



RESEARCH ARTICLE

Landscape alterations influence differential habitat use of nesting buteos and ravens within sagebrush ecosystem: Implications for transmission line development

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ABSTRACT

A goal in avian ecology is to understand factors that influence differences in nesting habitat and distribution among species, especially within changing landscapes. Over the past 2 decades, humans have altered sagebrush ecosystems as a result of expansion in energy production and transmission. Our primary study objective was to identify differences in the use of landscape characteristics and natural and anthropogenic features by nesting Common Ravens (*Corvus corax*) and 3 species of buteo (Swainson's Hawk [*Buteo swainsoni*], Red-tailed Hawk [*B. jamaicensis*], and Ferruginous Hawk [*B. regalis*]) within a sagebrush ecosystem in southeastern Idaho. During 2007–2009, we measured multiple environmental factors associated with 212 nest sites using data collected remotely and in the field. We then developed multinomial models to predict nesting probabilities by each species and predictive response curves based on model-averaged estimates. We found differences among species related to nesting substrate (natural vs. anthropogenic), agriculture, native grassland, and edge (interface of 2 cover types). Most important, ravens had a higher probability of nesting on anthropogenic features (0.80) than the other 3 species (<0.10), and the probability of nesting near agriculture was greatest for ravens (0.55) followed by Swainson's Hawk (0.28). We also describe changes in nesting densities over 4 decades at this site as related to natural and anthropogenic disturbances. Since the 1970s, the composition of the raptor and raven nesting community has drastically changed with anthropogenic alterations and loss of continuous stands of sagebrush (*Artemisia* spp.), favoring increased numbers of nesting ravens and fewer nesting Ferruginous Hawks. Our results indicate that habitat alterations, fragmentation, and forthcoming disturbances anticipated with continued energy development in sagebrush steppe ecosystems can lead to predictable changes in raptor and raven communities.

Keywords: anthropogenic, *Buteo*, energy development, Ferruginous Hawk, Red-tailed Hawk, raven, sagebrush, Swainson's Hawk, transmission line

Las alteraciones del paisaje en un ecosistema de *Artemisia* afectan el uso del hábitat en buteos y cuervos: Implicaciones para el desarrollo de líneas de transmisión

RESUMEN

Una meta en ecología de aves es entender los factores que promueven diferencias en el hábitat de anidación y en la distribución entre especies, especialmente en paisajes cambiantes. Durante las últimas dos décadas, los humanos han alterado los ecosistemas de *Artemisia* como resultado de la expansión en la producción y transmisión de energía. Nuestro principal objetivo fue identificar diferencias en el uso de las características del paisaje y de rasgos naturales y antropogénicos en individuos anidantes de *Corvus corax*, *Buteo swainsoni*, *B. jamaicensis*, y *B. regalis* en un ecosistema de *Artemisia* en el sureste de Idaho. Entre 2007 y 2009 medimos múltiples factores ambientales asociados con 212 sitios de anidación, usando datos recolectados remotamente y en el campo. Luego, desarrollamos modelos multinomiales para predecir la probabilidad de anidamiento de cada especie, y desarrollamos curvas predictivas de respuesta basados en los estimados promedio de los modelos. Encontramos diferencias entre especies relacionadas con el sustrato de anidación (natural vs. antropogénico) y la presencia de zonas agrícolas, pastizales nativos y bordes (interfaz entre dos tipos de cobertura). De máxima importancia fue que *C. corax* tuvo una mayor probabilidad de anidar en ambientes con características antropogénicas (0.80) que las otras tres especies (<0.10) y la probabilidad de anidar cerca de zonas agrícolas fue mayor para *C. corax* (0.55), seguido de *B. swainsoni* (0.28). También describimos cambios en la densidad de anidación durante cuatro décadas relacionados con disturbios naturales y antropogénicos en este sitio. Desde 1970, la composición de las comunidades anidantes de cuervos y aves rapaces ha cambiado drásticamente con las alteraciones humanas y la pérdida de parches continuos de *Artemisia*, lo que favorece el

incremento en el número de *C. corax* anidantes y la disminución del número de *B. regalis*. Nuestros resultados indican que las alteraciones del hábitat, la fragmentación y los disturbios futuros que se anticipan con el desarrollo continuo de la industria energética en los ecosistemas de *Artemisia* pueden conducir a cambios predecibles en las comunidades de cuervos y de aves rapaces.

Palabras clave: antropogénico, *Artemisia*, *Buteo*, *Buteo jamaicensis*, *Buteo regalis*, *Buteo swainsoni*, cuervo, industria energética, línea de transmisión

INTRODUCTION

The sagebrush steppe of the western United States has been altered substantially since European settlement. Agriculture, urbanization, infrastructure placement, and energy development have fragmented sagebrush ecosystems (Leu et al. 2008), diverted water, and diminished many wildlife populations. This transformation is ongoing and may accelerate with technological advances in the production and transportation of energy from fossil fuels, wind, solar, and geothermal sources in the western United States. One result of energy development is the placement of major energy transmission structures, including transmission “highways” consisting of high capacity electrical transmission lines that extend for hundreds of kilometers through sagebrush steppe, bisecting remaining tracts of intact sagebrush habitat.

Responses of predatory species to anthropogenic disturbance have been investigated (Rogers 1987, Crooks and Soulé 1999, Beckmann and Berger 2003, Prange et al. 2004, Quinn and Whisson 2005), including the response of raptors and Common Ravens (*Corvus corax*; hereinafter, raven) to transmission lines (Engel et al. 1992, Knight and Kawashima 1993, Steenhof et al. 1993, Howe et al. 2014). Transmission towers and poles often provide high-quality perching and nesting substrate in areas where natural perching and nesting substrates such as trees and cliff faces are otherwise rare. In the past, avian use of transmission towers sometimes was viewed as a beneficial outcome for wildlife, and utility companies were encouraged to enhance nesting opportunities for raptors by providing nesting platforms and tower fortifications (Knight and Kawashima 1993, Steenhof et al. 1993). Now, it seems that although transmission tower placement benefits raptors and ravens, predation risk for prey species increases as well, a potentially deleterious outcome for sagebrush steppe species previously isolated from high predation risk.

Raptors and ravens opportunistically select a wide variety of prey (Smith and Murphy 1973, Jaksić and Braker 1983, Heinrich 1989). One prey species of particular concern in sagebrush ecosystems is the Greater Sage-Grouse (*Centrocercus urophasianus*; hereinafter, sage-grouse). Raptors prey on sage-grouse (Hartzler 1974, Schroeder et al. 1999, Fletcher et al. 2003), and ravens prey on sage-grouse eggs and young (Coates et al.

2008, Lockyer et al. 2013). The use of perch deterrents now has been suggested to reduce raptor and raven use of transmission towers, thereby reducing indirect effects of transmission towers on the incidence of predation (Lammers and Collopy 2007, Prather and Messmer 2010, Slater and Smith 2010).

Although one investigation found that ravens were more prolific colonizers of new transmission structures than raptors (Steenhof et al. 1993), the propensity for raptors vs. ravens to nest on transmission towers is relatively undifferentiated in the literature. Many raptorial species avoid areas of human activity when selecting nest sites, however, and anthropogenic developments may act to reduce use of an area by some raptors (Newton 1979, Lehman et al. 1999). Raptors generally occur at relatively low densities and often range over large, sometimes remote areas (Newton 1979), likely rendering some raptorial species sensitive to anthropogenic environmental alterations (Newton 1979).

Conversely, some large predatory bird species tolerate human activity (Bird et al. 1996, Berry et al. 1998) and are even favored (Palomino and Carrascal 2007). For example, anthropogenically altered landscapes often subsidize raven populations by providing food and water resources (Heinrich 1989, Kristan et al. 2004, Boarman et al. 2006) and increasing population vital rates and recruitment (Kristan et al. 2004, Webb et al. 2004, Marzluff and Neatherlin 2006). At the Idaho National Laboratory (INL) and surrounding areas, raven numbers have increased 11-fold between 1985 and 2009 based on breeding bird surveys (D. Halford Gonzales-Stoller Surveillance, Idaho Falls, Idaho, USA, personal communication). A recent study on nest site selection of ravens at INL (Howe et al. 2014) indicated that ravens benefit from additive effects of anthropogenic structures and habitat fragmentation largely as a result of wildfires. Specifically, ravens selected nest sites closer to transmission lines than expected, and nests were located in areas with increased edge density and multiple edge types (Howe et al. 2014).

Given the recent influx of ravens within INL and other sagebrush ecosystems, we expanded on the Howe et al. (2014) study and investigated differences in the effects of landscape alterations on nesting ravens and other large nesting avian predators. Sympatric breeding buteos have been found to spatially partition nesting habitat (Schmutz et al. 1980, Bechard et al. 1990, McConnell et al. 2008);

therefore, we investigated how patterns of raven nesting differ from those of 3 buteos that occupy sagebrush ecosystems: Swainson's Hawk (*Buteo swainsoni*), Red-tailed Hawk (*B. jamaicensis*), and Ferruginous Hawk (*B. regalis*). For ravens and these buteo species, resource use is centered on nest sites during the breeding season. Our primary objective was to identify differences in use of natural and anthropogenic features between nesting ravens and buteo species. We were particularly interested in the use of nesting substrates and spatial attributes at multiple scales of dominant vegetation characteristics around nest sites, proximity of nests to vegetation edges, topography, and associations with other anthropogenic-related factors. With the exception of topography, these features currently are in flux in sagebrush ecosystems as a result of human activities.

We then qualitatively described changes in the composition of the buteo and raven nesting community, anthropogenic features, and vegetation communities at our study site. Differences in composition of avian species were based on our data compared with those reported in previous studies of raven and raptors conducted both entirely on and immediately adjacent to the INL from 1974 to 1993 (Craig 1979, Craig et al. 1984, Hansen 1994, Hansen and Flake 1995). The comparison in anthropogenic features and vegetation communities over time was possible largely because of extensive mapping and surveys at this site (McBride et al. 1978, Anderson 1986, Anderson and Inouye 1988, Bennett 1990, Foreman et al. 2010, 2013, Shive et al. 2011) using long-term vegetation (LTV) transects and permanent vegetation plots established in 1950 (Singlevich et al. 1951).

METHODS

Study Area

The study area is located in southeastern Idaho, USA (figure 1 in Howe et al. 2014) within and immediately adjacent to the INL. Encompassing more than 259,800 ha of cold desert, the INL and surrounding area represents one of the largest expanses of sagebrush steppe ecosystems remaining in the western United States. Public access has been restricted on most of the study site, and grazing by domestic livestock has been excluded within approximately half the area. The INL is bordered by public lands managed by the Bureau of Land Management and privately owned croplands (mainly irrigated alfalfa, cereal, and potato crops), as well as 3 small towns (U.S. Census Bureau 2010): Mud Lake (population = 297) to the north, Atomic City (population = 25) to the south, and Howe (population = 330) to the west. More than 269 vertebrate species and 400 species of plants have been documented on the site.

The study area also provides habitat to sagebrush-obligate species such as sage-grouse and pygmy rabbits

(*Brachylagus idahoensis*), as well as important nesting and wintering habitat for 12 raptorial species. The study area has been subject to differing degrees of anthropogenic alterations since the 1950s, including the development of nuclear research facilities, roads, communication and energy transmission towers and lines, and diversions of water away from the study area.

Although ~94% of the study area is undeveloped, the increase in anthropogenic disturbance on the study area is similar to trends in land-use practices across sagebrush steppe ecosystems in the western United States. Development includes multiple nuclear research facilities and related structures, houses and structures related to agriculture and livestock operations, a highway rest area, ~230 km of paved roads, and 297 km of electricity transmission and distribution lines. Over the past few decades, the INL has experienced an increase in the total extent of disturbed soil outside of facilities, the use of remote areas beyond facilities, and vegetation damage from livestock operations and off-road travel in grazing allotments (Forman et al. 2013).

Topography, climate, and vegetation communities for the study area have been previously described (Howe et al. 2014, Shive et al. 2011). Surface water diversion away from the study area began in 1965 through a series of artificial structures (Bennett 1990). Generally, historical native riparian plant communities consisting of willows (*Salix* spp.), wild rose (*Rosa* spp.), western water birch (*Betula occidentalis*), and large narrow-leaf cottonwood trees (*Populus angustifolia*) have not persisted (Rood et al. 2003), although remnant patches remain.

From 1994 through 2009, 103 wildfires have occurred on the study site, of which 77% were human-caused (Shive et al. 2011). Several large wildfires have altered the composition of vegetation communities across ~38% of the study area (Forman et al. 2013). Post-fire communities were characterized by resprouting shrubs (e.g., green rabbitbrush [*Chrysothamnus viscidiflorus*]), native perennial grasses, and forbs; however, some burned areas were colonized by nonnative species, including cheatgrass (*Bromus tectorum*). In addition, military ordnance impact scars and some burned areas were seeded with crested wheatgrass (*Agropyron cristatum*) during the 1950s and 1960s (McBride et al. 1978). Land managers have also conducted "green-stripping" practices by seeding roadsides with crested wheatgrass to minimize the spread of wildfire. These practices seem to have resulted in substantial encroachment of crested wheatgrass into adjacent shrub communities (Roger Blew, Gonzales-Stoller Surveillance LLC, Idaho Falls, ID, personal communication). Furthermore, results of LTV measurements indicated that the mean cover of crested wheatgrass, which was not planted on the LTV plots, steadily increased in native sagebrush steppe plant communities

in the absence of disturbances at a localized scale (Forman et al. 2010, 2013).

Historically, nearly 75% of the study area was dominated by big sagebrush (*Artemisia tridentata*; McBride et al. 1978), but currently only ~50% of the study area is classified as communities with a big sagebrush canopy (Shive et al. 2011). Although much of the loss of big sagebrush cover over the past few decades can be directly attributed to wildfire, LTV data indicate that some of this decline has not been the result of wildfire. Decreases in sagebrush and perennial grass cover were first documented by Anderson (1986). Continued decreases were reported again by Anderson and Inouye (1988) as well as an increase in the distribution of cheatgrass since the inception of the LTV study. Long-term trend analyses indicate that between 1975 and 2006, average big sagebrush ground cover on the unburned, core LTV plots declined from >20% to <10%, and the distribution of introduced annual forbs has increased considerably (Forman et al. 2010). Together, these anthropogenic and natural disturbances have led to some areas with increased vegetation edge consisting of the interface of 2 plant community types.

Nest Surveys

We located buteo and raven nests from April to July 2007–2009 across the study area by systematically searching all potential nesting substrates present on both the INL and adjacent lands within 4 km of the INL boundary. These substrates included buttes, cliffs and rock-outcrops, lava-tube caves, lone or small groups of juniper trees (*Juniperus osteosperma*), standing live or dead cottonwood trees, ornamental trees, and all areas of juniper woodland and juniper shrubland, as well as transmission and distribution lines, cell towers, cooling towers, weather towers, billboards, nest platforms, facilities, silos, irrigation pivots, and other structures associated with agriculture. Our nest sampling strategies were similar to the ground survey techniques previously used at the site (Craig 1979, Craig et al. 1984, Hansen 1994, Hansen and Flake 1995).

To ensure that all nests were detected within the study area, we supplemented the nest searches with extensive random point surveys aimed at observing territorial and courtship behaviors of the 4 focal species. Point survey methods, sample size, identification of occupied nest sites, and nest monitoring for buteos followed exactly those methods described for ravens in Howe et al. (2014). Although some nests were possibly undetected, we are confident that we located all nests of the 4 species during our study years, with the caveat that survey access within the perimeter of certain research facilities and firing ranges (representing a small area) was not allowed.

We used a geographical information system (GIS; ArcGIS 9.3, ESRI Redlands, CA) to map nest locations of

each species. We calculated nest densities for each species for each study year as the number of nests per total study area, a sufficient calculation assuming that we located essentially all nests within the study area each year. We also calculated the nearest neighbor distances between nests of the same species to assess adjacency of nests using a nearest neighbor distance analysis (Hawth's Analysis Tool; Beyer 2004). Reported values represent means \pm standard deviation (SD), unless otherwise noted.

Field Variables

We classified each nest (including new nests rebuilt at a location that was previously used) into 2 nest substrate categories: natural and anthropogenic. The natural category consisted of trees (juniper, cottonwood, willow, and planted ornamental trees) and rock (basalt outcrops, craters, lava-tube caves, and gravel and cinder excavation pit walls). The anthropogenic category consisted of platforms (artificial nesting platforms and nest boxes), electrical transmission towers (transmission and distribution line towers), and other towers (cell and other communication towers, weather instrument towers, cooling towers, and silos). These categories were used to develop a factor variable to estimate differential habitat use of anthropogenic subsidies between the focal species.

GIS Variables

We delineated land cover types using the GIS method described in Howe et al. (2014). For the modeling analyses, we condensed the 27 multispecies complexes into 4 landscape-level land cover types based on the dominant overstory cover and classified them as follows: sagebrush (Wyoming big sagebrush [*Artemisia tridentata wyomingensis*], basin big sagebrush [*A. t. tridentata*], little sagebrush [*A. arbuscula*], black sagebrush [*A. nova*], and three-tip sagebrush [*A. tripartita*]; non-sagebrush shrubland (green rabbitbrush, shadscale saltbush [*Atriplex confertifolia*], and spiny hopsage [*Grayia spinosa*]); grassland (native perennial grasses); and exotic (nonnative grasses and forbs). The remaining area (3.3%) consisted of land cover types that were relatively uncommon and thus not included in the analysis.

We evaluated landscape variables affecting nests at 3 spatial scales based on values derived from literature on home range or territory sizes for the 4 focal species. For our purposes, measurements conducted at the same spatial scale were required to compare use of land cover across nesting species, so separate scales were not used for each species. Instead, we selected 3 spatial scales relevant to the 4 focal species. Specifically, we calculated the mean of the reported averages (Fitzner 1980, Janes 1984, McAnnis 1990, Boarman and Heinrich 1999) and upper home range sizes (Bruggers 1988, Babcock 1995, Leary et al. 1998, Smith et al. 2003) as radii (1.09 km and 4.09 km) for 2

TABLE 1. Means \pm SE of explanatory variables used in multinomial models of differential habitat use between ravens and hawks from data collected in xeric sagebrush ecosystem of southeastern Idaho, 2007–2009.

Abbr.	Description	Species ^a							
		CORA		FEHA		RTHA		SWHA	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
ALL ROAD	Distance to improved and paved road (km)	1.94	0.286	2.67	0.517	2.19	0.374	2.74	0.487
HYW	Distance to highway (km)	2.63	0.340	3.51	0.643	3.46	0.476	3.57	0.534
EDGE	Distance to edge (km)	0.31	0.036	0.52	0.151	0.18	0.044	0.40	0.077
FAC	Distance to facility (km)	6.17	0.461	7.68	0.708	5.12	0.733	5.49	0.604
ELEV	Elevation (km)	1.53	0.006	1.53	0.007	1.52	0.009	1.53	0.008
RUGGED	Topographical ruggedness index	0.03	0.004	0.05	0.005	0.03	0.006	0.04	0.005
SAGE70	Sagebrush shrubland at 71 ha scale (%)	57.75	3.944	72.53	5.689	58.51	6.336	53.85	6.494
SAGE373	Sagebrush shrubland at 373 ha scale (%)	44.96	3.541	46.28	6.479	56.45	5.728	30.82	5.224
SAGE5253	Sagebrush shrubland at 5253 ha scale (%)	47.81	3.132	47.61	5.829	57.75	4.173	34.94	4.078
SHRUB70	Non-sagebrush shrubland at 71 ha scale (%)	15.98	2.893	17.45	5.146	30.90	6.957	17.55	4.658
SHRUB373	Non-sagebrush shrubland at 373 ha scale (%)	16.93	2.562	17.74	3.995	24.33	5.080	13.59	3.313
SHRUB5253	Non-sagebrush shrubland at 5253 ha scale (%)	18.37	2.098	16.53	3.183	23.80	3.798	15.55	2.764
EXO70	Exotic grassland at 71 ha scale (%)	7.74	1.985	2.11	1.582	3.85	1.968	1.78	1.286
EXO373	Exotic grassland at 373 ha scale (%)	3.95	0.578	2.97	0.876	2.35	0.575	3.96	0.853
EXO5253	Exotic grassland at 5253 ha scale (%)	5.87	1.429	5.29	2.427	3.17	1.177	3.15	1.494
GRA70	Native grassland at 71 ha scale (%)	6.45	1.768	1.26	1.254	2.55	1.027	7.58	3.164
GRA373	Native grassland at 373 ha scale (%)	4.84	0.917	0.76	0.616	4.71	1.366	7.72	2.719
GRA5253	Native grassland at 5253 ha scale (%)	5.90	0.757	4.15	1.108	4.59	1.370	7.81	1.085
SUB	Anthropogenic substrate (%; e.g., power pole)	73.20	—	27.30	—	31.00	—	2.00	—
	Natural substrate (%; e.g., tree)	26.80	—	72.70	—	69.00	—	98.00	—
AGR	Agricultural area present within 6.6 km (%)	33.00	—	30.30	—	7.00	—	46.00	—
	Agricultural area not present within 6.6 km (%)	67.00	—	69.70	—	93.00	—	54.00	—

^a Species Abbreviations: CORA = Common Raven; FEHA = Ferruginous Hawk; RTHA = Red-tailed Hawk; SWHA = Swainson's Hawk

scales of interest and averaged the recommended spatial buffer area used in published raptor protection guidelines for each of the buteo species (52.5 km²; Richardson and Miller 1997, U.S. Fish and Wildlife Service 2008) for the third scale. This resulted in 3 spatial scales: 71 ha, 373 ha, and 5253 ha. We created circular buffers centered on nest sites at each of the 3 scales and then, for each scale, calculated the area of each land cover type within buffer areas.

We also calculated variables to evaluate the effects of edge and anthropogenic features in relation to nest sites. To estimate the effects of proximity to edge, we calculated Euclidean distance (Conner et al. 2003) from each nest to the nearest interface between 2 land cover types by using the distance mapping tool in ArcGIS Spatial Analysis extension. We also calculated Euclidean distances between the nest and closest anthropogenic features, including paved road and facility. Our study site consisted of areas with agricultural activity, and because some species may include these areas within their nesting home range, we also measured the presence or absence of agricultural areas within a 6.6 km radius of each nest, which reflects the largest reported home range in the literature among the 4 study species (Leary et al. 1998).

In addition, we evaluated topography by including elevation (U.S. Geological Survey 2009) and a ruggedness

index (Riley et al. 1999), a measure of the topographical heterogeneity obtained by representing variation associated with changing elevation, calculated using the Geomorphometry and Gradient Metric Toolbox (ArcGIS 10.1, ESRI 2012, Redlands, CA).

Model Development

To estimate differential nest site use, we developed multinomial logistic models (Hosmer et al. 2013, Hosmer and Lemeshow 2000). The advantage of using multinomial outcomes was to allow >2 discrete outcomes and to predict the probabilities of categorically distributed dependent variables (i.e. species of nesting bird), given the set of independent variables (derived from field and GIS measurements). Specifically, we modeled the nominal response outcome of species of nesting bird as a function of multiple anthropogenic factors and environmental characteristics (covariates described in Table 1).

We carried out model comparisons in 2 steps. In step I, we evaluated evidence of factors by comparing performance among models that shared an overarching environmental theme but that used different factors within that theme, thus forming a set of candidate models. Each set of models consisted of 2–5 models and also included a simple null model that fitted the γ -intercept only for comparison with models that contained environ-

mental factors. For example, when we evaluated differences between spatial scales for a land cover type, the candidate model set consisted of 3 models, and each model consisted of the same land cover covariate (e.g., Exotic) at each of the 3 spatial scales. We sought the best (most supported) model that also was better supported than the null model. We evaluated evidence of support for models within each candidate set using Akaike's information criterion (AIC) with second-order bias correction (AIC_c; Anderson 2008). We evaluated uncertainty among models using AIC_c differences (ΔAIC_c). We also calculated model probabilities ($w_{\text{model } i}$; Anderson 2008) and evidence ratios ($\text{ER} = w_{\text{model } i}/w_{\text{model } j}$) and compared models among the set (Anderson 2008). Likelihood ratio tests (LRT) were used to evaluate each model fit relative to a null model ($\alpha = 0.05$).

In step II, we developed models using covariates from the most supported models in step I. These covariates satisfied 2 criteria: (1) they came from a model that fit the data significantly better than the null model based on LRT; and (2) ΔAIC_c was ≤ 2 within the candidate model set (Burnham and Anderson 1998). Because we used covariates from the most parsimonious models in step I, numerous additive effects were possible in step II. We therefore developed models with different combinations of covariates while not allowing >3 covariates in any model to avoid over-parameterizing any given model.

Although step II was exploratory, the factors being explored were based on objective a priori hypotheses from the literature. The purpose of step II was to better understand the relative ability of different variables to explain nest site selection among species. For each model in step II, we calculated ΔAIC_c , w , and ER. We also report a 95% confidence set of models identified by summing the top model probabilities (w), representing a cumulative probability (Cw), until 95% was reached. We then averaged parameter estimates (β) across all models within the 95% confidence set. The intent of this model analysis was not to identify a single "best" model, but rather to assess evidence for explanatory factors (a priori hypotheses) and to estimate average effects for each seemingly explanatory covariate (β) across the most parsimonious models.

Evidence for each factor included calculation of a variable likelihood (Anderson 2008), which consisted of summing w for all the models that included the variable of interest across the entire model set. This calculation was deemed appropriate because each variable was equally represented in the model set (Anderson 2008). To interpret effects of anthropogenic and land cover characteristics on the probabilities of nesting differences between species for each covariate, we calculated the exponent of the model-averaged β values.

Model Assumptions

Several assumptions were embedded into developing and interpreting the multinomial logistic models. (1) We assumed our data to be case-specific, meaning each model covariate (predictor) had a single value for each case (i.e. species of nesting bird; response), an assumption we met because all nests consisted of only one value for each covariate. Additionally, no values for any covariate were missing from the dataset. (2) We assumed that the observation-to-variable ratio was large enough for reliable parameter estimates, an assumption we likely met because no single model consisted of >3 covariates, resulting in observation-to-variable ratio of 69.9:1, substantially exceeding the recommended 10:1 (Hosmer and Lemeshow 2000) and 20:1 ratios (Peduzzi et al. 1996). (3) We assumed that the observations were independent; in other words, a choice of nesting location by one bird did not influence the choice of another bird. We recognize territoriality among the study species, but here we assumed, for example, that the selection of a tree by one individual did not influence the selection of another individual. (4) We assumed that the explanatory variables were measured with minimal or no error, a reasonable assumption based on the level of detail and high prediction accuracy of the land cover map (Shive et al. 2011) used to measure the explanatory variables. (5) We assumed that the explanatory variables within any one model were not a linear combination of each other; that is, we assumed negligible or no multicollinearity among variables. We sought to meet this assumption by excluding 1 of any 2 variables that were correlated ($r \geq |0.65|$) and those with variance inflation factors ≥ 10 (Menard 1995). (6) We assumed that the nests sampled from our study site are representative of the region because this study area presented buteos and ravens with ecological stressors similar to those occurring throughout sagebrush steppe ecosystems. (7) We assumed that the environmental characteristics available for use by buteos and ravens for nesting were constant over the study period, an assumption supported by imagery and mapping procedures (Shive et al. 2011) being conducted during the same 3 years of our study. Because multinomial logistic models predict the probability of a dependent categorical variable, assumptions of normality, linearity, and homogeneity of variance of the independent variable were relaxed.

Model Validation

To assess model predictions, we used each of the top models from the 95% confidence set to derive the most likely categorical outcome given the values from the explanatory field and GIS variables. The category with the greatest probability was chosen as the expected (predicted) outcome. We then calculated a Cohen's Kappa coefficient (κ) for each model using observed (actual) and expected outcomes, a value that represents the agreement between

these outcomes and is a more robust measure than a simple percentage of agreement because κ takes into account the agreement occurring by chance. We considered κ values >0.75 as excellent, 0.40 – 0.75 as acceptable, and <0.40 as poor (Fleiss 1981).

RESULTS

We located 212 nests (Swainson's Hawk, $n = 51$; raven, $n = 97$; Ferruginous Hawk, $n = 34$; Red-tailed Hawk, $n = 30$) across 3 yr at the study site. Nests were located on a variety of anthropogenic structures, such as cell towers, nest platforms, transmission towers, silos, cooling towers, and weather towers. Nests also were located on rock ledges of cliffs and lava tubes, in native trees including cottonwood and juniper, as well as ornamental, nonnative trees. Average nest density within our study area was 0.03 nests km^{-2} (SD 0.01). Although density was highest in 2009 (0.03 nests km^{-2}), we did not find strong differences among years (2007, 0.02 nests km^{-2} ; 2008, 0.03 nests km^{-2}); therefore, we calculated averages for each species across years. Average raven nest density (0.27 nests 10 km^{-2} , SD 0.05) was substantially higher than any of the buteo species (Swainson's Hawk, 0.07 nests 10 km^{-2} (SD 0.01), Ferruginous Hawk, 0.04 nests 10 km^{-2} (SD 0.02); Red-tailed Hawk, 0.03 nests 10 km^{-2} (SD <0.01). For example, raven nest density was 3.9, 6.8, and 9.0 times greater than Swainson's, Ferruginous, and Red-tailed Hawk nest density, respectively. We also found that the average distance between raven nests (4.71 km, SD 2.53) was less than that for each of the 3 buteos (Ferruginous Hawk, 7.83 km, SD 7.14); Red-tailed Hawk, 9.02 km, SD 8.14 ; Swainson's Hawk, 5.65 km, SD 4.00).

Incidentally, we found nests of other raptor and corvid species as well. These included: Burrowing Owls (*Athene cunicularia*; $n = 14$), American Kestrels (*Falco sparverius*; $n = 3$), Long-eared Owls (*Asio otus*; $n = 2$), Great Horned Owls (*Bubo virginianus*; $n = 3$), Prairie Falcons (*Falco mexicanus*; $n = 6$), and Black-billed Magpies (*Pica hudsonia*; $n = 6$).

Modeling Differential Habitat Use

We found the data substantially supported 6 covariates based on comparisons of single variable models with the null: nest substrate, presence of agriculture, ruggedness, distance to edge, amount of sagebrush at the 5253 ha scale, and amount of grassland at the 373 ha scale (Table 2). These covariates were then carried forward into our additive models in step II.

Of the 41 models considered in step II, we found that 5 models could account for 95% of the Akaike's cumulative weight (C_w , Table 3). The most parsimonious model ($w_{\text{model } 1} = 0.80$; Table 3) among the 5 models consisted of nest substrate, presence of agriculture, and the percent of

grassland (373 ha scale) as covariates. The performance index of agreement between model predictions and field observations from this model were acceptable (Cohen's $\kappa = 0.47$). All 5 models in the 95% confidence set included nest substrate and presence of agriculture as additive effects. The second-best model with support from the data ($w_{\text{model } 2} = 0.05$; $\kappa = 0.46$; Table 3) included nest substrate, agriculture, and distance to edge as covariates but had considerably less support than the most parsimonious model. Including grassland (model 1) instead of edge (model 2) was 16 times more likely to fit the data, although both variables showed some level of support. The third model with support from the data consisted of the covariates substrate, agriculture, and ruggedness index ($w_{\text{model } 3} = 0.04$; $\kappa = 0.47$; Table 3). An alternative model (4) that consisted of only substrate and agriculture had less support from the data but was retained in the 95% cumulative set ($\kappa = 0.49$). In comparing the top 3 models to model 4, we found that including the additive effects of grassland (model 1) and edge (model 2) increased the model probability by 20.0 and 1.25 times, respectively, and including ruggedness (model 3) did not influence the model probability. We did not find support for sagebrush in a model that also consisted of substrate and agriculture ($w_{\text{model } 5} = 0.03$).

We found the nest substrate measured in the field was the strongest covariate in our analysis and had a variable likelihood value of 0.99. This factor was more influential than any single GIS-derived covariate. Ravens most often nested on anthropogenic structures (73.2% of nests, $n = 71$), which was not the case for the buteos (2–31%; Table 1). The most common anthropogenic substrate for ravens was electrical transmission tower (53.0%, $n = 51$), followed by cooling towers, single radio-communication and cell towers (16.5%, $n = 16$), and nesting platforms (4.1%, $n = 4$). Natural nesting substrates for ravens included rock ledges (6.2%, $n = 6$) and a variety of native and cultivated trees (20.6%, $n = 20$). Although Red-tailed Hawks nested in both anthropogenic and natural substrate, their nests often were located in cottonwood trees (60.0%, $n = 18$) surrounded by sagebrush-dominated communities, followed by electrical transmission towers (26.7%, $n = 8$), junipers (10.0%, $n = 3$), and nesting platforms (3.3%, $n = 1$). Swainson's Hawks mostly nested in trees (98.0%, $n = 50$), with juniper most common (72.0%, $n = 36$), followed by ornamental trees (17.6%, $n = 9$), cottonwoods (9.8%, $n = 5$) and nesting platform (2.0%, $n = 1$). Ferruginous Hawks also nested primarily in trees. Most Ferruginous Hawk nests were in junipers (69.7%, $n = 23$), but one was in a cottonwood and another in an ornamental tree. Ferruginous Hawks also nested on platforms (14.7%, $n = 5$) and electrical transmission towers (11.8%, $n = 4$).

Using the model parameter estimates averaged across the model set of 95% C_w , the predicted probability of a raven nesting on an anthropogenic feature was substan-

TABLE 2. Step I of a differential habitat use analysis between Common Raven, Ferruginous Hawk, Red-tailed Hawk, and Swainson's Hawk using multinomial models from data collected in xeric sagebrush ecosystem of southeastern Idaho, 2007–2009. K = number of parameters; LL = log-likelihood; ΔAIC_c = difference between model of interest and most parsimonious model with second-order bias correction; w = model probability; and LRT = likelihood ratio test statistic (chi-square).

Model Set ^a	No.	Model ^b	K	LL	ΔAIC_c	w	LRT
Nest Substrate	1	SUB	6	-217.1	0.0	1.00	98.1*
		Intercept-only	3	-266.1	91.8	0	—
Anthropogenic	2	AGR	6	-258.2	0.0	0.99	15.8*
		FAC	6	-262.8	9.1	0.01	6.7
		Intercept-only	3	-266.1	9.5	0.01	—
Topographical	4	HYW	6	-264.3	12.1	0	3.7
		ALL ROAD	6	-264.5	12.6	0	3.2
		RUGGED	6	-261.2	0.0	0.83	9.81*
		Intercept-only	3	-266.1	3.5	0.14	—
		SLOPE	6	-265.4	8.4	0.01	1.36
Edge	8	ELEV	6	-265.5	8.6	0.01	1.17
		EDGE	6	-261.0	0.0	0.88	10.2*
Sagebrush Land Cover	9	Intercept-only	3	-266.1	3.9	0.12	—
		SAGE5253	6	-260.2	0.0	0.59	11.8*
		SAGE373	6	-260.7	1.0	0.35	10.8
Grassland Land Cover	10	Intercept-only	3	-266.1	5.5	0.04	—
		SAGE70	6	-263.6	6.7	0.02	5.1
		GRASS373	6	-259.8	0.0	0.89	12.6*
		Intercept-only	3	-266.1	6.3	0.04	—
Exotic Land Cover	13	GRASS5253	6	-263.0	6.3	0.04	6.3
		GRASS70	6	-263.1	6.6	0.03	6.0
		EXO70	6	-262.2	0.0	0.61	7.8
Shrubland Land Cover	16	Intercept-only	3	-266.1	1.5	0.29	—
		EXO373	6	-264.6	4.7	0.06	3.1
		EXO5253	6	-264.9	5.3	0.04	2.4
		Intercept-only	3	-266.1	0.0	0.52	—
Shrubland Land Cover	19	SHRUB70	6	-263.7	1.5	0.24	4.8
		SHRUB373	6	-264.4	2.9	0.12	3.4
		SHRUB5253	6	-264.4	2.9	0.12	3.4

^a Step I compared models within each candidate model set (total models, $n = 21$). Covariates of models that met 2 criteria ($\Delta AIC_c \leq 2$ and fit significantly better than null model, denoted by asterisks), were carried forward to step II.

^b Refer to Table 1 for model descriptions.

tially higher (probability = 0.80) than for the other 3 species (probabilities ranged from <0.01 to 0.10). The predicted probability of a nest belonging to a raven located on a natural feature was 0.23 (Figure 1), which was similar to Red-tailed Hawk (probability = 0.21) and Ferruginous

Hawk (probability = 0.18) but relatively much lower than that of Swainson's Hawk (probability = 0.38). Based on the averaged model β estimates, however, we found that a nest on anthropogenic substrate was nearly 100%, 89.4%, and 87.1% more likely to be a raven than that of a Swainson's

TABLE 3. Step II of a differential habitat use analysis between Common Raven, Ferruginous Hawk, Red-tailed Hawk, and Swainson's Hawk using multinomial models from data collected in xeric sagebrush ecosystem of southeastern Idaho, 2007–2009. K = number of parameters; LL = log-likelihood; ΔAIC_c = difference between model of interest and most parsimonious model with second-order bias correction; w = model probability; Cw = cumulative weight; ER = evidence ratio (e.g., $W_{\text{model 1}}/W_{\text{model 2}}$).

No.	Model ^a	K	LL	ΔAIC_c	w	Cw	ER
1	SUB + AGR + GRA373	12	-202.3	0.00	0.80	0.80	—
2	SUB + AGR + EDGE	12	-205.1	5.66	0.05	0.85	16.0
3	SUB + AGR + RUGGED	12	-205.2	5.78	0.04	0.89	20.0
4	SUB + AGR	9	-208.6	5.93	0.04	0.93	20.0
5	SUB + AGR + SAGE5253	12	-205.7	6.82	0.03	0.96	26.7

^a Top 5 models represent >95% cumulative weight of 41 candidate models. Abbreviations: SUB = nesting substrate (anthropogenic vs. natural); AGR = distance to agriculture; GRA373 = % grassland at the 373 ha scale; SAGE5253 = sagebrush steppe at the 5253 ha scale.

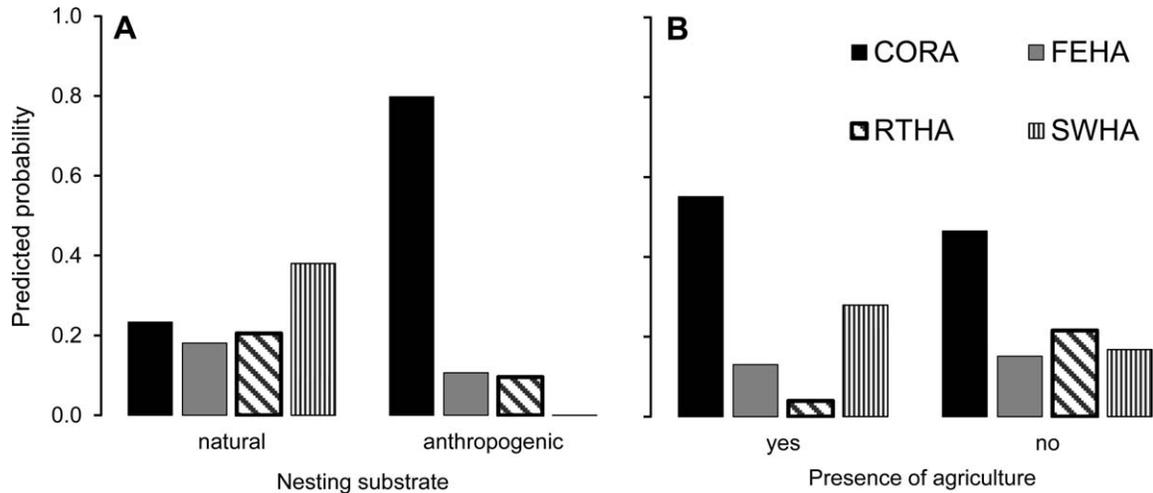


FIGURE 1. Predicted probabilities of nesting by Common Raven (CORA), Ferruginous Hawk (FEHA), Red-tailed Hawk (RTHA), and Swainson's Hawk (SWHA) based on (A) type of nesting substrate (natural or anthropogenic) and (B) presence of agriculture (yes or no). Data were collected in xeric sagebrush steppe environment of southeastern Idaho, 2007–2009.

Hawk, Red-tailed Hawk, and Ferruginous Hawk, respectively. The 95% CIs of the β estimates between ravens and Red-tailed Hawk and between ravens and Ferruginous Hawk did not overlap zero, indicating significant effects. Although we found the parameter estimate between ravens and Swainson's Hawk to be the relatively low ($\beta = -18.1$), indicating a strong relationship, the 95% CIs overlapped zero.

Of the GIS-derived covariates, the presence of an agricultural area within 6.6 km of nest locations was the most influential covariate, with a likelihood value of 0.96. Swainson's Hawks had a much greater percentage of nests within the spatial scale of 6.6 km of agriculture (46.0%) compared with other species (7.0–33.0%; Table 1). Based on model β estimates, however, the predicted probability for nesting within the 6.6 km spatial scale of agriculture was greatest for ravens (0.55) followed by Swainson's Hawks (0.28), and lowest for Red-tailed Hawks (0.04; Figure 1). Nests located near agriculture were predicted likely to be raven rather than Swainson's Hawk, even though Swainson's Hawks showed higher percentage of nests near agriculture due to the overall high number of ravens nests coupled with a relatively high proportion of ravens nesting near agricultural fields. In other words, our results account for the differences in numbers of nests between species. Nest sites near agriculture were 91.7%, 89.7%, and 83.6% more likely to be occupied by ravens, Swainson's Hawks, and Ferruginous Hawks, respectively, than Red-tailed Hawks. Although ravens and Swainson's Hawks were the most likely species to nest near agricultural areas, no substantial differences were found between these species and Ferruginous Hawks.

We calculated a likelihood value of 0.84 for the covariate of percentage of area dominated by grassland at the 373 ha

scale. Although we found Swainson's Hawks had a greater amount of grassland surrounding nest sites (7.7%, SD 2.7) compared with other species (0.8–4.8%), the only substantial difference was between Swainson's Hawks and Ferruginous Hawks (Table 1). Between those 2 species, the parameter estimate was moderately high ($\beta = 16.13$) with confidence intervals that did not overlap zero. The odds of a nest being that of a Swainson's Hawk were 100 times greater than it being a Ferruginous Hawk for every 1% increase in grassland at the 373 ha scale. The probability of raven and Red-tailed Hawk nests declined as grassland increased unless the nests for both species were located on anthropogenic substrate (Figure 2).

After accounting for additive effects, the variable likelihood for distance to edge was 0.06. Although Red-tailed Hawks were prone to nest within areas closer to edge (0.18 km, SD 0.04) compared with other species (0.31–0.52 km), we found the strongest difference to be between Red-tailed Hawks and Ferruginous Hawks (0.52 km, SD 0.15; Table 1). Based on averaged parameter estimates, we found the 95% CIs between Red-tailed Hawk and Ferruginous Hawk did not overlap zero. For every 1 km increase in distance away from the nearest edge, a nest was 83.8% less likely to belong to Red-tailed Hawk than Ferruginous Hawk. The 95% CI of estimates of differences between Red-tailed Hawk, Swainson's Hawk, and ravens, respectively, overlapped zero. Furthermore, raven nests were often relatively close to edges (0.31 km, SD 0.04), an effect that was pronounced where ravens nested on natural substrate (Figure 3). The parameter estimates overlapped zero between ravens and other species.

Although sagebrush cover was an influential variable in this analysis, sagebrush had the relatively low likelihood value of 0.06. We calculated a substantial difference

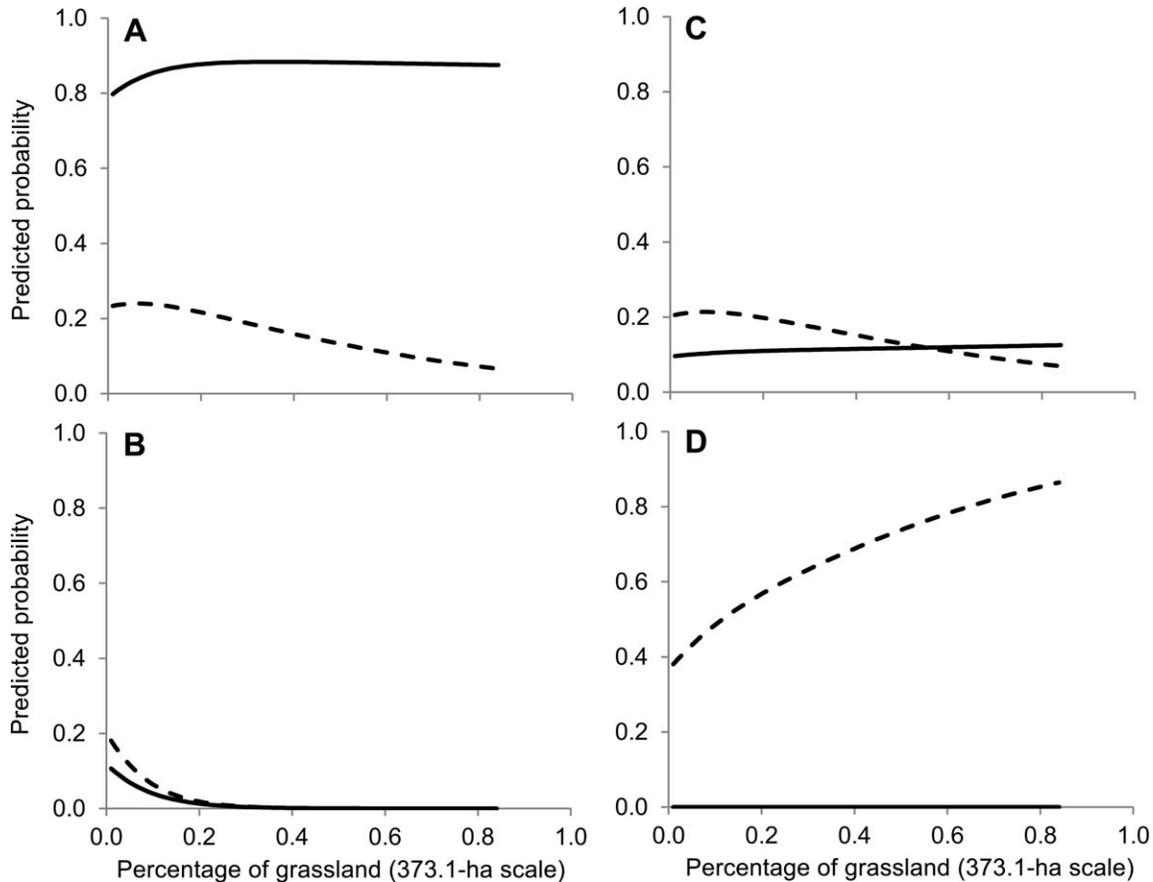


FIGURE 2. Predicted probability curves for nesting by (A) Common Raven (CORA), (B) Ferruginous Hawk (FEHA), (C) Red-tailed Hawk (RTHA), and (D) Swainson's Hawk (SWHA) based on grassland cover (%) at the 373 ha scale by nesting substrate type (anthropogenic = solid; natural = dashed). Data were collected in xeric sagebrush steppe environment of southeastern Idaho, 2007–2009. All predicted probabilities sum to 1 across all species for every given value of grassland (%).

between Swainson's Hawks (34.9%, SD 4.1) and other species (47.6–57.8%) for sagebrush. Numerically, the greatest difference occurred between Swainson's Hawk and Red-tailed Hawk (57.8%, SD 5.7; Table 1); however, all 95% CIs for the averaged parameter estimates between species overlapped zero, indicating a lack of variable evidence when considering additive effects. Ruggedness (likelihood value of 0.05) was the least important of those retained for step II. All 95% CIs for the averaged parameter estimates overlapped zero.

DISCUSSION

Our results provide strong evidence for differential use of anthropogenic features by 3 buteo species and ravens nesting in altered sagebrush steppe habitat. Similar to investigations conducted in other habitat types, our results also indicate that the 3 sympatric buteo species may spatially partition breeding territories according to differences in land cover (Schmutz et al. 1980, Bechard et al.

1990, McConnell et al. 2008). Four factors are associated with nest locations of buteos and ravens: (1) nest substrate, with ravens in particular showing high use of anthropogenic rather than natural nest substrate; (2) proximity to agriculture, with Swainson's Hawks and ravens nesting near agriculture; (3) amount of native grassland, with Swainson's Hawks associated with increased presence of native grassland; and (4) plant community edges, with Red-tailed Hawks nesting near habitat edges, unlike Ferruginous Hawks, which nest away from edges in native sagebrush communities.

Note that raven nest density is now substantially greater than buteo density and occurs in association with anthropogenic alteration of sagebrush habitat. This study informs land and resource management decisions in sagebrush steppe ecosystems by providing evidence of changes in species nesting patterns based on land use changes that can be used when predicting future scenarios related to the placement of energy infrastructure or other development.

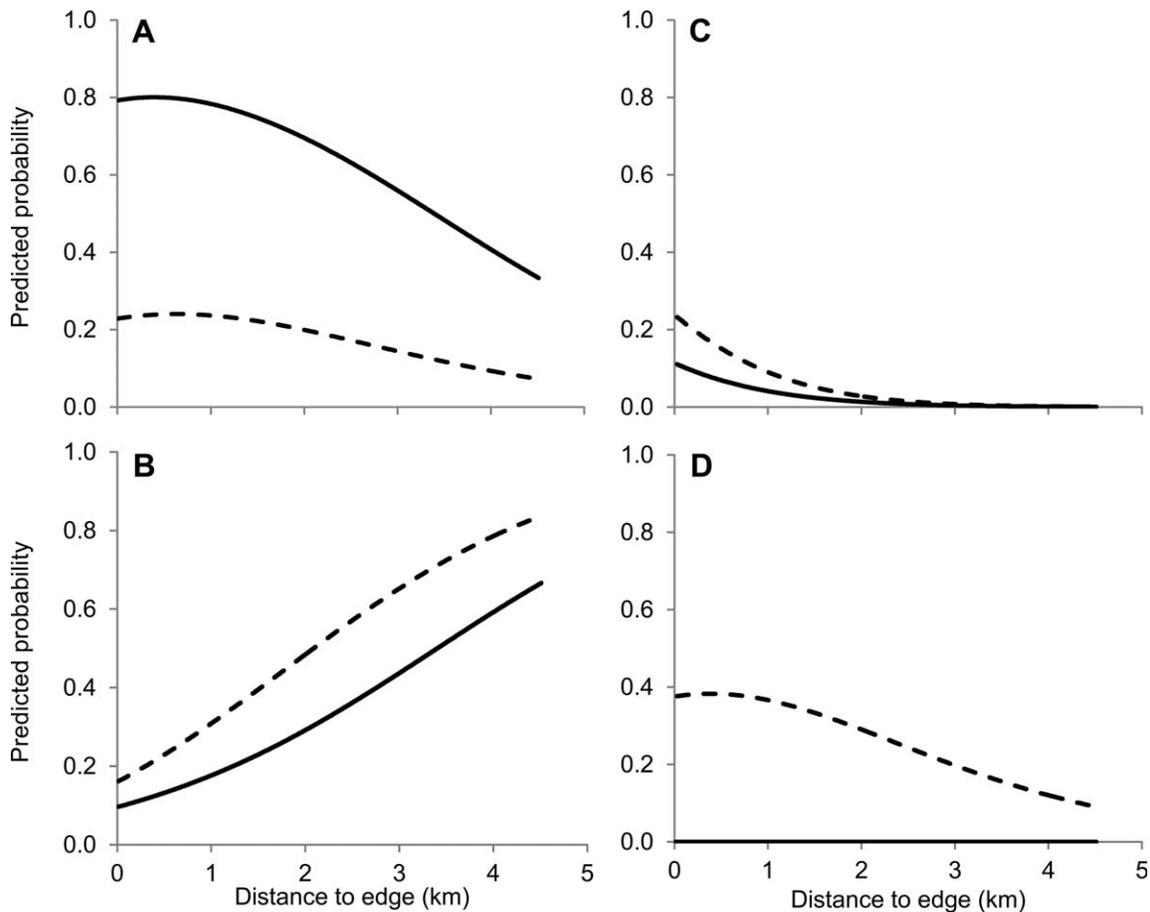


FIGURE 3. Predicted probability curves for nesting (A) Common Raven (CORA), (B) Ferruginous Hawk (FEHA), (C) Red-tailed Hawk (RTHA), and (D) Swainson's Hawk (SWHA) based on distance to edge (km) by nesting substrate type (anthropogenic = solid; natural = dashed). Data were collected in xeric sagebrush steppe environment of southeastern Idaho, 2007–2009. All predicted probabilities sum to 1 across all species for every given value of distance to edge (km).

These data contribute to our understanding of the dramatic expansion of territorial nesting ravens into sagebrush ecosystems, a process now recognized as occurring across much of the western United States (Boarman and Heinrich 1999, Leu et al. 2008). Ravens were classified as an uncommon breeder and year round resident within our study area as recently as 1986 (Reynolds et al. 1986). Studies of nesting raptors that date back to the late 1970s did not report the presence of nesting ravens within our study area (Craig 1979, Craig et al. 1984, Hansen 1994, Hansen and Flake 1995). Territorial ravens are now the most common predatory species nesting in the study area, accounting for 46% of nests among our 4 focal species and with the greatest nest density.

Although Swainson's Hawks showed higher probability of nesting in relation to agricultural areas, the greatest predicted probability of nesting by a given species was for ravens simply because ravens now account for more nesting overall than buteo species. Furthermore, distances

between raven nests were considerably less than distances between nests of buteos. Territorial ravens seem to be intrinsically capable of higher breeding densities than the buteos in altered sagebrush steppe. Perhaps ravens' space needs are less or they express an inherently higher conspecific tolerance; territorial ravens are likely more tolerant of each other than are the buteo species nesting in sagebrush ecosystems. Ravens receive substantial anthropogenic resource subsidies through their scavenging behavior (e.g., road kills) and other generalist foraging behaviors such as consuming agricultural waste grains when prey is unavailable.

Ravens had the highest probability of nesting on electrical transmission towers compared with the 3 buteos. Those structures were taller than nearly all other substrates in the study area and potentially reduced or eliminated mammalian-caused nest predation (Steenhof et al. 1993). Additionally, the probability of nesting increased substantially with reduced distance to nearest edge compared to the buteos. Howe et al. (2014) conducted a

resource selection function analysis on nesting ravens by contrasting used nest sites to random sites at INL and found that ravens chose nest areas with transmission lines and disproportionately greater amounts of edge compared to availability.

Fragmented landscapes (i.e. those with increased edge) may provide ravens with less visual obstruction than landscapes consisting of large contiguous patches of land cover, increasing opportunity to detect prey (Andr n 1992, Vander Haegan et al. 2002). Fine-scale analysis of edge-type selection revealed raven nests were often associated with prior habitat alterations by humans or wildfire (Howe et al. 2014). Specifically, ravens selected nest sites in edge-dominated areas where big sagebrush communities abut native grasslands and nonnative vegetation communities (Howe et al. 2014). Together, results from this investigation and Howe et al. (2014), coupled with recent shifts in vegetation composition identified by LTV trend analysis (Foreman et al. 2013), indicate that ravens are benefiting from fragmentation, loss of sagebrush cover, and increased patches of nonnative grasses and forbs, especially in landscapes transited by transmission lines.

The probability of nesting by Red-tailed Hawks also seems to be influenced by alterations to habitat features in the study area. The number and density of Red-tailed Hawks nesting in the study area increased dramatically from the mid-1970s ($n = 1$; Craig 1979) to the mid-1990s ($n = 33$; Hansen 1994) and have remained stable since that time ($n = 30$; this study). Increased density of Red-tailed Hawks has been reported elsewhere (Stout 2004), and previous studies indicate that this species' reproductive success is not adversely affected by anthropogenic structures and urbanization (Stout et al. 1996, 2006).

Although Swainson's Hawks have been known to aggressively exclude other species (Schmutz et al. 1980, Janes 1994), as the Red-tailed Hawk population increased in our study area, Hansen (1994) noted that this species displaced Swainson's Hawks from traditional nesting areas in cottonwoods along the Big Lost River. This trend has continued, with Red-tailed Hawks nesting in most of the surviving cottonwoods along the Big Lost River, Birch Creek, and contributing drainages. Red-tailed Hawks have been found to use areas with less canopy cover and few large trees and may avoid areas with high densities of trees due to their relatively large size and wingspan (Leyhe and Ritchison 2004), which may explain why Red-tailed Hawks have replaced Swainson's Hawks along the Big Lost River as the density of trees has substantially diminished over the years. Swainson's Hawks have, in turn, increased their use of lone or isolated groups of junipers as nest sites.

Electrical transmission towers were the second most utilized nesting substrate by Red-tailed Hawks. Hansen (1994) reported that Red-tailed Hawks chose nesting substrates that were tall and often nested higher above

ground than Swainson's and Ferruginous Hawks, as has been reported elsewhere (Schmutz et al. 1980, Bechard et al. 1990, Restani 1991). Red-tailed Hawks seem to select nest sites that provide unobstructed access and a high vantage point of the surrounding area (Bednarz and Dinsmore 1982, Smith et al. 2003, Preston and Beane 2009). Other evidence indicates these hawks will select tall cliff faces rather than trees located in areas with reduced visibility, such as canyon bottoms (Janes 1984). Continued loss of cottonwood trees from the study area and other sagebrush ecosystems will likely increase the use of electrical transmission towers as nesting substrates by Red-tailed Hawks.

We found an absence of strong association with any of the land cover variables for Red-tailed Hawks other than a significant association with edges and a potential avoidance of agriculture. Hansen (1994) reported an "affinity" for grassy areas by Red-tailed Hawks on our study site, but our data did not support that finding. Our study benefited from high quality vegetation maps and methods of analysis not available previously. Associations between nesting Red-tailed Hawks and cropland have been reported elsewhere (Peterson 1979, Bednarz and Dinsmore 1982); however, Red-tailed Hawks nested farther from agriculture relative to the other species in this study. This finding could be an artifact of the dispersion of remnant cottonwood tree stands within the study area rather than an avoidance of agricultural fields. Some dead or dying individual cottonwood trees persist along the Big Lost River channel, which extends linearly into the interior of the study site far from adjacent agricultural fields.

We found significantly more Swainson's Hawk nests ($n = 51$; 40 on INL and 11 offsite) during our study years than was reported by Craig ($n = 12$; 1979) and Craig et al. ($n = 7$; Craig et al. 1984) or by Hansen ($n = 28$; 1994). Although Swainson's Hawks reportedly will nest on electrical transmission towers (Blue 1996), this species overwhelmingly chose natural nest substrates in our study area. Only one nest was located on an artificial substrate—a nesting platform. Our finding of tree nesting behavior by Swainson's Hawks is similar to results from other studies (Fitzner 1980, Bechard et al. 1990). Swainson's Hawk is a grassland buteo, so the tendency to nest in closer proximity to agriculture and in areas with increased native grassland relative to the other focal species is consistent with its known natural history (Bechard et al. 1990, McConnell et al. 2008). Swainson's Hawks use trees associated with farmhouses for nesting substrate and agriculture fields to forage for insects and small mammals (Bechard et al. 2010, Nishida et al. 2013).

Swainson's Hawks are considered more versatile in their selection of prey species than Ferruginous Hawks, with prey ranging in size from invertebrates to small mammals (Fitzner 1980, Giovanni et al. 2007); however,

invertebrates were common in pellets found in this study area (Hansen and Flake 1995). Although not considered sensitive to urbanization (Berry et al. 1998), Swainson's Hawks chose nest sites in areas containing unbroken grassland habitat within 1.09 km of their nest sites and were, on average, farther from habitat edges than ravens and Red-tailed Hawks. Numerous wildfires since the mid-1990s have increased the amount of grassland habitat in the study area, which may have benefited Swainson's Hawks. Similar findings were reported in Arizona, where Swainson's Hawks nesting in grasslands and desert scrub selected open areas interspersed with mesquite (*Prosopis velutina*) and shrubs (Nishida et al. 2013).

Ferruginous Hawks may be quite vulnerable to future habitat alterations associated with energy development across sagebrush ecosystems. This buteo selected natural nesting substrates in areas with relatively contiguous sagebrush cover. MacLaren (1986) speculated that, of all the buteos, Ferruginous Hawks stand to benefit the most from electrical transmission towers; however, this species primarily chose juniper trees both in this study ($n = 34$) and Hansen's (1994) study ($n = 40$). Ferruginous Hawks also chose nest locations that were, on average, farther from vegetation edges, roads, and facilities, and they nested in habitats that were composed of a greater percentage of sagebrush cover within nest vicinity (71 ha scale) relative to the other focal species. Avoidance of fragmented habitats and anthropogenic developments is known for this species, which may be easily disturbed during the breeding season (Olendorff 1973, White and Thurow 1985, Gilmer and Stewart 1983; but see Keough and Conover 2012). In Colorado, Ferruginous Hawks avoided areas with >5% urban development (Berry et al. 1998) and will nest more than twice as far from humans than other buteos (Bechard et al. 1990).

Raptors with large home range requirements, such as Ferruginous Hawks, are more likely to be negatively affected by the loss and degradation of contiguous habitat (Newton 1979, Phillips et al. 1984). Raptors that prey on larger mammals are affected negatively by anthropogenic development, specifically urbanization and industrialization (Chace and Walsh 2006). Although Ferruginous Hawks have a diverse prey base, often varying geographically and by local prey abundance (Howard and Wolfe 1976, Steenhof and Kochert 1985), Giovanni et al. (2007) found that Ferruginous Hawks typically preyed on larger species while Swainson's Hawks consumed smaller prey. In southern Idaho, Ferruginous Hawks preyed primarily on northern pocket gophers (*Thomomys talpoides*) in grassland communities and primarily on black-tailed jackrabbits (*Lepus californicus*) in sagebrush ecosystems (Howard and Wolfe 1976) where jackrabbit numbers are relatively high (Stoddart and Anderson 1972, Westoby and Wagner 1973). The

loss of shrublands as a result of anthropogenic alterations and wildfire has long-term implications for jackrabbits (Knick and Dyer 1997) and likely Ferruginous Hawks.

Conclusion

Together, these data provide evidence that patterns of nesting by buteo species and ravens are predictable within this system based on changes in landscape characteristics and anthropogenic disturbance. Furthermore, comparison among 4 decades of raptor research at this study site provides further insight into long-term changes in composition and spatial structure of these species in altered landscapes in sagebrush ecosystems. Most important, we found that the composition of the avian predator community has shifted drastically with the substantial increase in generalists. Both ravens and Red-tailed Hawks are successful generalist species, and as such, further fragmentation of sagebrush steppe habitats will likely benefit these 2 species while reducing the number of suitable Ferruginous Hawk territories. Grasslands resulting from wildfire may have benefited Swainson's Hawks; however, their use of these areas was likely in part a result of their displacement by increased Red-tailed Hawk numbers beginning in the 1990s.

Furthermore, ravens are now exploiting anthropogenic resources that accompany infrastructure and transmission line development, and we found that the probability of use of electrical transmission towers for nesting by ravens far exceeds that of the buteo species. The use of electrical transmission towers as nesting substrate by Red-tailed Hawks, and to a lesser extent by Ferruginous Hawks, is a relatively recent occurrence on the INL because no previous raptor nest investigation in this study area reported any buteo species nesting on these anthropogenic subsidies when they were equally available. We believe the recent use of this substrate by these species reflect the deterioration of traditional nesting habitats in the study area, particularly the loss of cottonwoods as a result of hydrological diversions (Rood et al. 2003). Although these results were derived from a study site in southeastern Idaho, these results can help land and resource managers predict outcomes of energy development and other anthropogenic changes to sagebrush ecosystems across the western United States, especially in areas with similar landscape characteristics.

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