hills. Elevation ranged from 1393 to 2345 m. Land ownership was a mix of public and private lands with land use consisting of a complex of irrigated and dry land agriculture, grass/shrub rangeland, and forest. Public lands were administered variously by the U.S. Bureau of Land Management (BLM), the U.S. Forest Service, and the State of Idaho. We surveyed for ravens in Arbon Valley and Curlew Valley, as well as surrounding foothills and mountains within these boundaries.

Prior to agricultural development, the study area was an expansive sagebrush steppe landscape with forests occurring at higher elevations. The Curlew National Grassland encompassed approximately 19 020 ha, of which 4856 ha remained in native vegetation. Private lands included Conservation Reserve Program (CRP) lands and dry land and irrigated croplands. Primary use of private land across the study area consisted of livestock grazing, dry land wheat, oat and barley farming, and irrigated alfalfa production (McGrath et al. 2002, Idaho Agricultural Statistics Services 2005). Irrigated agriculture was restricted to the valley floor where both surface and groundwater were accessible. Dry land farming occurred in the foothills. Primary surface and ground water flow was associated with Deep Creek, Rock Creek, and springs generally flowing from north to south and from mountains toward valley bottoms (Bendixsen 1994, Hurlow and Burk 2008).

Lower elevations of the study area were characterized by a mix of introduced and native grass species with an overstory of desert shrubs including: Wyoming big sagebrush (*Artemisia tridentata*), basin big sagebrush (*A. t. tridentata*), mountain big sagebrush (*A. t. vaseyana*), low sagebrush (*A. arbuscula*), black sagebrush (*A. t. nova*), threetip sagebrush (*A. tripartita*), green rabbitbrush (*Chrysothamnus viscidiflorus*), rubber rabbitbrush (*C. nauoseosus*), bluebunch wheatgrass (*Agropyron spicatum*), brome (*Bromus* spp.), festuca (*Festuca* spp.), poa (*Poa* spp.), stipa (*Stipa* spp.), and wheatgrass (*Agropyron* spp.).

Higher elevations were characterized by Rocky Mountain juniper (*Juniperus scopulorum*), Utah

juniper (*J. osteosperma*), Rocky Mountain maple (*Acer glabrum*), subalpine fir (*Abies lasiocarpa*), curl-leaf mountain mahogany (*Cercocarpus ledifolius*), lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), and quaking aspen (*Populus tremuloides*). Average annual precipitation in the region was 336 mm, with the majority occurring as snow (National Climatic Data Center). The average daily temperature range in summer was 9–29°C, and –9 to 0°C in winter (National Climatic Data Center).

Raven point surveys

During the spring and summer months of 2010–2012, we conducted raven point count surveys based on techniques recommended by Ralph et al. (1995). In 2010 and 2011, we conducted surveys during the sage-grouse brood-rearing period (July–August). In 2012, we conducted surveys during the sage-grouse nesting and brood-rearing period (May–July). The turn-out date for cattle on the Curlew National Grassland (16 April; USDA 2002) preceded primary raven nesting season in southeastern Idaho (May–July; Howe et al. 2014). The surveys included breeding and non-breeding ravens and it usually was not possible to differentiate the breeding status of ravens detected during surveys.

Survey points were generated in a stratified random design across the study site (Fig. 1) to ensure sampling across all available habitat types and at various distances up to 1500 m from paved, gravel, and two-track roads. Points were surveyed only once per season and up to three times over the course of the study. To prevent double-counting, survey points that were located within 3 km of each other were not surveyed on the same day. Surveys were not conducted in winds ≥ 32 km/h or during moderate or heavy precipitation (Luginbuhl et al. 2001). We surveyed for ravens during random intervals between one half-hour before sunrise and one half-hour following sunset. Sage-grouse nest depredation by ravens can occur at any time of the day. However, most nest depredations occur under low-light conditions at dawn and dusk (Coates and Delehanty 2008). As such, surveys that span the entire daylight period adequately represent raven foraging opportunity. During each survey, we visually scanned the ground and sky using binoculars and unaided eyes for a period of 10 min. For each raven observed, the

time of sighting, bearing relative to survey point, distance (m) from the survey point (estimated using a handheld rangefinder), and behavior of the bird (perching, on the ground, hunting/circling, nest sentry, copulation, etc.) was recorded. We estimated bearing and distance for ravens that were heard vocalizing but not visually located.

Presence of livestock and anthropogenic features

At each field survey point, we scanned the area for presence of livestock. Because livestock at this study area consisted almost entirely of domestic cattle (*Bos primigenius taurus*), hereafter we usually refer to cattle instead of livestock. When cattle were present, we estimated the distance from cattle to the survey point using rangefinders. For the analysis, we included cattle within 2 km of the survey point based on field estimation. We also recorded all anthropogenic features, defined as any structures that were built and placed within the environment by humans. These features specifically consisted of electrical transmission and distribution lines, telephone lines and towers, communication towers, buildings, campground facilities, fences, stock ponds and water troughs, irrigation pivots, grain silos, and other structures associated with agriculture. Similar to livestock, we included presence or absence of these features within 2 km of the survey point. Incorporating presence data collected from surveys allowed us to use these types of features in our analysis, which typically are not available as GIS layers.

Landscape characteristics

We measured multiple landscape characteristics associated with each survey point using land cover maps. Because raven occurrence is associated with landscape-level factors (Bui et al. 2010, Coates et al. 2014), we included these important factors in the analysis that might otherwise confound our site-level effects (e.g., presence of livestock). Our underlying land cover data was based on Landscape Fire and Resource Management Planning Tools (LANDFIRE 2006), which consisted of classified vegetation communities using 30-m resolution Landsat imagery (Rollins 2009). We condensed the multispecies complexes into 14 landscape-level cover types based on the dominant overstory, which consisted of annual grassland, big

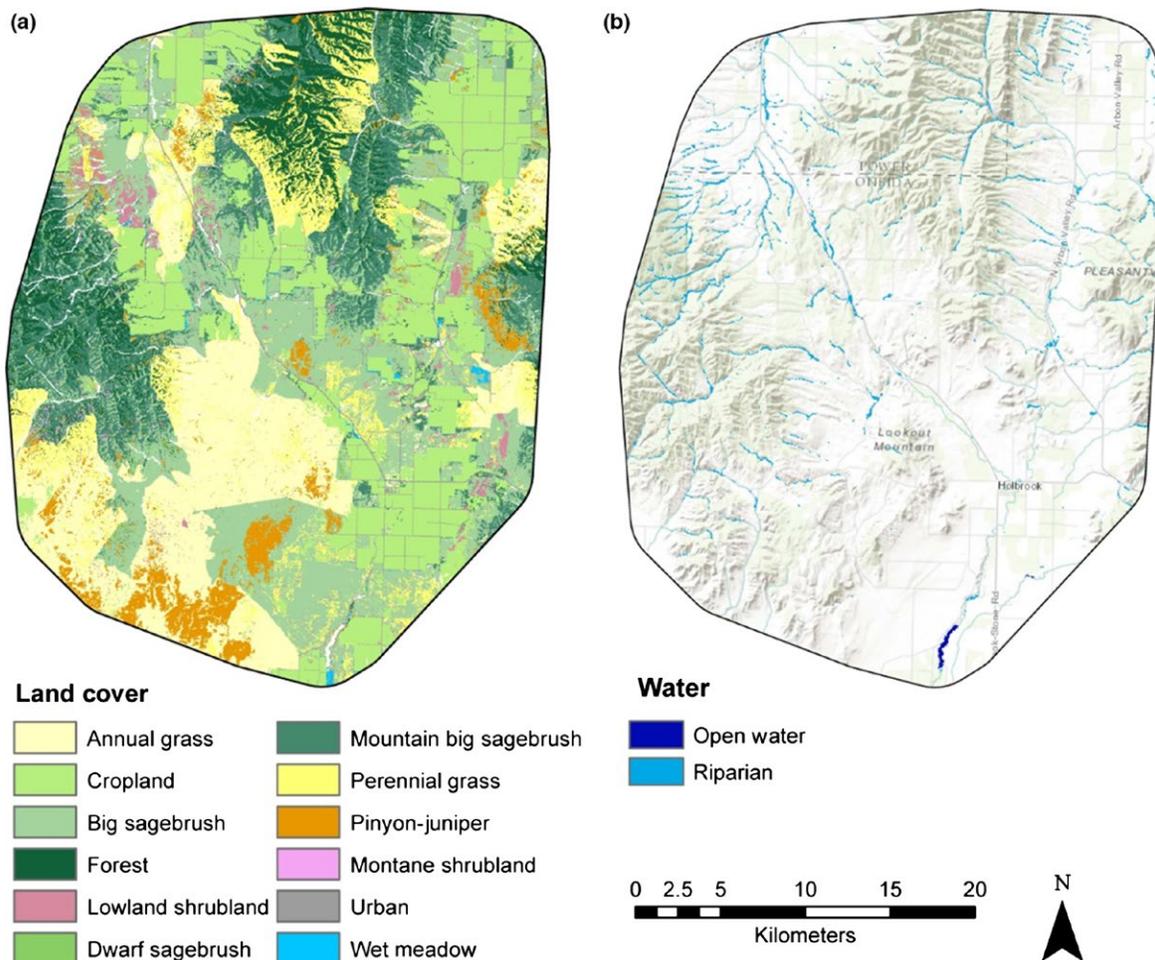


Fig. 2. Map of cover classifications for all land (a) and water (b) cover types that were used as explanatory variables for modeling the occurrence of common ravens in southeastern Idaho, 2010–2012.

sagebrush, cropland, forest, lowland shrubland, dwarf sagebrush, mountain big sagebrush, perennial grassland, pinyon-juniper, upland other shrub, wet meadow, urban, riparian, and open water (Fig. 2a,b). We mapped the location of each raven survey into the GIS by importing survey location UTM coordinates.

Because relationships between wildlife and environmental factors are inherently scale-dependent (Mayor et al. 2009), we evaluated landscape covariates at three spatial scales. The scales were based on reported average distance ravens travel from nest sites (570 m; Boarman and Heinrich 1999), and home range (6.6 km²; Smith and Murphy 1973) or territory size (40.5 km²; Bruggers 1988) for breeding ravens. These

distances equated to spatial scales of 102.1, 660.5, and 4048.9 ha, respectively. We used the Neighborhood Analysis tool in Spatial Analyst (ArcGIS 10.1, ESRI 2012) to carry out a moving window analysis, which calculates the percent of each land cover type within each spatial scale (circular) centered on every 30 m × 30 m grid cell across the study area. Percentages of each land cover type at each spatial scale were then assigned to the raven survey points to be used in the analyses. Because open water and riparian represented relatively small amounts of cover across the landscape, we investigated the effects of Euclidean distance between survey points and nearest open water and riparian source, which is considered a useful approach to estimate effects of features that are

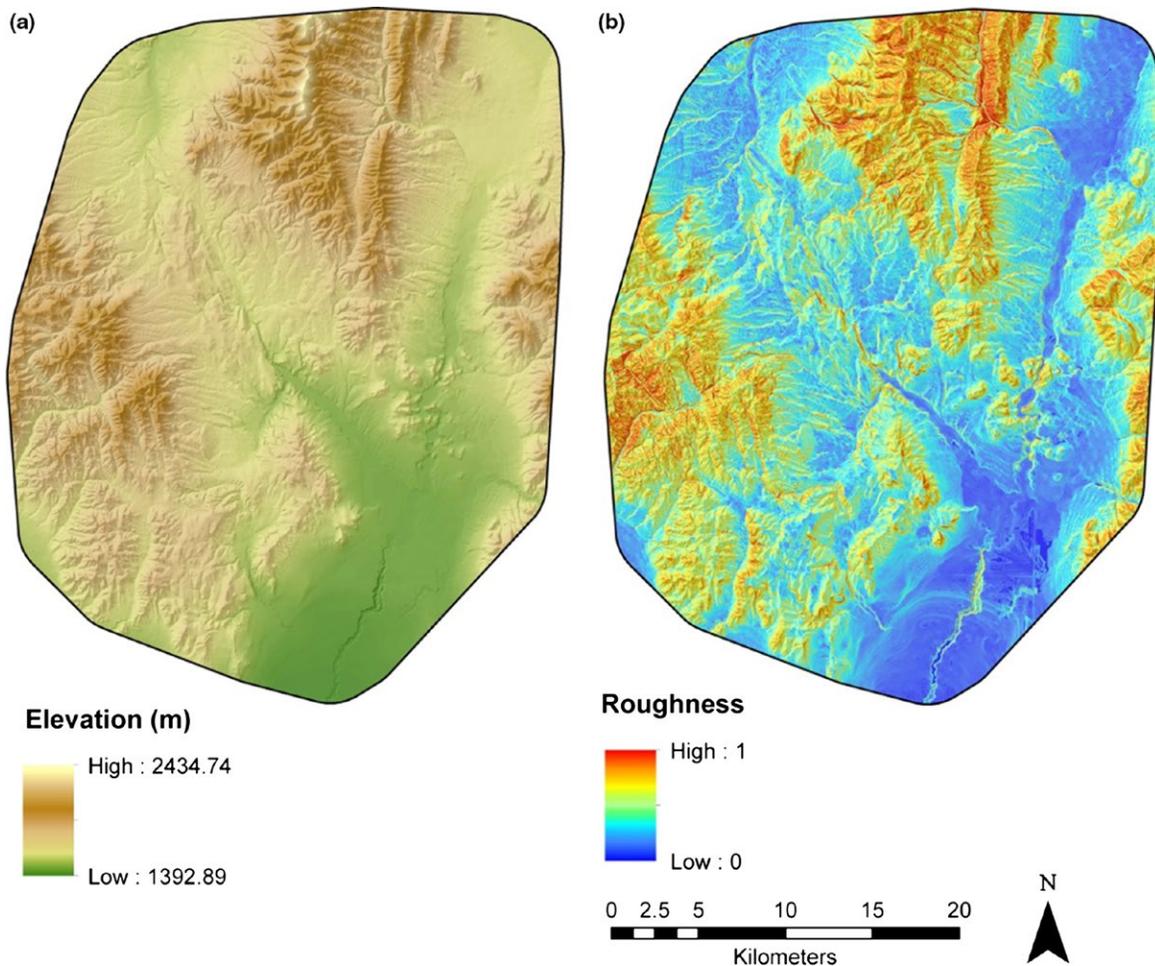


Fig. 3. Map of elevation (a) and roughness index (b) that were used as explanatory variables for modeling the occurrence of common ravens in southeastern Idaho, 2010–2012.

points, linear, or relatively small in area on the landscape (Conner et al. 2003). To investigate the effects of proximity to cropland, we also calculated the distance to nearest cropland, either irrigated or dry land agriculture, and the distance to nearest permanent human dwelling. We also accounted for physiographic factors, such as elevation (Fig. 3a; U.S. Geological Survey 2009) and an index of roughness (Fig. 3b). Roughness was a measure of the topographical diversity obtained by representing small-scale variation in elevation (Riley et al. 1999), which was calculated using the Geomorphometry and Gradient Metric Toolbox (ArcGIS 10.1, ESRI 2012).

We included roads as a landscape-level anthropogenic feature into the models because studies

indicate that roads provide road-killed animals and land cover edges which influence resource selection by ravens at both fine- and coarse-scales in sagebrush environments (Austin 1971, Knight and Kawashima 1993, Webb et al. 2011, Howe et al. 2014). Specifically, we calculated nearest distance from survey points to state highways, major paved roads, improved gravel roads, and to any road including unimproved two-track roads (Fig. 4a).

To incorporate presence of breeding sage-grouse into the models, we calculated the distance to nearest active sage-grouse lek (traditional breeding ground; Fig. 4b). Our basis for using active leks as an indicator of sage-grouse reproductive life stages was literature reporting that leks occur within core areas of sage-grouse nesting (Autenrieth 1969,

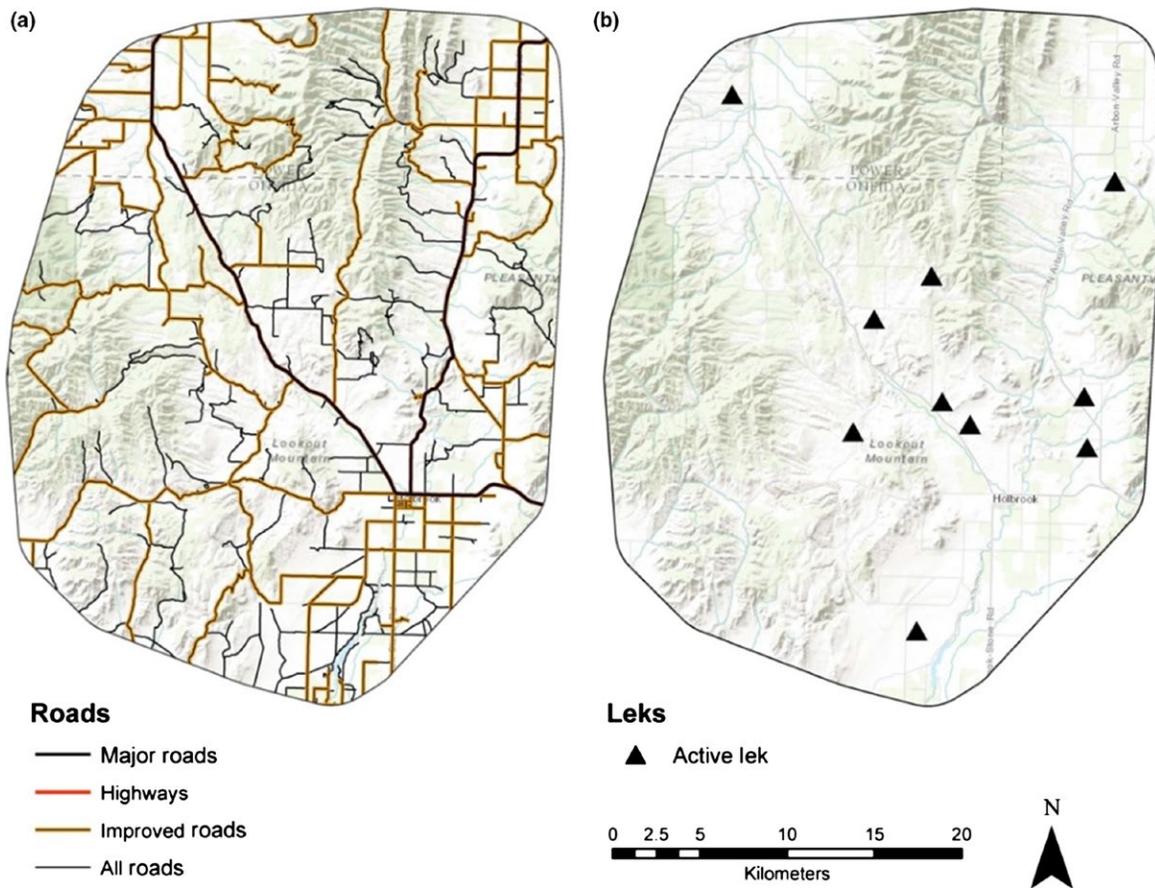


Fig. 4. Map of roads (a) and greater sage-grouse lek sites (b) that were used as explanatory variables for modeling the occurrence of common ravens in southeastern Idaho, 2010–2012.

Lyon and Anderson 2003, Fedy et al. 2012, Coates et al. 2013), and that areas near leks are important for sage-grouse during brood-rearing stages (Connelly et al. 2004). We assumed that the degree to which ravens were present in areas near active leks reflected the degree to which ravens occupied areas with breeding female sage-grouse in the nesting or early brood-rearing phases of reproduction.

To further investigate the distance-based effects, we carried out an exponential decay transformation on the distance value as an alternative effect (Nielsen et al. 2009), using $e^{-d/\alpha}$ where d was the distance (m) from each survey point (i.e., points with and points without observed ravens) to the feature of interest, and α represented the mean distance between each survey point at which ≥ 1 raven was observed and the feature of interest. The mean represented the most reliable measure of central tendency based on the distribution of

these data. This decay form allowed us to estimate the degree to which the effect of a feature of interest strengthened or weakened exponentially as distance from that feature changed.

Raven occurrence modeling

We developed GLMMs (specified binomial error distribution; Zuur et al. 2009), which allowed us to estimate the influence of each factor using a logistic regression approach (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006) on the odds of raven occurrence. In this case, we contrasted measurements between survey points where ravens were present to those where ravens were absent to make inferences about the influence on raven occurrence within a 10-min survey duration. Predictor variables that were considered in the modeling framework are listed in Table 1. We also included year as a random effect in the

Table 1. Groups of predictor variables representing overarching explanatory themes, covariate descriptors, and explanation of covariates used to develop generalized linear mixed models for raven occurrence within sagebrush steppe in southeastern Idaho during 2010–2012.

Model groups	Abbr.	Description
Road	D_ALLR	Distance (km) to nearest road (includes two-track)
	D_ALLR_e	Exponential decay form of D_ALLR
	D_IMPR	Distance (km) to nearest improved road
	D_IMPR_e	Exponential decay form of D_IMPR
	D_HWY	Distance (km) to nearest highway
	D_HWY_e	Exponential decay form of D_HWY
	D_MJR	Distance (km) to nearest major road
Distance to cropland	D_MJR_e	Exponential decay form of D_MJR
	D_CPL	Distance (km) to nearest cropland
Sage-grouse leks	D_CPL_e	Exponential decay form of D_CPL
	D_LEK	Distance (km) to nearest sage-grouse lek location
Annual grassland	D_LEK_e	Exponential decay form of D_LEK
	AG_102	Annual grass (%; 102.1 ha scale)
	AG_660	Annual grass (%; 660.5 ha scale)
Big sagebrush	AG_4048	Annual grass (%; 4048.9 ha scale)
	BS_102	Big sagebrush (%; 102.1 ha scale)
	BS_660	Big sagebrush (%; 660.5 ha scale)
Cropland	BS_4048	Big sagebrush (%; 4048.9 ha scale)
	CPL_102	Cropland (%; 102.1 ha scale)
	CPL_660	Cropland (%; 660.5 ha scale)
Dwarf sagebrush	CPL_4048	Cropland (%; 4048.9 ha scale)
	DS_102	Dwarf sagebrush (%; 102.1 ha scale)
	DS_660	Dwarf sagebrush (%; 660.5 ha scale)
Forest	DS_4048	Dwarf sagebrush (%; 4048.9 ha scale)
	FOR_102	Forest (%; 102.1 ha scale)
	FOR_660	Forest (%; 660.5 ha scale)
Lowland shrubland	FOR_4048	Forest (%; 4048.9 ha scale)
	LOS_102	Lowland non-sagebrush shrub (%; 102.1 ha scale)
	LOS_660	Lowland non-sagebrush shrub (%; 660.5 ha scale)
Mountain big sagebrush	LOS_4048	Lowland non-sagebrush shrub (%; 4048.9 ha scale)
	MBS_102	Mountain big sagebrush (%; 102.1 ha scale)
	MBS_660	Mountain big sagebrush (%; 660.5 ha scale)
Perennial grass	MBS_4048	Mountain big sagebrush (%; 4048.9 ha scale)
	PG_102	Perennial grass (%; 102.1 ha scale)
	PG_660	Perennial grass (%; 660.5 ha scale)
Pinyon-Juniper	PG_4048	Perennial grass (%; 4048.9 ha scale)
	PJ_102	Pinyon-juniper (%; 102.1 ha scale)
	PJ_660	Pinyon-juniper (%; 660.5 ha scale)
Upland other shrub	PJ_4048	Pinyon-juniper (%; 4048.9 ha scale)
	UOS_102	Upland shrubland (%; 102.1 ha scale)
	UOS_660	Upland non-sagebrush shrub (%; 660.5 ha scale)
Urban	UOS_4048	Upland non-sagebrush shrub (%; 4048.9 ha scale)
	URB_102	Urban area, human inhabitants (%; 102.1 ha scale)
	URB_660	Urban area, human inhabitants (%; 660.5 ha scale)
Wet meadow	URB_4048	Urban area, human inhabitants (%; 4048.9 ha scale)
	WM_102	Wet meadow (%; 102.1 ha scale)
	WM_660	Wet meadow (%; 660.5 ha scale)
Water	WM_4048	Wet meadow (%; 4048.9 ha scale)
	D_OW	Distance (km) to nearest open water source
	D_OW_e	Exponential decay form of D_OW
Elevation	D_RIP	Distance (km) to nearest riparian area
	D_RIP_e	Exponential decay form of D_RIP
	ELEV	Elevation (m)

(Continued)

Table 1. Continued.

Model groups	Abbr.	Description
Roughness	ROUGH	Roughness index
Livestock	P_LIVE	Presence or absence of livestock (within 2 km)
Subsidy	P_SUB	Presence of a subsidy feature (within 2 km)

models to account for temporal correlation (Zuur et al. 2009) that may otherwise confound the fixed effects (e.g., amount of cropland; Faraway 2006, Gillies et al. 2006, Koper and Manseau 2009).

We employed a multistep information theoretic modeling approach, following procedures conducted in similar studies (Coates and Delehanty 2008, Aldridge et al. 2012, Coates et al. 2014). We first reduced the number of variables by comparing evidence within a biological theme and comparing to an intercept-only model (see Appendix A; Coates et al. 2014). Using those variables that were found to have support from the data, we developed additive models that consisted of predictor variables (covariates) carried forward from the variable reduction process, which produced more realistic models by including multiple biological themes (Coates and Delehanty 2008, Aldridge et al. 2012). Because numerous combinations of additive models were possible, we developed sets of models with different combinations between covariates. We did not allow >3 covariates in each model to prevent over parameterization (Coates and Delehanty 2008). By design, this approach is exploratory, seeking covariates that explain observed occurrence of ravens in altered sagebrush steppe habitat. However, the environmental factors represented by the covariates were based on *a priori* hypotheses from the literature (Coates et al. 2014, Howe et al. 2014). In other words, our approach was an exploration of those habitat features at our study site that previously have been hypothesized to be important to the occurrence of ravens elsewhere. To reduce potential effects of multicollinearity within each model, we removed models that consisted of covariates that covaried ($r \geq |0.65|$).

We used Akaike's information criterion with second-order correction (AIC_c ; Anderson 2008) to evaluate evidence of support for models, and then we used the AIC differences (ΔAIC_c) between two models to compare the relative utility of the models. We also calculated Akaike's weights (w ;

Anderson 2008) and model-averaged the parameter estimates (β s) for each covariate across models (Anderson 2008) included within 90% of the cumulative w (Cw). Model-averaging was appropriate because variables were standardized and multicollinearity had been reduced by removing those models with predictors that covaried. We also calculated unconditional standard errors, 85% confidence intervals (CI), and 95% CIs of the β s. Covariates with model-averaged 95% CIs that did not overlap zero demonstrated the greatest support from the data. We considered estimates with 85% CI that overlapped zero as lacking support from the data (Arnold 2010). We also report the 95% CIs for mean values of each variable across survey sites where ravens were and were not sighted. The purpose of these calculations was not to identify a single "best" model, but instead to recognize the degree of support for explanatory covariates representing habitat features (i.e., hypotheses from the literature) and to estimate the model-averaged β s of these covariates in explaining the observed occurrence of ravens while allowing for additive effects. For example, we model-averaged the effect of the presence of livestock on raven occurrence while accounting for additive effects from influential landscape-level covariates. To facilitate the interpretation of the effects of explanatory covariates on raven occurrence, model-averaged standardized β s were back-calculated and expressed in original measurement units and then expressed as odds ratios. We estimated a relative importance of each explanatory covariate in terms of its explanatory contribution by summing w across models that included the covariate of interest (Burnham and Anderson 2002), adjusted for unequal number of models representing each covariate.

Model assumptions

This study relies on multiple assumptions. We first assumed that the detection probability of ravens in our study area was one or the

difference from one was negligible. We right truncated data to exclude observations that exceeded 1.5 km because at that distance raven detection probability may become lower and we sought to prevent misclassification with other large bird species. We are confident that this assumption was not violated because ravens are large, vocal birds, easily identified with binoculars given our distance cutoff, and the dominant land cover in our study area consists of relatively low vegetation. Furthermore, Bui et al. (2010) found that most land covers (sagebrush, riparian woodland, agricultural land, oil fields, and human settlement) had no effect on the detection of ravens, and density estimates adjusted for detection probability were strongly correlated with the unadjusted estimates.

Second, variation in the detection probability by observer is also negligible in this study because all observers were trained to use standardized procedures and initial comparisons between double blind observers were carried out to ensure consistency. We assumed that surveyed points represented open plots, which ravens may move through following the survey. Therefore, results should be interpreted as odds of occurrence within a 10-min period, based on sampling whether or not one or more ravens visited our survey area within the 10-min survey.

Third, we assumed independence among observations. Although ravens often form groups, interact with each other, and are territorial (Boarman and Heinrich 1999), this assumption likely was met because surveys were scored as presence or absence of ravens at each point. In other words, it is highly unlikely that resource selection by ravens at one survey point influenced raven resource selection at a distant point. It is also important to note that we did not differentiate between breeding ravens vs. nonbreeding ravens. Thus, our model predictions were limited to ravens regardless of life-history stage. Last, we assumed resource availability to be known without error and to be the same for all ravens in the study area and to be constant over the period of the study. Ravens are capable of long-distance movements (e.g., 320 km; Mahringer 1970). Thus, ravens were capable of selecting any area within the extent of the study area.

RESULTS

Raven surveys

We conducted 341 raven surveys and detected 264 raven occurrences among 83 (24.3%) of those surveys. For those surveys in which ravens were detected, we observed single ravens on 29 occasions (34.9%), two ravens on 28 occasions (33.7%), and >2 ravens on 26 occasions (31.3%). Observations of single or pairs of ravens during spring and early summer are consistent with breeding raven territoriality, while the groups of ravens were more likely to be nonbreeding, transient adults, or juveniles. The greatest number of ravens observed in a single survey was 38.

Effects on raven occurrence

Thirteen covariates were supported in the variable reduction process and were used to model environmental factors in more complex and realistic multifactor additive models (Appendix A). The covariate for presence of livestock was included in all of the most parsimonious models (P_LIV; Table 2) and provided the greatest relative importance of all covariates considered (Table 3). All models with this covariate indicated that ravens were more likely to be present in areas with cattle than those without, with strongest support from the most parsimonious model (Fig. 5). Based on the model-averaged parameter estimates, the odds of occurrence of raven increased 45.8% where livestock was present.

A covariate for elevation was in the most parsimonious model (ELEV; Table 2) and was the second most important variable of those considered across the model set (Table 3). The averaged 95% CI of the β estimates for elevation did not overlap zero (Table 3), which met the highest standard of evidence. Ravens selected areas at lower elevation (Fig. 6a). Based on model-averaged parameter estimates, a 100-m increase in elevation decreased the odds of raven occurrence by 9.5%. In areas where ravens were detected, elevation was 1612.4 m (95% CI = 1584.6–1640.2 m) compared to where ravens were not detected 1676.3 m (95% CI = 1658.8–1693.8 m; Table 4). Roughness did not lack support from the data, as 85% CI of β estimates did not overlap zero (Table 3).

Table 2. Evaluation of models explaining occurrence of raven within sagebrush steppe in southeastern Idaho, 2010–2012.

Model†	K	LL‡	ΔAIC_c	w
P_LIV + D_CPL_e + ELEV	5	-177.05	0.00	0.11
P_LIV + D_CPL_e + D_LEK	5	-178.02	1.94	0.04
P_LIV + ELEV + URB_4048	5	-178.09	2.08	0.04
P_LIV + ELEV + WM_4048	5	-178.18	2.27	0.03
P_LIV + D_CPL_e + FOR_4048	5	-178.38	2.66	0.03
P_LIV + ELEV	4	-179.46	2.76	0.03
P_LIV + D_CPL_e + ROUGH	5	-178.50	2.89	0.03
P_LIV + D_CPL_e + WM_4048	5	-178.52	2.94	0.02

Notes: K = number of estimated parameters; LL = Log (*Likelihood*); ΔAIC_c = difference (Δ) in Akaike's Information Criterion (AIC) with sample size adjustment (c) between best approximating model and model of interest; w = model probability.

† Models consisted of ≤ 3 covariates to prevent overparameterization and all models consisted of year as a random effect (Zuur et al. 2009). Covariate abbreviations: P_LIV = presence of livestock; D_CPL_e = exponential decay form of distance to cropland; ELEV = elevation; D_LEK = distance to lek; URB_4048 = urban area (%; 4048.9 ha scale); WM_4048 = wet meadow (%; 4048.9 ha scale); FOR_4048 = forest (%; 4048.9 ha scale); ROUGH = roughness index.

‡ Log (*Likelihood*) of the null model (random effect only) was -189.24.

Table 3. Model-averaged parameter estimates of landscape-level covariate effects on raven occurrence within sagebrush steppe in southeastern Idaho during 2010–2012.

Covariate†	Averaged Estimate	Covariate Weight‡	Interpretation§
P_LIV#	0.68	0.71	Selected areas where livestock were present
ELEV#	-2.98	0.52	Selected areas at lower elevations
D_CPL_e#	0.94	0.49	Selected areas near cultivated fields
WM_4048¶	52.80	0.23	Selected increased wet meadows at largest scale
URB_4048¶	17.73	0.20	Selected areas of urbanization at largest scale
ROUGH¶	-2.15	0.18	Avoided topographically diverse areas
D_LEK¶	-0.09	0.18	Selected areas near active sage-grouse lek sites
FOR_4048¶	-2.43	0.11	Avoided forested areas at largest scale
UOS_4048	-72.46	0.10	–
BS_4048	1.30	0.10	–
D_OW	0.62	0.09	–
P_SUB	0.30	0.07	–
D_MJR_e	0.25	0.05	–

† Covariate abbreviations: P_LIV = presence of livestock; ELEV = elevation (km); D_CPL_e = exponential decay form of distance to cropland; WM_4048 = wet meadow (%; 4048.9 ha scale); URB_4048 = urban area (%; 4048.9 ha scale); ROUGH = roughness index; D_LEK = distance to lek; FOR_4048 = forest (%; 4048.9 ha scale); UOS_4048 = upland non-sagebrush area (%; 4048.9 ha scale); BS_4048 = big sagebrush area (%; 4048.9 ha scale); D_OW = distance to open water; P_SUB = presence of anthropogenic subsidy; D_MJR_e = exponential form of distance to major road.

‡ Covariate weight represents a ranking for the relative importance, calculated by summing Akaike's weights (Anderson 2008) across models that included the covariate corrected for unequal representation in model set due to removal of models with correlated predictors.

§ Interpretation of model-averaged parameters estimates with 85% confidence interval that did not overlap zero (Arnold 2010). Standardized estimates were back-calculated for interpretation. Dashes indicate those estimates with 85% CIs that overlapped zero.

¶ Indicates 85% CI of the averaged estimates across all models with additive effects did not overlap zero.

Indicates 95% CI of the averaged estimates across all models with additive effects did not overlap zero.

Ravens were more likely to be detected in areas with decreased topographic diversity (detected = 0.21, 95% CI = 0.19–0.23; not detected = 0.26, 95% CI = 0.24–0.27; Table 4; Fig 6b). Taken to-

gether, these physiographic covariates indicate that ravens were more likely to occur at lower elevations such as valleys with relatively flat, not rugged, terrain.

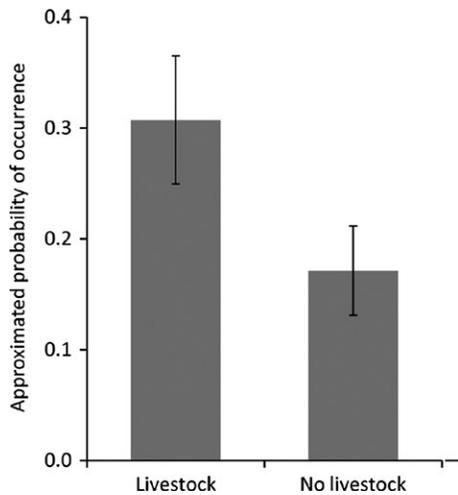


Fig. 5. Approximated probability of raven occurrence (bars = SE) as a function of presence of livestock in southeastern Idaho, 2010–2012. For illustrative purposes, predictions were derived using parameter estimates from the most parsimonious model while additive effects were held at their means.

The exponential decay form of distance to cropland (D_{CPL_e}) was included in the most parsimonious model and was found in three of five models with the lowest AIC_c (Table 2). This covariate was the third most supported covariate (Table 3). Surveys with ravens present were closer to cropland than those with ravens absent (Table 4). Furthermore, model evidence indicated that the odds of raven occurrence decreased as distance to cropland increased but not at a constant rate. Specifically, the odds of raven occurrence decreased most notably up to approximately 500 m (Fig. 6c), but beyond 500 m the odds remained relatively constant.

The fourth most supported covariate was percent of wet meadow at the 4048.9 ha scale (WM_{4048} ; Table 3). Although the extent of wet meadow areas was relatively restricted compared to other land cover types, surveys in which ravens were present were associated with nearly twice as much area classified as wet meadow than surveys in which ravens were absent (Table 4, Fig. 6d). Ravens were more likely to select areas as urbanization increased at the 4048.9 ha scale (Table 3; Fig. 6e). Ravens were present in areas containing 2.50% (95% CI = 2.15–2.84%) urbanization, on average, and not detected

in areas containing an average of 1.92% (95% CI = 1.73–2.11%) urbanization (Table 4). The final land cover characteristic that showed evidence from the data was forest. We found that the averaged 85% CI of the β estimates for forest at the largest scale (FOR_{4048}) did not overlap zero (Table 3). Ravens were associated with areas with less forest than was available (Table 4; Fig. 6f). Distance to nearest sage-grouse lek (D_{LEK}) influenced raven occurrence. This covariate was in the second most parsimonious model (Table 2). We observed an 8.9% increase in the odds of raven occurrence for every 1 km decrease in distance to lek (Fig. 7).

Those covariates that received limited support from the data included upland other shrub land (4048.9 ha scale), big sagebrush (4048.9 ha scale), proximity to relatively large open water sources, presence of anthropogenic subsidies, and proximity to major roads. Although these models influenced the variable reduction process, the averaged 85% CI estimates across additive models employing these covariates included zero (Table 3).

DISCUSSION

This study reveals empirical support for a strong, positive association between presence of cattle and likelihood of presence of ravens within an altered sagebrush ecosystem used by breeding sage-grouse while accounting for landscape-level characteristics, such as vegetative land cover. The presence of livestock and associated animal husbandry practices can provide ravens with resource subsidies. For example, water is a critical resource for domestic cattle and, behaviorally, cattle are central place foragers with proximity to water for daily drinking influencing their foraging movements and habitat occupancy (Kaufmann et al. 2013). At the same time, water is a critical resource for ravens in semiarid environments (Boarman 2003), and ravens are associated with stock ponds, watering troughs, and other water sources intended for cattle (FaunaWest Wildlife Consultants 1989, Boarman et al. 2006). To that extent, our results are supported by a previous study that quantified use of stock tanks, natural springs, and control sites by ravens (Knight et al. 1998). Interestingly, Knight

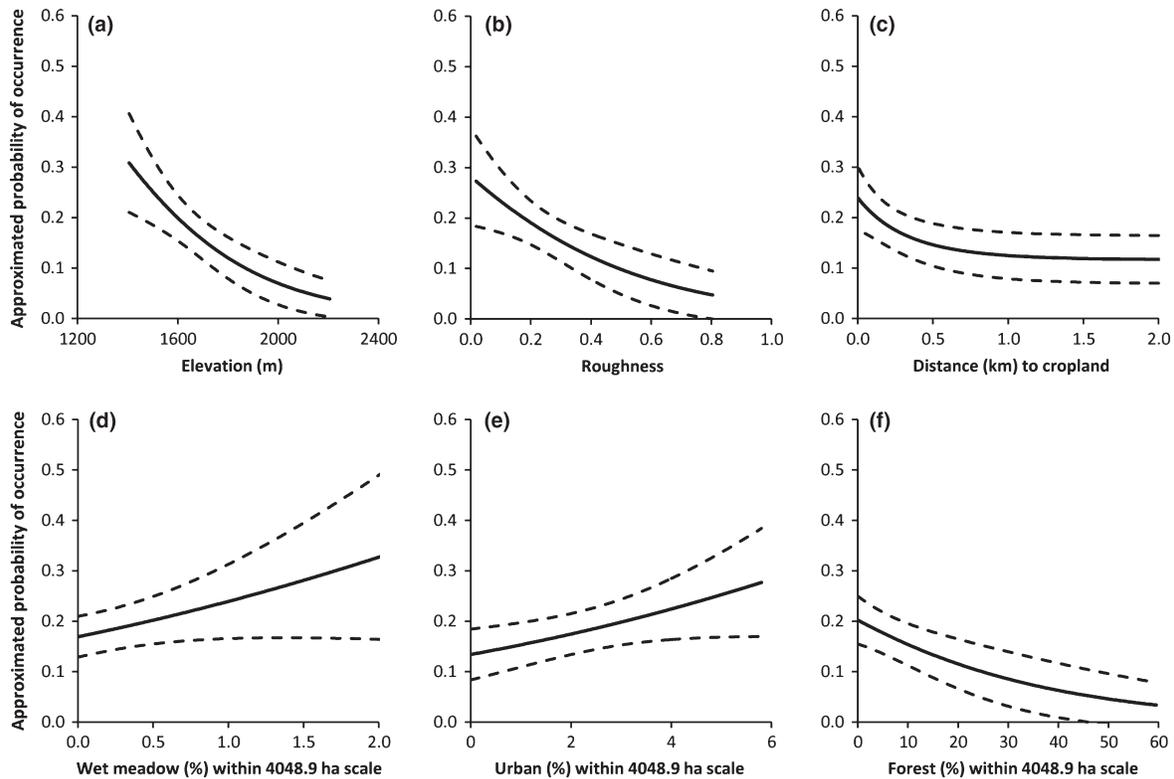


Fig. 6. Approximated probability of raven occurrence (dashed lines = 85% CIs) with respect to (a) elevation, (b) roughness, (c) distance (km) to cropland, (d) percent of wet meadow within 4048.9 ha scale, (e) percent of urban within 4048.9 ha scale, and (f) percent of forest within 4048.9 ha scale in southeastern Idaho, 2010–2012. For illustrative purposes, predictions were derived using parameter estimates from the most parsimonious model while additive effects were held at their means.

Table 4. Mean and standard errors of landscape-level characteristics describing survey locations where common ravens were present or absent during a 10-min survey within sagebrush steppe in southeastern Idaho during 2010–2012.

Group	Covariate†	Absent		Present	
		Mean	SE	Mean	SE
Roads (km)	D_MJR	4.36	0.21	3.50	0.37
Agriculture (km)	D_CPL	0.66	0.05	0.41	0.07
Leks (km)	D_LEK	5.06	0.18	3.96	0.28
Land cover (%)	BS_4048	25.59	0.94	31.03	1.78
	FOR_4048	7.27	0.82	3.39	0.88
	UOS_4048	0.21	0.03	0.10	0.03
	WM_4048	0.21	0.02	0.40	0.07
	URB_4048	1.92	0.10	2.50	0.18
Water source (km)	D_OW	18.04	0.50	15.68	0.94
Elevation (m)	ELEV	1676.3	8.94	1612.4	14.17
Topographical Index	ROUGH	0.26	<0.01	0.21	0.01

† Covariates were carried forward from the variable reduction process described in Appendix A. Covariate abbreviations: D_MJR_e = exponential form of distance to major road; D_CPL_e = exponential decay form of distance to cropland; D_LEK = distance to lek; BS_4048 = big sagebrush area (%; 4048.9 ha scale); FOR_4048 = forest (%; 4048.9 ha scale); UOS_4048 = upland non-sagebrush area (%; 4048.9 ha scale); WM_4048 = wet meadow (%; 4048.9 ha scale); URB_4048 = urban area (%; 4048.9 ha scale); D_OW = distance to open water; ELEV = elevation; ROUGH = roughness index.

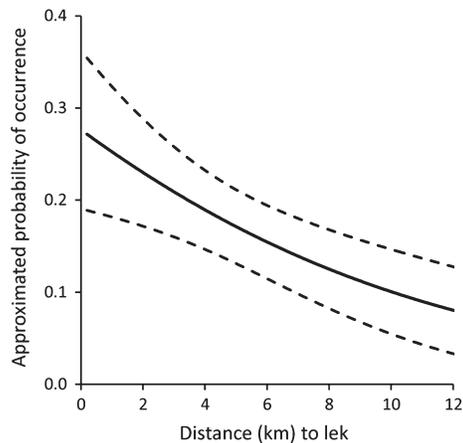


Fig. 7. Approximated probability of raven occurrence (dashed lines = 85% CIs) as a function of distance (km) to active greater sage-grouse lek in southeastern Idaho, 2010–2012. For illustrative purposes, predictions were derived using parameter estimates from the most parsimonious model while additive effects were held at their means.

et al. (1998) reported that ravens were only detected at stock tanks, and 80% of the observations involved ravens drinking water directly from the tank. In our study area, water troughs were often permanent infrastructure on the landscape (concrete pads and steel structures), though some mobile water troughs were dispersed across the range.

Distance to open surface water was not an explanatory covariate in our selection models. Unfortunately, the 30-m cell size mapping resolution of LANDFIRE was limited to relatively large water sources and did not include small open water sources as features in the GIS component of the analysis. Nonetheless, our anthropogenic site-level covariate did include relatively small anthropogenic water sources on the landscape (e.g., stock ponds and water troughs) and was only moderately supported by the data (Appendix A). Water troughs were observed at 17% of the survey points, and 22% of the sites where anthropogenic subsidies were present. The remaining 78% consisted of other anthropogenic features (e.g., powerlines, fences, facilities, etc.). Notably, the cattle covariate showed more evidence of support from the data than did the anthropogenic covariate, indicating that ravens might occupy areas with cattle for reasons un-

related to anthropogenic alterations designed to improve conditions for cattle. Some research has demonstrated that livestock feeding operations unintentionally provision juvenile ravens by providing concentrated and continually replenished sources of food (Webb et al. 2009). Ravens have been observed feeding on a variety of livestock-related subsidies in other studies (Knight and Call 1980, Boarman and Heinrich 1999), and we observed similar raven foraging behavior at our study site.

Ravens selecting areas near breeding locations of sage-grouse was consistent with findings that ravens actively hunt sage-grouse eggs and chicks (Coates et al. 2008, Lockyer et al. 2013) and are drawn to areas important for sage-grouse reproduction (Bui et al. 2010). We found stronger support for the linear form of the distance effect to sage-grouse leks than the exponential decay form. A simple linear effect of distance is consistent with sage-grouse behavior in that sage-grouse nesting and brood-rearing typically do not occur directly on or immediately near lek sites. Although utilization of areas near leks by sage-grouse has been reported as relatively high near the lek sites during the reproductive period (Coates et al. 2013), average distance from lek to nest varies from 1.1 to 5.0 km (Autenrieth 1981, Wakkinen et al. 1992, Coates et al. 2013) and is influenced by habitat quality (Autenrieth 1981). Therefore, spatial scales of which sage-grouse are associated with lek sites may help explain evidence for linear form and not one of which the effect weakens rapidly with distance from lek.

The co-occurrences of ravens and cattle and of ravens and breeding sage-grouse lead to important questions regarding the presence of cattle in sage-grouse breeding areas. Leks of other grouse sometimes are located near livestock handling or watering areas (Haukos and Smith 1999) and some evidence suggests that sage-grouse establish leks in livestock salting areas (Beck and Mitchell 2000). In our study, however, an *a posteriori* test for correlation between presence of cattle and presence of sage-grouse leks does not support the idea that cattle and leks intrinsically co-occurred. For example, we found that points where cattle were present did not differ in distance to leks (4.97 km, 95% CI 4.47–5.46) than those points where cattle were absent (4.65 km,

95% CI 4.28–5.02). In other words, our data are consistent with ravens selecting areas near cattle and areas near sage-grouse leks independently. However, ravens were most likely to occur at sites that were close to leks with livestock in the area.

Evidence for the effects of anthropogenic subsidies on raven occurrence in this study was not as strong as evidence recently reported elsewhere (Bui et al. 2010, Coates et al. 2014, Howe et al. 2014). One explanation for this inconsistency is the inherent differences between anthropogenic subsidies across these studies. For example, the most common anthropogenic features observed at survey sites were relatively small vertical poles for fencing livestock and wooden poles for energy or telephone transmission lines. Studies that have identified substantial effects of anthropogenic structures have included much higher voltage transmission lines, communication towers, and facilities (Bui et al. 2010, Coates et al. 2014, Howe et al. 2014). These vertical structures provide valuable perching and nesting substrate (Knight and Kawashima 1993) in areas where natural substrates (e.g., tall trees) are otherwise rare. In this study, vertical poles were observed at 29.8% of all sample sites, and at 40.0% of sites where anthropogenic subsidies were present. However, it is important to consider that at 69.8% of sites where vertical poles were observed, other subsidies were also present. Nevertheless, these findings still contribute to a growing body of work demonstrating that ravens are attracted to anthropogenic structures in environments to some degree regardless of type (Engel and Young 1992, Knight and Kawashima 1993, Bui et al. 2010).

Our results indicate that ravens select cropland, and we routinely observed groups of ravens perched on irrigation water pivots within irrigated agricultural fields. These areas likely provide food and water sources beneficial to nonbreeding, transient groups of ravens. Data from southwestern Idaho suggest that agriculture fields, particularly cereal grains, are a primary food source for ravens and presence of these subsidies support increased raven populations (Engel and Young 1989, 1992). Alfalfa and other seeded crops can attract insects and rodents (Martin et al. 1961), important food sources for ravens (Stiehl 1978, Engel and Young 1989, Boarman and

Heinrich 1999). Also, cultivation acts to fragment sagebrush stands, and ravens select areas with increased edge (Coates et al. 2014, Howe et al. 2014). In Washington, nest predation by corvids was greatest in shrub-steppe communities that were fragmented (Vander Haegen et al. 2002). Furthermore, shrub canopy cover usually is reduced near edges of sagebrush cover types and ravens are most efficient at finding sage-grouse nests where sage-grouse overhead cover is low (Coates and Delehanty 2010). This is likely because ravens use visual cues to locate their prey and decreased overhead cover diminishes the capacity for sage-grouse to conceal their nests and to incubate cryptically (Coates et al. 2008).

For sage-grouse, nest survival decreases as a function of increased raven numbers (Bui et al. 2010, Coates and Delehanty 2010, Dinkins 2013). Unnaturally, high numbers of ravens resulting from anthropogenic subsidies that support groups of nonbreeding ravens, such as rich food and water resources associated with cropland, may cause spillover predation (Schneider 2001, Kristan and Boarman 2003). Regarding ravens and sage-grouse, spillover predation would occur when ravens move from subsidized areas supporting high raven densities into adjacent “natural” areas and cause inflated sage-grouse nest predation rates. In addition, some authors have expressed concern that anthropogenic resource subsidies can increase opportunity for territory establishment by ravens and lead to a hyperpredation effect (Kristan and Boarman 2003). In the case of hyperpredation, subsidies result in ravens nesting where they otherwise would not, leading to increased predation rates as ravens breeding in these locations seek to feed themselves and their young. The relative importance of these two types of subsidy driven amplifiers of predation by ravens on sage-grouse nests remains unclear and merits investigation.

We also found that ravens select wet meadows and relatively low elevations while avoiding topographically diverse areas and forested habitats. Although wet meadows in our study usually consisted of mesic sites located in topographically low areas and generally did not contain large trees, wet meadow areas were not correlated with those with low roughness indices. Nevertheless, ravens may be selecting wet meadows because they are rich food sources for insects, rodents,

and many other animals, including sage-grouse broods (Connelly et al. 2004, Casazza et al. 2011). Some wet meadows in this study were adjacent to agricultural lands and it is likely that conversion into agriculture occurred in these areas because wet meadows create soils amenable to cultivation (Galatowitsch et al. 2000). We also found some evidence for selection of areas dominated by big sagebrush communities (Appendix A), consistent with the propensity of ravens to occupy areas near breeding sage-grouse (Patterson 1952). As visually-cued predators, ravens may select lower elevations and uniform terrain because rough, broken terrain may hinder hunting efficiency. If true, this may also explain why ravens in our study area avoided forested areas, as has been observed previously (Dorn 1972, Howe et al. 2014).

The effects of cattle, agriculture, and other anthropogenic subsidies on raven occurrence within a sagebrush ecosystem are of interest to wildlife and land managers concerned with sage-grouse and other species vulnerable to predation by ravens. However, one limitation of our investigation is that these findings pertain to our study area which encompasses a patchwork of sagebrush steppe habitat interspersed with multiple land-use practices such as homesteads, integrated ranching operations, agricultural production, and recreational activities. The effects of cattle on raven occurrence may vary among sagebrush steppe ecosystems. Further study is needed to understand if more remote environments where open-range livestock grazing occurs far from other anthropogenic influences are consistent with these findings. In addition, the effects of cattle might be inherently different between breeding and nonbreeding ravens. Our survey method did not differentiate ravens by breeding status, but it is plausible that nonbreeding ravens are more likely to be directly associated with cattle to obtain food and water resources because of their transient nature, whereas breeding ravens forage in established territories and often forage within 570 m of their nest site (Boarman and Heinrich 1999, Howe et al. 2014). However, this does not preclude indirect effects of cattle or associated land use designed to benefit cattle on territorial distribution of ravens. For example, territory establishment and nest site selection may be influenced by permanent resource subsidies, like

water troughs, placed in the environment to improve conditions for cattle.

Raven population numbers have grown rapidly in recent decades across the western United States (Sauer et al. 2008) and further increases in raven abundance in sagebrush steppe habitats likely will further diminish reproduction by prey species of conservation concern, such as sage-grouse. Recognition of these dynamics opens the way for designing countervailing management practices. Although lethal raven control can result in reduced raven abundance for short time periods and in the immediate area of treatment (Coates et al. 2007, Dinkins 2013), long-term raven suppression through lethal control has not been demonstrated (Hagen 2011). Management actions aimed at reducing anthropogenic resource subsidies likely will be most effective at reducing raven densities for longer time periods, maintaining raven numbers at “natural” levels, and avoiding unnaturally elevated predation by ravens. For example, land and wildlife managers could consider reducing fragmentation of previously contiguous sagebrush stands through sagebrush restoration and reducing raven access to anthropogenic food and water resources like water troughs, road kills, livestock carcass dumps, and municipal dumps as feasible long-term conservation actions.

These findings may help to inform the difficult decisions faced by land managers regarding stipulations associated with livestock grazing on public land in areas occupied by sage-grouse such as the timing or location of grazing or the placement of water sources for livestock that may also benefit ravens in arid sagebrush steppe environments. Though controversial, our findings suggest that limiting livestock around sage-grouse leks during sage-grouse nesting and brood-rearing periods would reduce the exposure of breeding sage-grouse to predatory ravens, and likely aid sage-grouse reproduction. Managers also might carefully consider placement of livestock water sources to avoid areas around sage-grouse leks.

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