

Resource selection of apex raptors: implications for siting energy development in sagebrush and prairie ecosystems

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Abstract. There is an urgent need to understand ecological responses of avian species to the rapidly expanding human footprint of conventional and renewable energy development in sagebrush and prairie ecosystems. The ferruginous hawk (*Buteo regalis*) and golden eagle (*Aquila chrysaetos*) are two sympatric raptors of conservation concern that occupy and flourish in the most intact sagebrush steppe region remaining in North America. To understand these species' use of habitat relative to energy development, we built resource selection functions using a spatially representative sample of occupied nesting territories collected in 2010–2011 and remotely sensed environmental variables across an extensive study area (186,693 km²). We used the resulting predicted resource selection maps to evaluate spatial overlap between the nesting habitats of these sympatric raptor species, as well as overlap of predicted habitat with potential development of oil/gas and wind energy resources. Remotely sensed variables were very effective in modeling patterns of nest-site selection based on fivefold cross-validation (>0.93 Spearman-rank correlation) and validation with an independent dataset of historical nests collected from 2000 to 2009. Topographic roughness and intermediate levels of spring precipitation were the strongest drivers of differences in habitat use between ferruginous hawks and golden eagles. We did not detect a strong signal of avoidance of energy infrastructure by either species at current levels of development and both nested closer than expected to gravel/dirt roads associated with oil and gas infrastructure. However, extensive overlap of nesting habitat more selected by ferruginous hawks and golden eagles with areas of actual and potential energy development suggests both species are at risk from future habitat fragmentation. Given that 80% of nests are > 1 km from oil/gas wells, we believe the density of energy-related disturbance present during our study was insufficient to drive patterns of resource selection for ferruginous hawks when considered at broad spatial scales. However, it was beyond the scope of our study to predict long-term, population-level responses. We suggest rigorous monitoring of long-term trends in occupancy, productivity, and distribution is warranted for populations of ferruginous hawk and golden eagle in sagebrush and prairie ecosystems exposed to increased energy development.

Key words: artificial nest structure; *Aquila chrysaetos*; *Buteo regalis*; energy development; ferruginous hawk; golden eagle; human disturbance; oil and gas development; resource selection; sagebrush ecosystems; wind energy; Wyoming.

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INTRODUCTION

Sagebrush (*Artemisia* sp.) and prairie ecosystems of North America support 65 taxa of sagebrush-associated plants of conservation concern and 40 vertebrates, of which seven are considered sagebrush obligates (Hanser et al. 2011); the basins of Wyoming, USA, include some of the most intact sagebrush and prairie ecosystems. However, sagebrush and prairie communities are at risk through degradation caused by direct removal of sagebrush by cutting, spraying, and chaining, as well as indirect threats such as overgrazing, agriculture, forest encroachment, energy development, and non-native invasive species (Braun et al. 2002, Davies et al. 2011). Physical disturbance to this community is long term, such as the vegetative recovery time from oil and gas well development that takes from 60 to 100 yr for recovery (Monroe et al. 2020). In addition, sagebrush and prairie ecosystems are being increasingly fragmented as the human footprint from urbanization, agriculture, grazing, and energy development expands throughout the western United States (Leu et al. 2008). An estimated 14% of sagebrush steppe has been converted to agricultural, urban, or industrial uses, 27% has been converted to other vegetation types, and 59% remained relatively intact throughout the native range of sagebrush and prairie ecosystems in the western United States (Miller et al. 2011).

State and federal agencies administer ~ 70% of remaining sagebrush and prairie ecosystems in the United States, including the activities of energy-extraction industries that operate mostly in these landscapes (Knick et al. 2003). Demand for energy has global consequences to biodiversity in sagebrush and prairie ecosystems (Jones et al. 2015). Technological innovation associated with energy extraction greatly increased the production of unconventional gas wells (coal-bed methane via hydraulic fracturing, shale gas, tight gas) and nearly doubled the number of unconventional gas wells in the United States since 1990 (U.S. Energy Information Administration 2018). Sagebrush and prairie ecosystems are further at risk from climate change, as frost-intolerant vegetation expands northward across an estimated 87,000 km² of sagebrush habitat for each 1°C increase in temperature (Nielsen et al.

2005). Thus, there is a pressing need to understand how ecological and anthropogenic impacts to sagebrush and prairie ecosystems relate to the persistence and viability of wildlife populations (Knick et al. 2003, Davies et al. 2011).

Of particular urgency is the need to understand how avian species respond to the ecological and anthropogenic changes to the structure and composition of sagebrush and prairie ecosystems, as well as long-term responses to human disturbance (Knick et al. 2003, Brennan and Kuvlesky 2005, Copeland et al. 2011). The causes for the well-documented decline of avian populations in sagebrush and prairie ecosystems are complex (see Knick et al. 2003 for a review, Gilbert and Chalfoun 2011, Hethcoat and Chalfoun 2015) and result from the cumulative impact of habitat fragmentation, non-native vegetation replacement, and afforestation of grass and shrublands (Brennan and Kuvlesky 2005). Raptors, similar to mammalian carnivores, represent an avian taxa that can be vulnerable to ecological changes because they typically occur at low densities (Newton 1979) and frequently depend on intact vegetation communities that support prey populations (Morrison et al. 2007, Ripple et al. 2014).

Ferruginous hawk (*Buteo regalis*) and golden eagle (*Aquila chrysaetos*) are sympatric raptors that provide ideal focal species to evaluate changes in resource selection in sagebrush and prairie ecosystems given the demand for conventional (e.g., oil, coal, natural gas), unconventional (e.g., tight gas, coal-bed methane), and alternative (e.g., wind, solar) energy (U.S. Energy Information Administration 2018). Ferruginous hawks are a species of conservation concern (Ng et al. 2017) with reported sensitivities to human disturbance (White and Thurow 1985, Ng et al. 2017) and habitat alteration, especially land conversion to tillage agriculture (Schmutz 1987, Coates et al. 2014). Similar to ferruginous hawks, golden eagles exhibit sensitivity to human disturbance (Richardson and Miller 1997) as evidenced by a reduction of nest occupancy and egg laying in response to outdoor recreation from off-road vehicles and early-season pedestrian use (Spaul and Heath 2016). Golden eagles are also vulnerable to illegal shooting and secondary poisoning (Kochert and Steenhof 2002), electrocution, and collisions with powerlines (Harness and Wilson

2001, Lehman et al. 2007), and mortality from collisions with turbine blades at wind energy developments (Pagel et al. 2013, Watson et al. 2018). Thus, ferruginous hawks and golden eagles are sympatric avian predators that secure resources in sagebrush and prairie ecosystems that are increasingly fragmented and disturbed by an expanding human footprint.

In this paper, we evaluated patterns of nest-site selection for ferruginous hawks and golden eagles in sagebrush steppe and prairie ecosystems of Wyoming, USA, an area that supports the most intact native sagebrush steppe found in North America. We focused our study on the conservation and management of nesting habitat at multiple scales rather than investigating the site-specific placement issues associated with energy infrastructure. The basins of Wyoming within our study area are central to the geographic distribution of ferruginous hawks in North America (Ng et al. 2017) and provide important habitat for golden eagles (Nielson et al. 2014). This region also includes an estimated proved reserve of approximately 20 trillion cubic feet of natural gas (U.S. Energy Information Administration 2018). In addition, this region is central to the development of renewable energy and includes some of the best on-shore development sites for wind power in North America, including 1017 existing wind turbines in 2018 (Elliott et al. 1986, Hoen et al. 2018).

Our first step was to obtain a representative sample of occupied nests for ferruginous hawks and golden eagles using aerial surveys across sagebrush and prairie ecosystems in Wyoming (186,693 km²). Based on this sample, we built resource selection function (RSF) models that considered patterns of selection for nesting ferruginous hawks and golden eagles based on remotely sensed covariates of environmental heterogeneity, including measures of energy-related infrastructure (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). Understanding resource-use patterns of non-breeders or recent fledglings was beyond the scope of our study. Given that artificial nest structures (nest platforms placed by wildlife managers) are important mitigation to energy development for ferruginous hawks (Neal et al. 2010, Wallace et al. 2016b), we created separate models for

hawks nesting on natural substrates (i.e., rock outcrops, hill sides, trees, erosional spires) vs. artificial nest structures in view of human influence on structure placement.

An important motivation of resource selection analyses is to provide maps of predicted use to inform conservation planning (Johnson et al. 2006, Hebblewhite et al. 2014, Morris et al. 2016). Similar to Smith et al. (2010) and Carr and Melcher (2017), we used RSF models to create predictive spatial maps of nesting habitat for golden eagles and ferruginous hawks to display gradients of habitat quality relative to current and projected energy development (e.g., wind, oil/gas). This provides a valuable tool for land planners to evaluate how anthropogenic impacts from areas of current and potential energy development may relate spatially to selected habitat for these species. Furthermore, this provides a defensible basis to develop conservation strategies for these sympatric raptors in sagebrush and prairie ecosystems impacted by expanding energy development.

We evaluated the following predictions: (1) Ferruginous hawks and golden eagles would select areas of low-energy infrastructure to avoid disturbance; (2) ferruginous hawks nesting on artificial nest platforms would differ in patterns of resource selection compared to pairs selecting natural nest substrates given the human involvement in nest placement; (3) both raptor species would select nesting areas of high topographic relief relative to the surrounding landscape since golden eagles often nest on cliffs and ferruginous hawks on erosional spires and hills; and (4) both species would avoid areas of greater sagebrush cover, given the negative relationship of potential prey abundance (sciurids, family Sciuridae, and leporids, family Leporidae) to shrub cover at a landscape scale (Olson et al. 2017).

METHODS

Study area

Our study area included sagebrush and prairie grasslands of Wyoming, USA, that are central to the conservation of ferruginous hawks and golden eagles in North America (Nielson et al. 2014, Ng et al. 2017, Fig. 1). Our 186,693-km² study area supported a mixed land ownership consisting of 42% federal, 7% state, and 51%

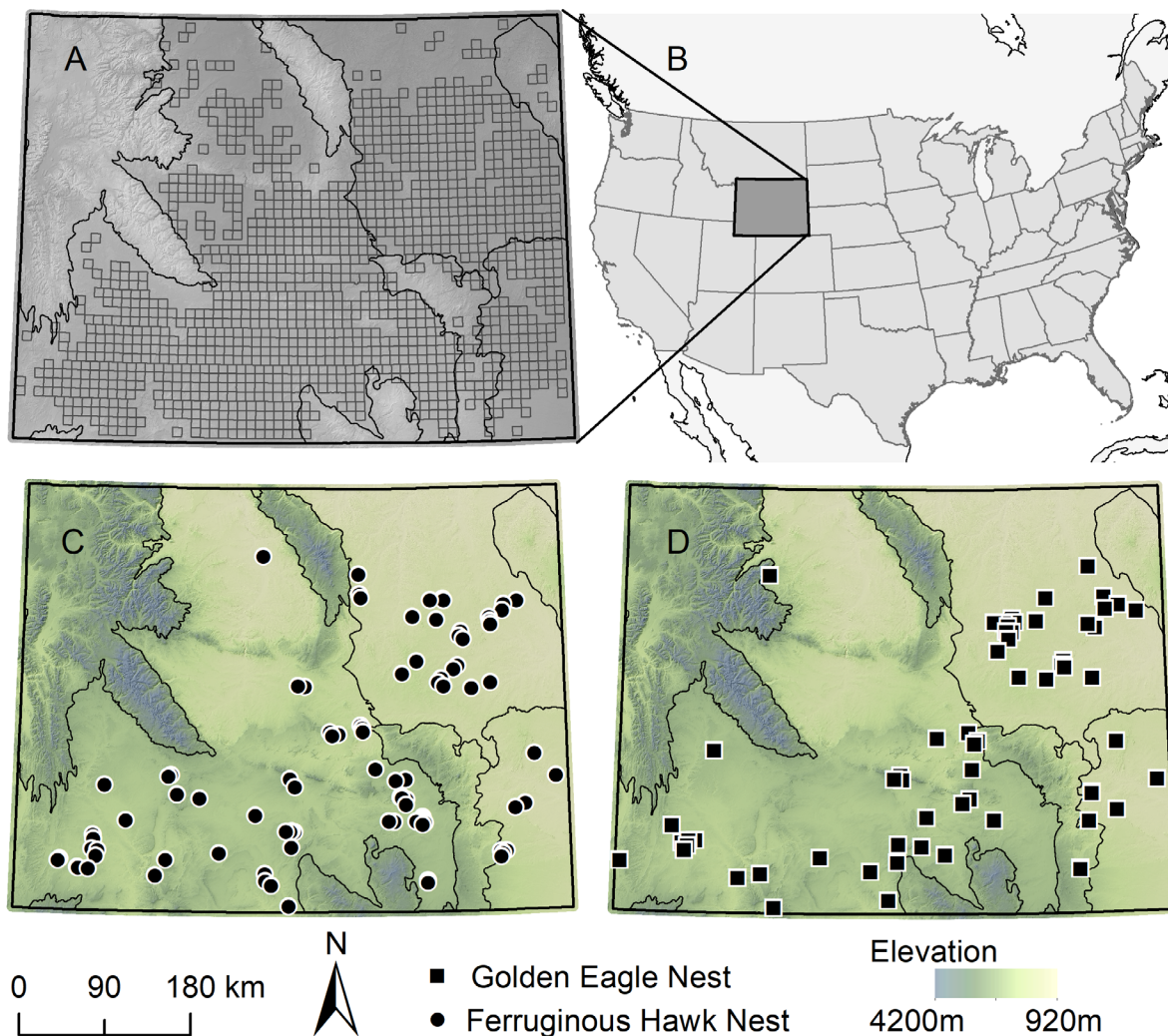


Fig. 1. Study area for investigating resource selection of nesting ferruginous hawks and golden eagles in the sagebrush steppe and grassland habitat of Wyoming, USA. (A) The distribution of survey units (i.e., townships) that were available (open squares) and surveyed (filled squares). (B) The location of Wyoming in the United States. (C, D) The distribution of nests occupied by ferruginous hawks (circles, C) and golden eagle (squares, D) detected during surveys in 2010 and 2011; mountainous areas (light shading in A) were excluded from surveys.

private lands. This area encompassed approximately 45% of the state (Wallace et al. 2016a) within three level III ecoregions (Wyoming Basin, Northwestern Great Plains, High Plains) and 20 level IV ecoregions as defined by Chapman et al. (2004) based on dominant vegetation and environmental conditions (Appendix S1: Fig. S1). Northern portions of the Wyoming Basin included the Salt Desert Shrub sub-ecoregion (15–25 cm annual precipitation) dominated by

alkaline-tolerant shrubs and grasses such as greasewood (*Sarcobatus* spp.), saltbush (*Atriplex* spp.), Indian ricegrass (*Achnatherum hymenoides*), and needle-and-thread grass (*Hesperostipa comata*). Central and southern portions of the Wyoming Basin supported big sagebrush (*Artemisia tridentata*), black sagebrush (*Artemisia nova*), and silver sagebrush (*Artemisia cana*) within wheatgrass (*Agropyron* spp.) mixed prairies. The Northwestern Great Plains in the northeastern

portion of the study area included the Powder River Basin sub-ecoregion (30–46 cm annual precipitation) and was dominated by mixed-grass prairies, including wheatgrasses, needle-and-thread grass, rubber rabbitbrush (*Ericameria nauseosa*), and fringed sage (*Artemisia frigida*). Similarly, the High Plains (30–36 cm annual precipitation) was dominated by mixed-grass prairies of western wheatgrass (*Agropyron smithii*), prairie junegrass (*Koeleria macrantha*), blue grama (*Bouteloua gracillis*), and various forbs and shrubs. Elevation ranged from 940 to 2200 m asl, with a mean of 1780 m asl (Olson et al. 2015). The primary land use of the study area was cattle grazing, with only approximately 4% of the state in irrigated and non-irrigated cropland. Our study area included extensive energy-related infrastructure from coal, natural gas, petroleum, and wind power development (U.S. Energy Information Administration 2018), and this region is recognized as one of the most important in the United States to understand potential impacts for species of concern from energy-related disturbance (Copeland et al. 2009).

Nest surveys

We conducted aerial surveys to locate occupied ferruginous hawk and golden eagle nests across sagebrush and grasslands of Wyoming. Surveys were conducted during mid-April to mid-May 2010 and 2011 when ferruginous hawks and golden eagles were likely present at nesting territories. Nests were considered occupied and suitable for inclusion in the study if we observed an incubating adult or pair associated with a nest structure (Steenhof and Newton 2007). Our survey unit for aerial surveys was the township ($N = 104$), a square area of 93.3 km² delineated by the Public Land Survey System (9703-km² total survey area). Our sampling frame was all townships with centroids in the distribution of ferruginous hawks in Wyoming, as modeled by Keinath et al. (2010). Thus, survey townships were in open, non-forested environments characteristic of ferruginous hawks, and we did not sample golden eagles that nested in forested and mountainous terrain. In each township, we flew 16 equidistant (600-m spacing) north–south transects the length of our sample unit (9.7 km; Appendix S1: Fig. S2; see Olson et al. (2015) and Wallace et al. (2016) for survey

details and nest densities). The probability of detection of occupied nests in our survey townships from fixed-wing aircraft was 0.71 (95% CI 0.25–0.95) and 0.74 (95% CI 0.20–0.97) for ferruginous hawks and golden eagles, respectively (Olson et al. 2015). Townships were large enough to be efficiently searched by fixed-wing aircraft and sufficient in size to potentially support multiple nesting pairs of ferruginous hawks and/or golden eagles. After searching townships, we augmented the sample by checking historical nest locations that could have been missed and we retained any nest observed while flying between survey townships. Our use of a randomized grid-based design helped to ensure that occupied ferruginous hawk and golden eagle nests used for modeling were representative of these species in sagebrush and prairie ecosystems.

Environmental variables

We considered predictor covariates that related to the life histories of both ferruginous hawks and golden eagles (Kochert et al. 2002, Ng et al. 2017) and were easily accessible to land managers for conservation planning. We quantified the environmental heterogeneity associated with energy development, vegetation, physical environment, and prey abundance around nest sites compared to locations randomly available using remotely sensed covariates (Table 1). Given that ferruginous hawks and golden eagles exhibit some sensitivity to human disturbance (White and Thurow 1985, Spaul and Heath 2016), we measured the density and Euclidean distance of oil and gas wells as indices of energy-related disturbance (Table 1; Wyoming Oil and Gas Conservation Commission). We also quantified road density as an index of energy disturbance using a road layer (2010) developed by the Bureau of Land Management (BLM) from NAIP imagery (Wyoming BLM, *unpublished data*). We quantified secondary roads, including those with dirt, gravel, and aggregate surfaces, but excluded both paved highways and primitive, non-graded dirt roads; paved state and federal highways were too sparse on our study sites to model effectively. We generally matched these data layers that indexed energy infrastructure to the temporal period that we searched for nest occupancy.

Table 1. Environmental covariates used to predict resource selection of nesting ferruginous hawks and golden eagles across spatial scales, Wyoming, USA, 2011–2012.

Variable name	Description	Scale	Source
Bare	Mean % bare ground	A, B	Homer et al. (2009, 2012)
Bare_SD	Standard deviation of mean % bare ground	A	Homer et al. (2009, 2012)
Crop	Mean % agricultural crop cover	A, B	National Agricultural Statistics Service Cropland Data Layer (2010)
NDVI	Normalized difference vegetation index, MODIS data, 2010	A, B	Pettorelli et al. (2005)
Precip_Sp	Average spring precipitation (cm; April–May, 1981–2010)	B	PRISM Climate Group (2006)
Prey	Modeled index of prey abundance for four prey groups, based on empirical count data, grouped into 10 equal-area bins, and added across bins	A, B	Olson et al. (2017)
Rd_den	Density of secondary roads including dirt, gravel, and aggregate-surfaced roads per km ² ; excludes interstate and state highways and primitive non-graded dirt roads.	A, B	BLM road layer
Rd_dist	Distance to secondary roads including dirt, gravel, and aggregate-surfaced roads (km); excludes interstate and state highways and primitive non-graded dirt roads.	B	
Roughness	Mean surface area based on digital elevation model	A, B	Jenness (2004)
Sage	Mean % sagebrush cover	A, B	Homer et al. (2009, 2012)
Sage_SD	Standard deviation of mean % sagebrush	A	Homer et al. (2009, 2012)
Shrub_Ht	Mean shrub height (cm)	A, B	Homer et al. (2009, 2012)
Shrub_Ht_SD	Standard deviation of mean shrub height	A	Homer et al. (2009, 2012)
Temp_Sp	Average spring temperature (Centigrade; April–May, 1981–2010)	B	PRISM Climate Group (2006)
TPI	Topographic position index	A, B	Weiss (2001), Jenness (2006)
Well_den	Density of oil/gas wells per km ²	A, B	Wyoming Oil and Gas Conservation Commission (2012)
Well_dist	Distance to oil/gas wells (km)	B	Wyoming Oil and Gas Conservation Commission (2012)

Note: Nest-site scale (A: 250 m radius circle, 500, 1000 m) and landscape scale (B: 1.5, 5, 10, and 25 km).

We considered covariates that indexed structure and composition of shrubland and grassland vegetation given the potential impact to habitat of prey for both raptors (Table 1; Hanser and Huntly 2006, Olson et al. 2017). We quantified percent sagebrush (*Artemisia* spp.) cover, shrub cover, bare ground, and shrub height (cm) based on remotely sensed spatial products developed for sagebrush steppe habitat (Homer et al. 2009, 2012), while recognizing that shrub-cover estimates from remote sensing were not directly proportional to mean cover values measured in the field (Aldridge et al. 2012, Homer et al. 2012). We included the standard deviation of mean sagebrush cover and shrub height as indices of shrub-cover heterogeneity. We used the Normalized Difference Vegetation Index (NDVI) based on MODIS data to index the productivity of green growing vegetation (Carlson and Ripley 1997, Pettorelli et al. 2005). High values of NDVI correlate with dense vegetation cover, whereas

low values correlate with areas barren of vegetation (e.g., snow, dirt, and rock; Gamon et al. 1995). Although conversion of native grasslands to crop lands was low on our study area, we considered nest-site selection in relation to crop lands mapped at broad scales using satellite imagery interpreted by the USDA National Agricultural Statistics Service Cropland Data Layer (2010). Mapped crop lands included irrigated fields primarily composed of alfalfa, mustard, wheat, and cultivated crops.

We also considered covariates that indexed the physical environment, since ferruginous hawks and golden eagles nest on a variety of physical structures (e.g., ridges, cliffs, erosion spires; Kochert et al. 2002, Ng et al. 2017) whose presence or absence may constrain breeding densities (Kochert and Steenhof 2002, Kochert et al. 2002). We considered surface roughness and topographic position index (TPI) to quantify potential nest substrates associated with a highly dissected

topography (Table 1). We calculated surface roughness based on the average three-dimensional surface area of 30×30 m pixels using a digital elevation model across moving windows at different scales (Jenness 2004). Topographic position index was a measure of landscape slope position (e.g., ridges and valleys; Weiss 2001, Jenness 2006). Positive TPI values represented locations that were ridge-like, and negative values indicated valleys (Weiss 2001). Since raptors are sensitive to weather conditions during nesting, we also considered mean spring temperature and precipitation to evaluate whether nest-site selection was affected by relatively warmer and wetter regions of the landscape (Wallace et al. 2016b, Reynolds et al. 2017).

Ferruginous hawks and golden eagles depend primarily on mammalian prey during nesting (Bedrosian et al. 2017, Ng et al. 2017). Thus, from 2010 to 2012, we sampled the relative abundance of sciurid and leporid populations at 86 locations, along 6, 1-km line transects per location (~516 km per sample occasion) as indices of aboveground prey abundance (i.e., prey potentially available to raptors). We tallied sciurids at point counts sampled at 333-m intervals, and leporids along transects. From these data, Olson et al. (2017) modeled abundance at a broad spatial scale corrected for probability of detection for ground squirrels, chipmunks, and rabbits/hares (leporids) across our study area. We used these predictive prey surfaces as covariates relative to raptor resource selection.

Model framework and spatial predictions

We assumed that raptors selected nest-site locations based on a broad perception of environmental heterogeneity across multiple spatial scales (Orians and Wittenberger 1991, Mayor et al. 2009). Thus, we considered how ferruginous hawks and golden eagles responded to environmental heterogeneity at nest site (0.25–1 km), landscape (1.5–25 km), and a combination (combined) of these spatial scales. Given that we had no a priori knowledge of the ecological scale of raptor perception when selecting nesting locations (Johnson et al. 2004), we calculated environmental metrics using moving window averages in circular neighborhoods with radii of 250, 500 m, 1, 1.5, 5, 10, and 25 km. We assumed scales from 250 m to 1 km could be

biologically meaningful as potential post-fledging areas, similar to other raptors (Reynolds et al. 1992, Kennedy et al. 1994). We chose the smallest landscape scale (1.5 km) as approximately one half the nearest-neighbor distance between ferruginous hawk nests (Wallace et al. 2016a, Ng et al. 2017). This scale was considered a putative home range based on Ng et al. (2017) and was generally verified by our field observations of territory defense against conspecifics and other raptors. We considered the 25-km radii as appropriate to accommodate the large scale of energy development and potential raptor movement.

To evaluate resource selection of nest sites, we constructed RSFs with generalized linear logistic regression models within a use-availability framework (Manly et al. 2002, Johnson et al. 2006). We created available locations (i.e., pseudo-absence points; $N = 1000$) distributed randomly throughout the level III ecoregions (see *Study area*) that defined our inference area (Fig. 1), and compared values of environmental variables at those locations to occupied nests located during surveys (Johnson et al. 2006, Northrup et al. 2013). The large number of random locations across Wyoming provided a general measure of environmental heterogeneity associated with available sites, excluding mountain ranges with forest cover. We based RSF models only on occupied nests of golden eagles and ferruginous hawks. We assigned weights to random locations so they balanced with occupied nest sites to avoid inflating statistical precision, while still providing for a representative sample of habitat availability. We conducted separate analyses for ferruginous hawk nests on natural vs. artificial structures to understand whether environmental characteristics at nest structures built and placed by humans differed from those selected by ferruginous hawks that selected naturally occurring nest substrates. We documented too few golden eagles nesting on artificial nest structures ($N = 2$) to conduct separate analyses for this species.

We screened potential covariates to include only top-performing variables in global models for each raptor species consistent with Hosmer and Lemeshow (2000). Since covariates were closely correlated across scales, we used only the single most predictive scale (nest-site or landscape) for each covariate, based on comparison

of univariate models with Akaike's information criteria (AIC; Burnham and Anderson 2002). We discarded all variables that performed worse than a null model based on AIC. Next, we screened remaining variables for multi-collinearity using a variance inflation factor (VIF). We performed this procedure separately for variables within the nest-site and landscape scales, and sequentially removed variables with the highest VIF until the VIF for all covariates was < 2.5 (Zuur et al. 2010). The remaining variables became our final covariate set. For these variables, we also considered whether a quadratic form would be more predictive by comparing the AIC from a univariate model with only the linear form to a model containing both a linear and a quadratic form; we included the quadratic form in models if it was more supported. We used this variable selection procedure to generate a single global model for each scale (nest-site and landscape) and each dataset (ferruginous hawk natural nests, ferruginous hawk artificial nests, and golden eagle natural nests). We also considered a combination scale, which followed the same procedure as above, but included both nest-site and landscape-scale predictors in the same model to evaluate potential improvements in model performance. For each dataset (ferruginous hawk natural nests, ferruginous hawk artificial nests, and golden eagle natural nests), we used fivefold cross-validation (Boyce et al. 2002) and independent validation on a dataset of historical nests (details below) to select a single best-performing scale; we considered this the top-performing RSF model for each dataset, and conducted all further analyses using this scale.

Based on the most predictive RSF model for each dataset, we produced spatial predictions of the relative probability of nest-site selection for ferruginous hawks and golden eagles. We estimated the relative probability of selection (w) using the equation.

$$w(x) = \frac{\exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i)}{1 + \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i)} \quad (1)$$

where β_i is the estimated beta coefficient for each covariate (i), and x_i is the value of each covariate (i ; Boyce et al. 2002). We split spatial predictions into seven equal-area bins; this was done for ease of interpretation of the mapped predictions, since

predictions generated from a use-available design are relative probabilities, and thus, the continuous nature of predictions is difficult to interpret (Boyce et al. 2002, Morris et al. 2016) and to generate data that were consistent with grouping of the wind power class covariate layer into seven bins (Spatial mapping and species overlap).

Model validation

We validated resource-use models using a five-fold cross-validation to identify the best spatial scale (nest-site, landscape, combination) at which to predict nest-site selection using the methods of Boyce et al. (2002). For each model, we randomly split the data into five equal-sized folds and sequentially withheld one fold, refitting the model on the remaining four folds and using this model to predict RSF values for the withheld fold. We determined the Spearman-rank correlation between binned predictions of RSF probabilities from the withheld data in each of the five folds and the binned predicted probabilities of available habitat across the landscape; we expected models with good fit to have high Spearman-rank correlations. Due to our sample sizes of occupied nests, we repeated our fivefold validation 100 times per model and recorded the average and range of Spearman correlations produced at each iteration, to ensure stable estimates of model performance.

We also evaluated model performance based on an extensive sample of independent (i.e., nests not used to build RSF models) historical nests of ferruginous hawks ($N = 101$) and golden eagles ($N = 237$) that were occupied between 2000 and 2009 as documented in the Wyoming Game and Fish Wildlife Observation Database (Wyoming Natural Diversity Database, <http://www.uwyo.edu/wyndd/>). We believed this second, and possibly more rigorous evaluation of model performance, provided the best estimate of how RSF models would actually perform when applied to conservation planning. If the underlying RSF models were truly predictive of nest-site selection, we would expect that independent ferruginous hawk and golden eagle nests would generally occur in areas predicted as high relative probability from RSF models. This evaluation also allowed us to use independent nests to

provide a binary definition of habitat quality (e.g., more-selected, less-selected) for ferruginous hawks and golden eagles as an additional tool for land managers (see Holbrook et al. 2017). For this analysis, we calculated the cumulative percentage of independent nests within each RSF bin to identify a threshold that managers could use to split the continuous spatial predictions from RSF models into more-selected and less-selected habitat when assessing habitat fragmentation from current and potential siting of energy infrastructure.

Spatial mapping and species overlap

Managers and policymakers are often required to manage anthropogenic stressors of wildlife populations based on imperfect knowledge regarding spatial patterns of risk (Duggan et al. 2015). To better understand potential impacts, we used methods similar to others (Neal et al. 2010, Tack and Fedy 2015, Carr and Melcher 2017, Juliusson and Doherty 2017) to assess the overlap of spatial distribution of high-quality ferruginous hawk and golden eagle habitat with areas of likely energy (oil/gas, wind) development. As an index of wind energy development potential, we used data from the National Renewable Energy Laboratory (NREL), which categorized potential wind power into seven classes (from 1 to 7, low–high) based on modeled wind speed (NREL 2002; <https://eerscmap.usgs.gov/uswtdb/>). For oil and gas development, we used a model of development potential created by Juliusson and Doherty (2017), which used the known locations of producing and non-producing oil and gas wells to predict the probability of the presence of oil or gas deposits. Since the wind potential data were binned into categories, for comparison purposes we binned the potential oil and gas development layer, which was originally on a continuous scale from 0 to 1, into seven equal-area quantiles by sampling the data at 100,000 random locations distributed across our study area. The indices we used to delineate areas of wind, oil, and gas development were derived from sources that used differing methods, and were binned into categories using different methods, and thus are not directly comparable. However, bins indicate relative potential development and thus can be rank compared. Based on RSF spatial predictions, we

used our binary (less-selected or more-selected) determination of habitat quality for ferruginous hawks and golden eagles to overlay with development risk layers using ArcGIS (ESRI 2017). This created an output raster containing all possible combinations of habitat quality/development risk bins: 1–2 for raptor habitat quality and bins 1–7 for development risk. This resulted in 14 possible values that we used to calculate and map the amount of overlap of each development risk bin relative to the habitat quality (more-selected vs. less-selected) for ferruginous hawks and golden eagles.

Raptor resource selection and energy siting potential

To provide a more detailed understanding of the current distribution of energy development relative to ferruginous hawk and golden eagle nests, we reported the density of oil/gas infrastructure within circular buffers around nests and we compared the Euclidian distance from nests to this infrastructure in relation to random expectation. Using the location of producing oil and gas wells provided by the Wyoming Oil and Gas Conservation Commission (retrieved 6 July 2015 from <http://wogcc.state.wy.us>), we determined the number of natural ferruginous hawk nests and golden eagle nests within a 500-m, 1-km, or 5-km radius of one or more producing wells. We then did the same for our sample of random locations ($N = 1000$), and compared the number of nests within each distance category to the random locations within each distance category for each species, using a chi-square analysis (Agresti 2007). We calculated the average density (wells/km²) of producing oil and gas wells within a 25-km radius around each ferruginous hawk, golden eagle, or random location. We also determined the distance to the nearest producing oil or gas well from each ferruginous hawk or golden eagle nest, and from the random locations, and produced summary statistics of this value for each group to provide a metric of nest proximity to oil wells during the time of this study.

To compare the distribution of ferruginous hawk and golden eagle nests to the binned energy development potential layers on the landscape, we spatially overlaid the nest locations on top of the potential oil/gas and wind layers, and

extracted the bin value (1–7) at each nest for each layer. We then counted the number of nests in each bin, and compared this to a random expectation of equal numbers of nests per bin using a chi-square test. We examined the chi-square residuals to determine which bins contained a disproportionately high or low number of nests. We also overlaid the current existing numbers of oil and gas wells (WOGCC 2015) and existing wind turbines (Hoen et al. 2018) with the development potential layers, to determine the distribution of existing energy development on the binned potential development layers. All spatial analyses were performed in ArcGIS and statistical analyses in program R (R Core Team 2019).

RESULTS

During 2010–2011, we located 96 occupied territories of ferruginous hawks. Of these, 77 territories were located during aerial surveys of 104 townships randomly distributed across our study area and 19 when the aircraft ferried between survey townships (Fig. 1). Most of the ferruginous hawks that nested on natural substrates choose cottonwood trees (26%) followed by rock outcrops (21%), ground/hillsides (19%), and juniper trees (7%). In addition, we documented 80 occupied nests of ferruginous hawks on artificial nest structures: 24 were located during surveys of random townships and 56 from historical records. We located a total of 63 occupied territories of golden eagles, with 53 in surveys of random townships and 10 while ferrying between townships (Fig. 1). Golden eagle nests were mostly on cliffs (44%), cottonwood trees (40%), and rock outcrops (6%).

Resource selection and model validation

Environmental covariates in our most parsimonious and predictive models suggested resource selection by ferruginous hawks and golden eagles varied between species and spatial scales. The top-performing RSF model for ferruginous hawks at natural nest sites included only covariates quantified at the landscape scale. Ferruginous hawks exhibited strongest selection for areas with lower surface roughness within 5 km, moderate spring temperature within 1.5 km, lower proportion of cropland within 10 km, and closer proximity to roads (Table 2, Fig. 2).

Marginal response curves indicated that habitat suitability for nesting ferruginous hawks was most sensitive to topographic roughness and declined sharply as terrain became more highly dissected (Table 2, Fig. 2). In contrast, there was a linear increase in habitat suitability as percent bare ground increased, although this relationship was not statistically significant. There was a sharp curvilinear decrease in predicted suitability with higher proportions of cropland that was statistically significant. However, agricultural lands were present at low levels across our study area, with an average of only 3% (standard error [SE] = 22%) cover from cultivated land within a 1-km radius of ferruginous hawk nest sites. The landscape-scale RSF model was highly predictive with a Spearman-rank correlation coefficient of 0.98 for fivefold cross-validation (range of 0.79–0.96 for individual folds; Table 3). The landscape model was also highly predictive when applied to the independent validation set of ferruginous hawk nests (i.e., nests not used to build RSF models; $N = 101$) with a Spearman-rank correlation of 0.96 (Table 3). The high validation of independent nests suggested the underlying model provided an effective tool for conservation planning applications.

The best-performing model for ferruginous hawks nesting on artificial nest platforms included covariates quantified at the combined scale. Ferruginous hawks nesting on artificial platforms selected areas with low surface roughness at a 1-km scale, moderate amounts of spring precipitation within 25 km, moderate shrub height within 1.5 km, and shorter distances to roads (Appendix S1: Table S1). Models for ferruginous hawks nesting on artificial nest platforms validated similar to models for nests on natural substrates with a Spearman-rank correlation of 0.94 at the nest-site scale, 0.95 at the landscape scale, and 0.96 at the combination scale (Table 3); no independent data were available to validate on the model for artificial nest structures since all nest structures were used to build the model.

The combined-scale RSF model was most predictive for golden eagles and included covariates at the nest-site and landscape scales. Golden eagles selected nest sites with high surface roughness within 250 m of nests and moderate ($\sim 0.5 \text{ km/km}^2$) road density within 25 km

Table 2. Standardized model parameters for resource selection models of ferruginous hawks on occupied natural nests in Wyoming at three spatial scales, 2010–2011.

Scale	Coefficient	SE	CI	
			2.5%	97.5%
Nest-site				
Roughness 1k	-1.09	0.34	-1.81	-0.48
Shrub_Ht250	-0.20	0.33	-0.86	0.44
Shrub_Ht250 ²	-0.22	0.24	-0.72	0.13
Sage250	-0.28	0.29	-0.85	0.29
Sage250 ²	-0.29	0.24	-0.79	0.14
Crop1k	-0.61	0.31	-1.29	-0.07
Rd_dist	-0.39	0.19	-0.77	-0.03
Prey	0.21	0.18	-0.14	0.57
Landscape (best-performing scale)				
Roughness 5k	-1.72	0.44	-2.64	-0.94
Temp_Sp1500	-0.32	0.30	-0.91	0.26
Temp_Sp1500²	-0.49	0.25	-1.01	-0.03
Bare1500	0.35	0.28	-0.21	0.91
Crop10k	-0.61	0.31	-1.27	-0.08
Precip_Sp25k	0.10	0.34	-0.57	0.76
Precip_Sp25k ²	-0.39	0.26	-0.91	0.10
Sage25k	-0.15	0.30	-0.75	0.44
Sage25k ²	-0.07	0.18	-0.45	0.24
Rd_dist	-0.41	0.20	-0.81	-0.04
Combination				
Roughness 1k	-0.99	0.35	-1.74	-0.36
Sage250	-0.43	0.27	-0.98	0.08
Sage250 ²	-0.25	0.20	-0.67	0.11
Crop1k	-0.41	0.38	-1.22	0.29
Rd_dist	-0.40	0.19	-0.79	-0.03
Prey	-0.06	0.32	-0.69	0.57
Shrub_Ht25k	-0.53	0.38	-1.33	0.18
Shrub_Ht25k ²	-0.52	0.32	-1.19	0.05
Temp_Sp1500	-0.45	0.33	-1.11	0.20
Temp_Sp1500²	-0.56	0.25	-1.08	-0.09
Crop10k	-0.37	0.36	-1.13	0.30
Precip_Sp25k	-0.03	0.33	-0.68	0.61
Precip_Sp25k ²	-0.20	0.27	-0.74	0.33

Notes: Spatial scales are nest site, 0.25–1 km, landscape, 1.5–25 km, and combined, nest-site and landscape scale in combination. Significant covariates (i.e., 95% confidence intervals not overlapping 0) appear in boldface. Superscript numbers indicate quadratic terms in the model. SE, standard error.

(Table 4). Marginal response curves for covariates in the top-performing model indicated that golden eagles exhibited a sharply increasing and curvilinear selection response to landscape roughness that was essentially opposite to that observed for ferruginous hawks (Fig. 2).

However, the positive response of golden eagles to roughness was at a fine scale (250 m) immediately surrounding the nest site, compared to selection for low roughness by ferruginous hawks at a landscape scale (5 km). Golden eagles also exhibited a strong curvilinear response to roads that indicated selection for areas of moderate road density at a landscape (25 km) scale (Table 4, Fig. 2). Although not significant for either species, there was some evidence that golden eagles exhibited a curvilinear response to percent bare ground compared to the positive linear relationship with this covariate exhibited by ferruginous hawks (Fig. 2). Both species tended to avoid croplands, but ferruginous hawks responded at a broad scale (10 km) and golden eagles weakly at a finer scale (1 km; Table 4, Fig. 2). The combined RSF model for golden eagles was highly predictive with a Spearman-rank correlation of 0.93 (range of 0.67–0.92) for the individual folds (Table 3). The predicted values associated with the independent validation set of golden eagle nest locations also indicated strong model performance with a Spearman-rank correlation of 0.93 (Table 3).

Spatial mapping and species overlap

We used RSF coefficients from our most parsimonious and best-performing models (Tables 2, 4) to develop resource selection maps for ferruginous hawks and golden eagles (Fig. 3). These maps delineated spatial predictions of habitat suitability on a continuous scale (90 × 90 m pixel) across our study area. We also extracted the values associated with our validation sample ($N = 101$) of independent nests to provide an empirically based delineation of more-selected vs. less-selected habitat, where the more-selected bin accounted for 90% of independent nests for each species. For ferruginous hawks, 90% of nests from the independent sample were contained within bins 5 and higher of the top-performing RSF model (Appendix S1: Table S2; Fig. 4). The golden eagle model was less efficient, requiring RSF bins 3, and higher to capture 90% of historical nests (Appendix S1: Table S2; Fig. 4).

We intersected the simplified binary surfaces (i.e., more-selected vs. less-selected) for each species to evaluate the spatial overlap of selected nesting habitat between ferruginous hawks and golden eagles (Fig. 5). Approximately 35%

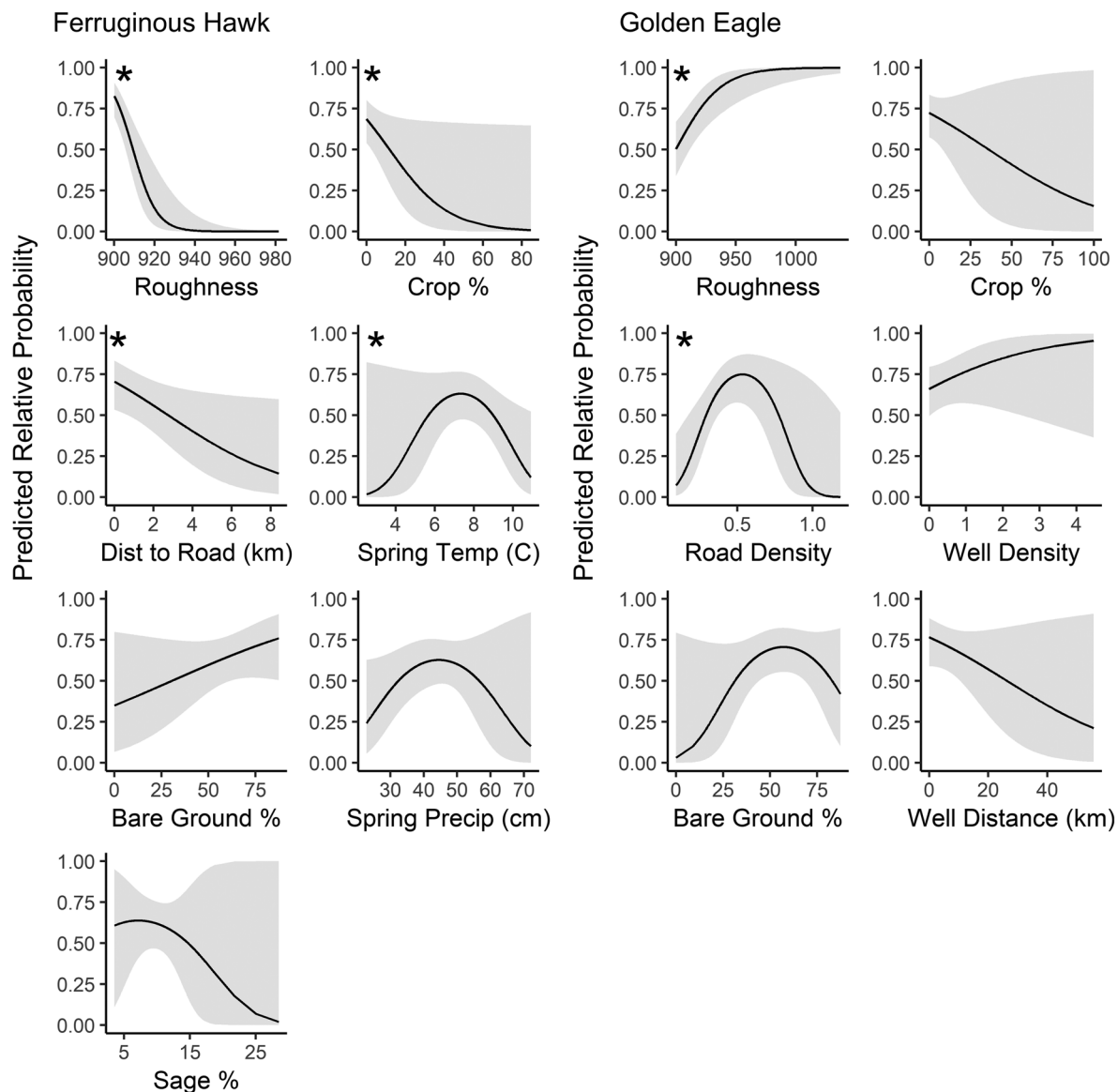


Fig. 2. Marginal response curves of each environmental covariate (see Tables 2, 3; model summary) in the top resource selection model for ferruginous hawks nesting on natural substrates (landscape scale) and golden eagles (combined scales) composed of environmental covariates (see Tables 2, 3; model summary). Plots were created by varying each covariate from the minimum to maximum, while holding all other covariates at their mean. The change in predicted relative probability indicates the strength of the individual contribution of each covariate to the model. Plots show standardized covariates with mean values of 0 to allow comparison across covariates with differing ranges. Significant variables with CI not overlapping zero are indicated by an asterisk.

(63,021 km²) of our study area was classified as more-selected by both ferruginous hawks and golden eagles (Fig. 5). This area was 48% within the Rolling Sage Steppe sub-ecoregion (Appendix S1: Fig. S1) that supports a sagebrush-

and wheatgrass-dominated vegetation community. However, golden eagles exhibited a broader spatial distribution in predicted nesting habitat than ferruginous hawks (Fig. 5). Golden eagles selected areas that intersected those that were

Table 3. Validation of resource selection function (RSF) models for nesting ferruginous hawks and golden eagles in sagebrush steppe, Wyoming, USA, 2010–2011, based on fivefold cross-validation for each spatial scale (nest-site, landscape, and combined).

Scale	Average	SE	Range	Historical nests
Ferruginous hawks–natural nests				
Nest-site	0.81	0.08	0.53–0.78	0.96
Landscape	0.98	0.02	0.79–0.96	0.96
Combined	0.95	0.03	0.69–0.94	0.89
Ferruginous hawks–artificial nest substrate				
Nest-site	0.94	0.05	0.60–0.90	n/a
Landscape	0.95	0.06	0.70–0.88	n/a
Combined	0.96	0.02	0.75–0.90	n/a
Golden eagles				
Nest-site	0.86	0.08	0.37–0.77	0.94
Landscape	0.68	0.12	0.33–0.64	0.67
Combined	0.96	0.05	0.67–0.92	0.93

Notes: Validation was bootstrapped 100 times to ensure stable estimates that were averaged with standard errors (SE) over iterations. Range was the range of correlations calculated for each of the five folds. Historical nests are correlations of independent nests (not used in selection modeling) imposed on RSF predictions. Best-performing model scales appear in boldface.

less-selected by ferruginous hawks on 39% (69,756 km²) of the study area, whereas areas that were less selected by golden eagles and more selected by ferruginous hawks accounted for only 10% (17,370 km²; Fig. 5). The broader predicted distribution for golden eagles was most evident in the Salt Desert Shrub and Big-horn Basin ecoregions of the Wyoming Basin (Appendix S1: Fig. S1; Fig. 5). These sub-ecoregions generally supported greasewood- and salt-bush-dominated shrublands that were largely avoided by nesting ferruginous hawks. Approximately 17% (30,802 km²) of the study area was less-selected by both species (Fig. 5).

Raptor resource selection and energy siting potential

For ferruginous hawks, 10 of the 96 nesting pairs (10% of total) had one or more producing oil or gas wells within 500 m of the occupied nest, 17 pairs (18%) had one or more wells within 1 km, and 42 (44%) had one or more wells within

Table 4. Standardized model parameters for resource selection models of golden eagles at occupied nests in Wyoming at three spatial scales, 2010–2011.

Scale	Coefficient	SE	CI	
			2.50%	97.50%
Nest-site				
Roughness 250	0.70	0.22	0.32	1.17
Crop1k	−0.60	0.46	−1.78	0.09
Well_dist	−0.74	0.29	−1.36	−0.21
Landscape				
Crop1500	−0.62	0.47	−1.76	0.10
Rd_den25k	0.50	0.33	−0.13	1.15
Rd_den25k²	−0.58	0.24	−1.11	−0.15
Well_den10k	0.27	0.23	−0.15	0.77
Well_dist	−0.26	0.28	−0.85	0.28
Bare1500	0.31	0.25	−0.17	0.82
Bare1500²	−0.38	0.23	−0.86	0.03
Combination (best-performing scale)				
Roughness 250	0.82	0.24	0.40	1.35
Crop1k	−0.41	0.46	−1.64	0.30
Well_dist	−0.39	0.33	−1.10	0.20
Bare1500	0.26	0.26	−0.24	0.81
Bare1500 ²	−0.38	0.24	−0.88	0.07
Well_den10k	0.30	0.24	−0.14	0.81
Rd_den25k	0.89	0.39	0.17	1.70
Rd_den25k²	−0.74	0.28	−1.35	−0.25

Notes: Spatial scales are nest site 0.25–1 km, landscape 1.5–25 km, and combined: nest-site and landscape scale in combination. Significant covariates (i.e., 95% confidence intervals not overlapping 0) appear in boldface. Superscript numbers indicate quadratic terms in the model. SE, standard error.

5 km. For golden eagles, 9 of the 63 nests (14%) had one or more producing oil or gas wells within 500 m, 13 nests (21%) were within 1 km of one or more wells, and 31 nests (49%) were within 5 km. At random locations, 70 of the 1000 (7%) had at least one well within 500 m, 127 (13%) had at least one well within 1 km, and 392 of the 1000 (39%) had at least one well within 5 km. The number of energy wells associated with occupied nests did not differ from random expectation for ferruginous hawks ($\chi^2 = 0.95$, $df = 2$, $P = 0.63$) or golden eagles ($\chi^2 = 1.70$, $df = 2$, $P = 0.43$). The median distance to the nearest producing oil or gas well was 5990 m (range 115–41,693 m) for occupied ferruginous hawk nests on natural substrates ($N = 96$ pairs), 3623 m (range 49–21,796 m) for occupied ferruginous hawk ($N = 80$ pairs) nests on artificial nest platforms, 54,18 m (range 134–32,278 m) for

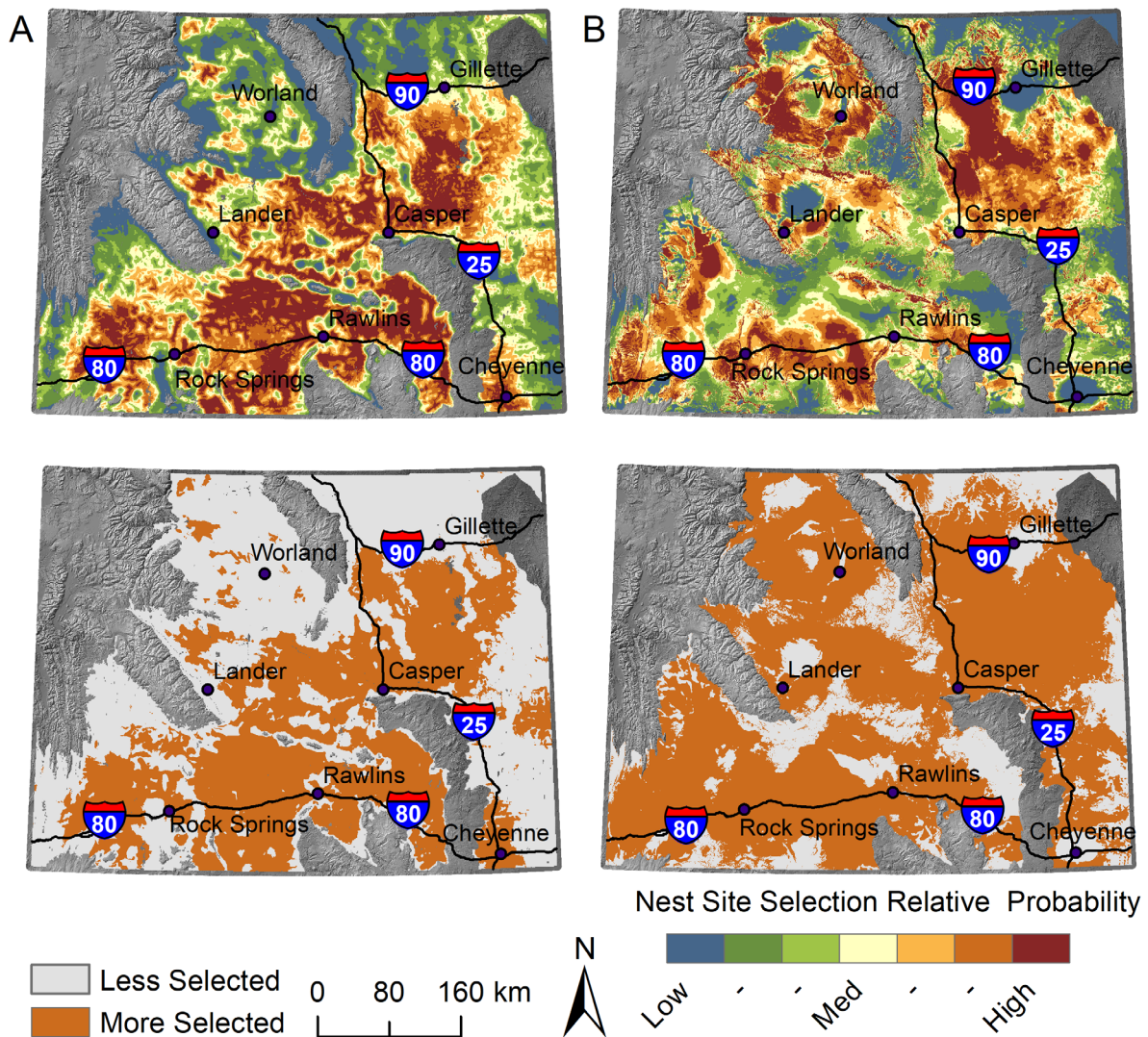


Fig. 3. (Top) Predicted relative probability of use for (A) ferruginous hawks and (B) golden eagles nesting in Wyoming, USA, 2010–2011, based on top-performing resource selection function (RSF) models. (Bottom) Spatial depiction of binary maps showing more-selected and less-selected (A) ferruginous hawk and (B) golden eagle nesting habitat based on a threshold determined to include 90% of historical nests (independent from RSF model development; ferruginous hawks: $N = 101$, golden eagles $N = 237$; see Fig. 4).

occupied golden eagle nests ($N = 63$), and 7198 m (range 36–59,430 m) for random points ($N = 1,000$) across the inference area. The average density of producing oil and gas wells within a 25 km radius circle around occupied nests was 0.002 wells/km² for ferruginous hawks and 0.01 well/km² for golden eagles, compared to 0.01 wells/km² in a 25-km radius around random locations across our inference area. Comparative

measures to wind turbines were not meaningful due to the clumped distribution and low density of wind infrastructure in Wyoming during our study period.

Distributions of potential oil/gas and wind power reserves varied spatially across the study area; areas of highest potential oil/gas reserves occurred mostly in the northeastern and in the southcentral/southwestern portions of Wyoming,

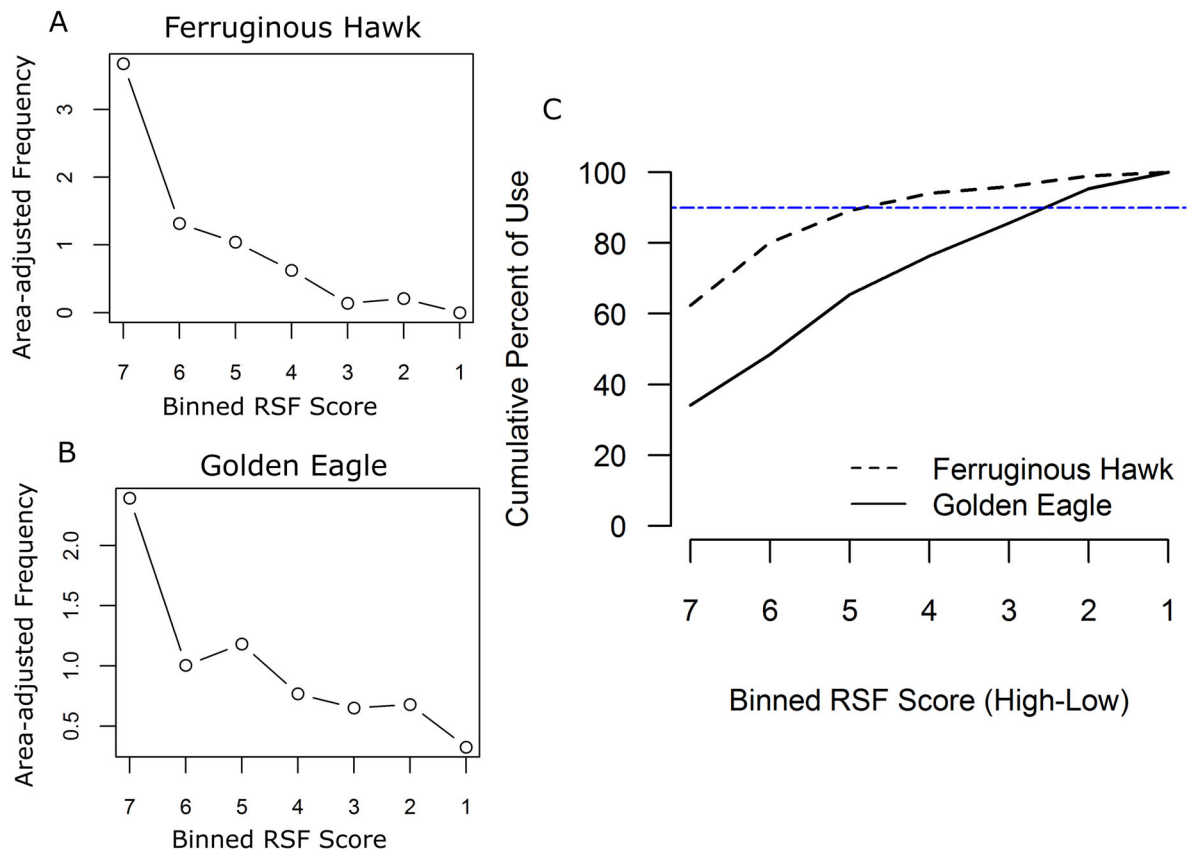


Fig. 4. Resource selection function (RSF) scores associated with historical independent nests from (A) ferruginous hawks ($N = 101$) and (B) golden eagles ($N = 237$) binned from low (1) to high (7) relative scores from predicted RSF values across sagebrush steppe in Wyoming, USA, as stratified based on equal-area intervals. Good model predictive ability is indicated when the number of nests per bin is positively correlated with bin rank. (C) Cumulative percent of historical nests included within binned predicted probabilities of nest-site selection (high to low) for ferruginous hawks (dashed line) and golden eagles (solid line). The bins below the horizontal line include 90% of historical nests (i.e., more-selected habitat) as defined by RSF bins 5–7 and 3–7 for ferruginous hawk and golden eagle nests, respectively.

whereas most potential wind power occurred in the southcentral/southeastern portions of the state (Table 5, Fig. 6). Areas of more-selected nesting habitat for ferruginous hawks (binned predicted RSF values 5–7; Fig. 4) and golden eagles (binned predicted RSF values 3–7; Fig. 4) largely overlapped areas of high-potential oil/gas development (Fig. 7; see Appendix S1: Fig. S3 for oil/gas overlap with less-selected nesting habitat). The spatial intersection between more-selected nest habitat and high-potential oil/gas development (bins 5–7) across the study area was 44,132 km² for ferruginous hawks and

72,601 km² for golden eagles (Appendix S1: Table S5). Observed ferruginous hawk nests on natural substrates ($\chi^2 = 28.26$, $df = 6$, $P < 0.001$) and golden eagle nests ($\chi^2 = 28.47$, $df = 6$, $P < 0.001$) differed from random expectation relative to intensity of potential for oil/gas development (oil/gas bins adapted from Julissson and Doherty 2017; Appendix S1: Table S3). Chi-squared residuals indicated the energy bin with the highest potential for oil/gas development (bin 7) contained a disproportionate number of occupied nests of ferruginous hawks and golden eagles when compared to random expectation

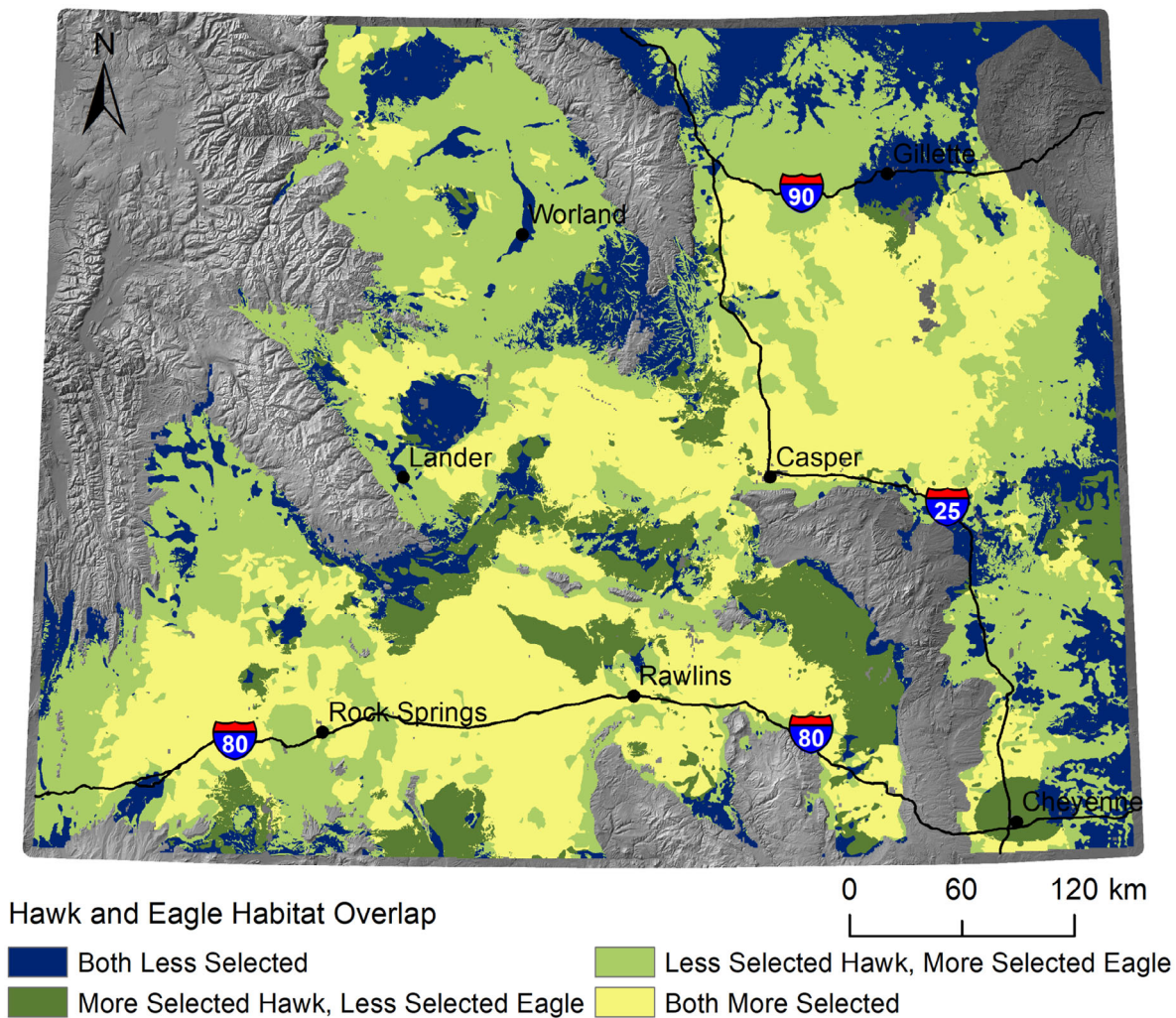


Fig. 5. Spatial overlap of areas less selected vs. more selected by ferruginous hawks and golden eagles across Wyoming, USA, 2010–2011. More-selected regions were defined as resource selection bins 5 and higher for ferruginous hawks and 3 and higher for golden eagles (see Fig. 4).

(Appendix S1: Fig. S4). Similarly, 87% of all active oil/gas wells ($N = 66,144$) on the study area (Wyoming Oil and Gas Conservation Commission) were located in this same bin of highest oil/gas development potential (Appendix S1: Table S4).

Areas of more-selected nesting habitat for ferruginous hawks (binned predicted RSF values 5–7; Fig. 3) and golden eagles (binned predicted RSF values 3–7; Fig. 3) also overlapped broadly to areas of potential wind power development based on wind power class (Fig. 8; see Appendix S1: Fig. S5 for potential wind power

overlap with less-selected nest habitat). The spatial distribution of ferruginous hawk nests on natural substrates ($\chi^2 = 46.52$, $df = 6$, $P < 0.001$) and golden eagle nests ($\chi^2 = 24.04$, $df = 6$, $P < 0.001$) differed from chance expectation relative to the wind power bins (Appendix S1: Table S3, Fig. S4). Ferruginous hawks located their nests more frequently than random expectation in wind power bins 3–5 and golden eagles in bins 3, 4, and 6 (Appendix S1: Table S3; Fig. 8). However, the current locations of wind turbines ($N = 1004$; Hoen et al. 2018) in the sagebrush and prairie ecosystem of Wyoming differed from random expectation

Table 5. The area (km²) and percent coverage of potential oil/gas (Juliusson and Doherty, 2017) and wind (NREL 2002; <https://eerscmap.usgs.gov/uswtdb/>) energy development across Wyoming, USA.

Area	Energy bin number						
	1	2	3	4	5	6	7
Wind area (km ²)	633,89	61,653	64,571	32,983	14,266	10,782	5506
Percent coverage	25	24	26	13	6	4	2
Oil area (km ²)	32,606	32,457	36,028	32,517	37,052	34,840	35,399
Percent coverage	14	13	15	13	15	14	15

Notes: We binned the original continuous (from 0 to 1) oil/gas development model (Juliusson and Doherty, 2017) into seven equal-area quantiles across the study area. Bins (from 0 to 7) for potential oil/gas development (see Fig. 6) were equal-area and not directly comparable to the geometric bins for potential wind power development.

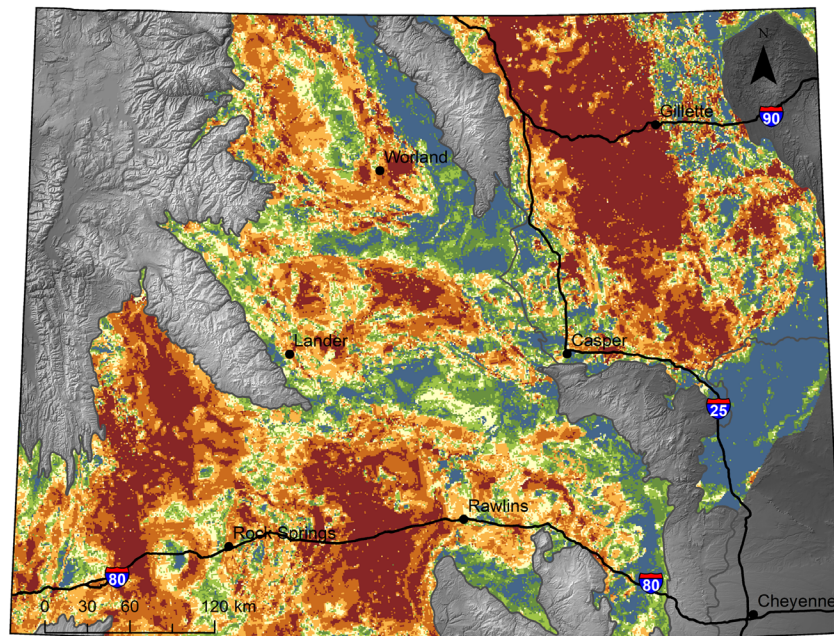
($\chi^2 = 2720.7$, $df = 4$, $P < 0.001$). Existing wind turbines were mostly in wind power bins 4–7 (Appendix S1: Table S6). Thus, the pattern of current wind turbine development on the landscape was similar to the current locations of ferruginous hawk and golden eagle nests.

DISCUSSION

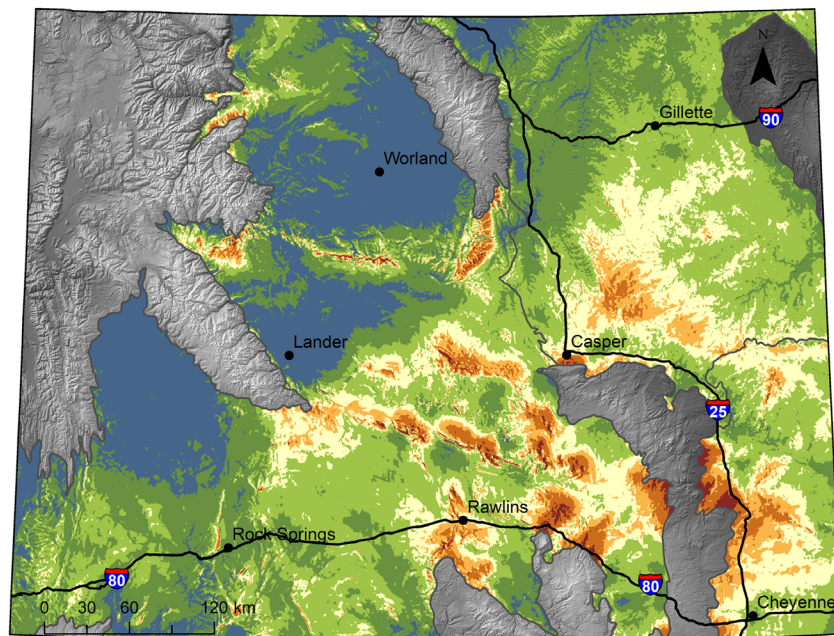
We studied patterns of resource selection for nesting ferruginous hawks and golden eagles across some of the most intact tracts of native sagebrush and prairie grasslands found in North America, but that are increasingly impacted by energy development and transmission. We demonstrated that ferruginous hawks and golden eagles exhibited differences in their habitat selection as represented by remotely sensed predictors of environmental heterogeneity (type 2 selection sensu Johnson 1980). Ferruginous hawks selected areas of low topographic roughness at the landscape scale with moderate spring temperatures, low cropland coverage, and in close proximity to roads. Golden eagles, in comparison, selected areas of high topographic roughness in the immediate nest area (250 m) within areas of moderate road densities at a landscape (25 km²) scale. Patterns of resource selection for both species were effectively modeled with remotely sensed covariates based on high standards of model validation. Contrary to our predictions, we found no evidence that ferruginous hawks or golden eagles overtly avoided energy infrastructure at the current density of development across our study area in selection of nesting sites/territories. For example, ferruginous hawks nested closer to roads compared to random expectation and golden eagles nested in

areas of moderate road density. In addition, the actual number of energy wells present near occupied nests did not differ from random expectation for either species.

An important caveat to this finding is that we investigated current patterns of nest-site selection for a relatively short study period. The patterns of selection we observed were after the construction of energy infrastructure so we lacked the ability to understand potential changes before and after development of long-term demographic responses of raptor or prey populations that could ultimately affect nearest-neighbor distance and raptor nest density (Skalski et al. 2005, Barbar et al. 2018). However, we also demonstrated that more-selected habitat (90% of use based on independent historical nests) for ferruginous hawks and golden eagles intersected the areas of greatest potential and current development of oil/gas reserves and wind energy. Thus, the risk of increased habitat fragmentation from conventional and renewable energy development is an important conservation issue, including how increased human disturbance may alter distributions or population trajectories over the long term. Selection of nesting habitat in areas with increased energy development for both species could create an ecological trap, if energy infrastructure and associated activities negatively impact demography (e.g., reproductive success, Kolar and Bechard 2016, Wiggins et al. 2017; survival of fledglings, Kolar and Bechard 2016; or survival of adults, Pagel et al. 2013). Alternatively, the birds could adapt to this novel infrastructure as suggested by ferruginous hawk use of artificial nest structures and given evidence that novel ecosystems can provide suitable habitat to some wildlife



A



B



Fig. 6. Spatial distribution of (A) modeled potential oil/gas development model reserves (Julusson and Doherty 2017) and (B) potential wind power based on modeled wind speed (NREL 2002; <https://eersmap.usgs.gov/>)

(Fig. 6. Continued)

uswtb/ in Wyoming, USA; see Table 5 for area (km²) and percent coverage of potential oil/gas and wind development potential. We binned the original continuous (from 0 to 1) oil/gas development model (Juliussjon and Doherty 2017) into 7 equal-area quantiles across the study area. Bins (from 0 to 7) for potential oil/gas development (see Fig. 6) were equal-area and not directly comparable to the geometric bins for potential wind power development.

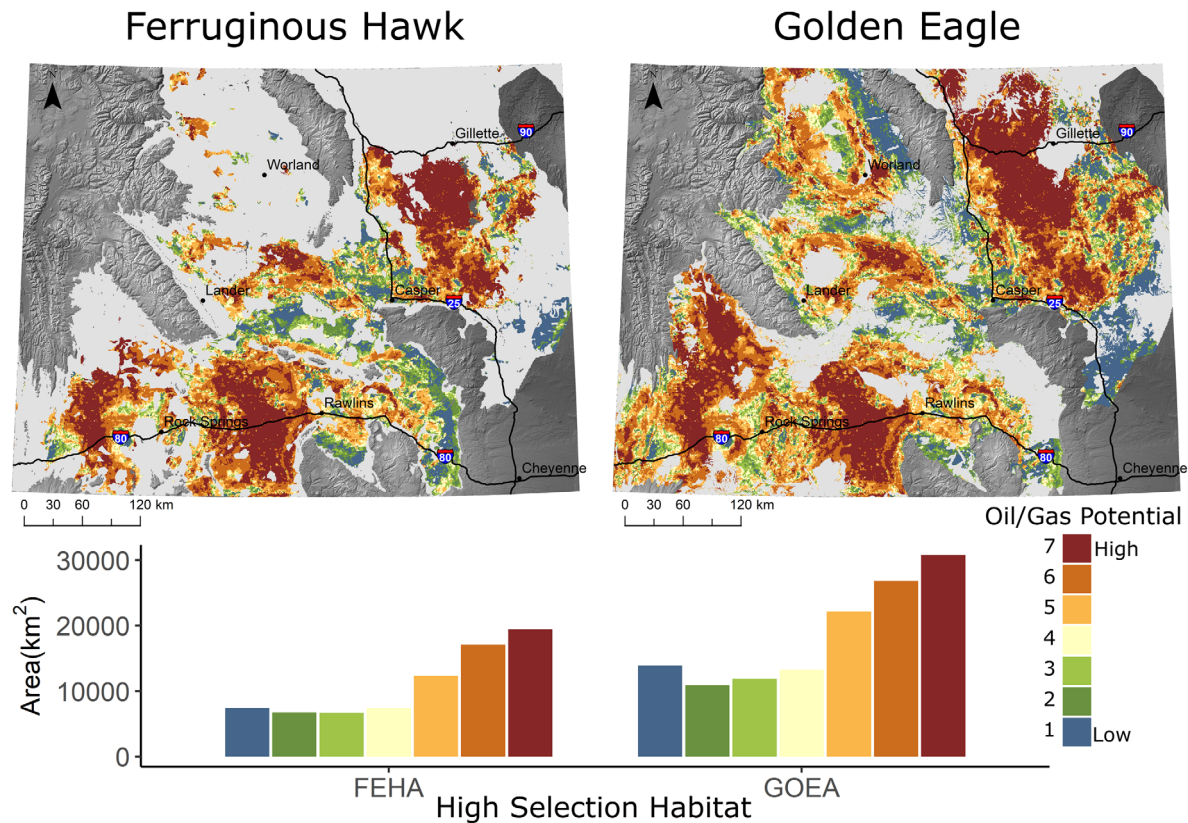


Fig. 7. Spatial distribution of oil/gas development potential (colors; bins 1–7 = low to high development potential; adapted from Juliussjon and Doherty 2017) within the more-selected nesting habitat for ferruginous hawks (binned predicted resource selection function [RSF] values 5–7; Fig. 4c) and golden eagles (binned predicted RSF values 3–7; Fig. 4c); light gray delineates less-selected habitat for each raptor. Bar plots show the area (km²) of each bin of oil/gas development potential within more-selected habitat for each raptor species.

(Kennedy et al. 2018) provided they do not reduce survival and productivity in a manner that threatens population persistence.

Resource selection of sympatric raptors

We demonstrated that ferruginous hawks and golden eagles were similar to other sympatric avian species in their differential partitioning across gradients of environmental heterogeneity (Siepielski and McPeck 2010, Beaulieu and Sockman 2012). Contrary to our listed prediction that

both raptors would select nesting areas of high topographic relief, topographic roughness was the strongest driver of habitat separation between ferruginous hawks and golden eagles compared to the other factors we considered. Ferruginous hawks exhibited a sharp decline in habitat suitability with increased roughness at a landscape scale compared to golden eagles that selected rough topography in the immediate (250 m) nest areas. We assumed this difference in selection for roughness was due to golden eagles frequently

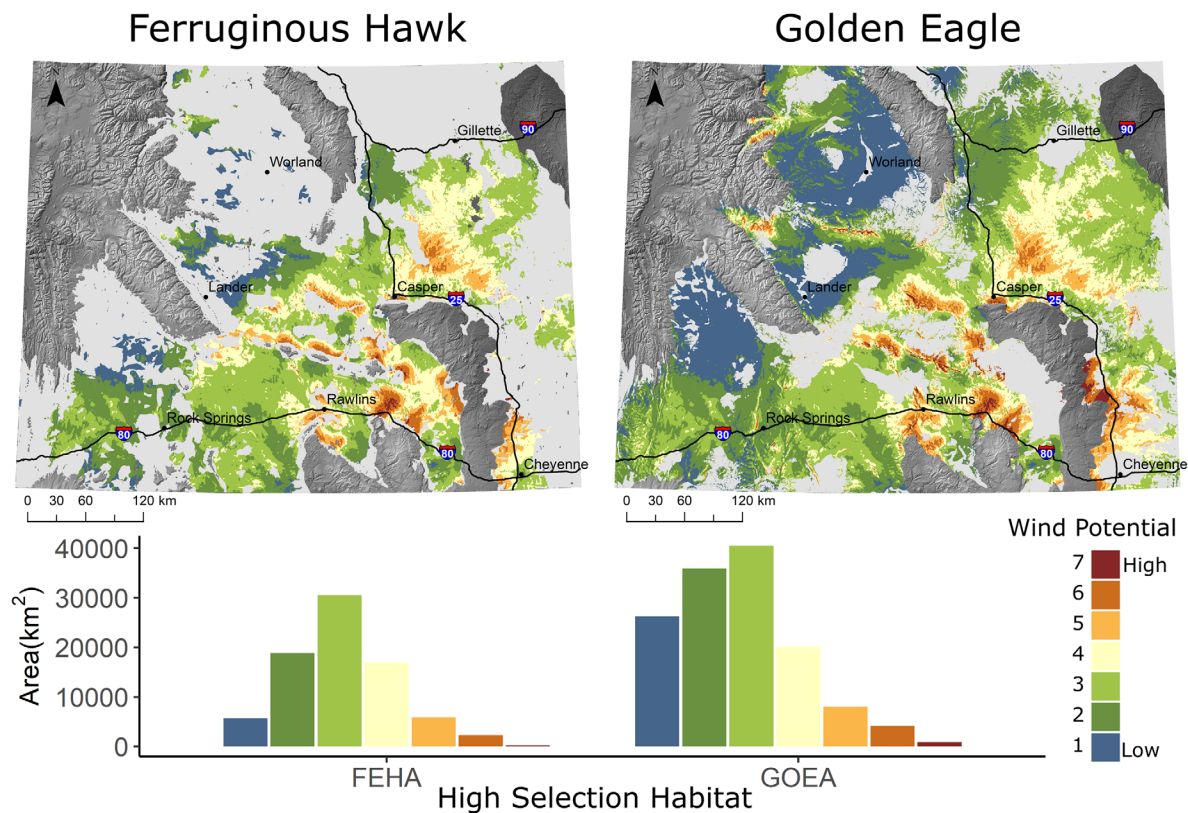


Fig. 8. Spatial distribution of potential wind resource development represented by wind power classes (colors; bins 1–7 = low to high wind speeds; NREL 2002; <https://eerscmap.usgs.gov/uswtdb/>) within the more-selected nesting habitat for ferruginous hawks (binned predicted RSF values 5–7; Fig. 4c) and golden eagles (binned predicted RSF values 3–7), Wyoming, USA; light gray delineates less-selected habitat for each raptor. Bar plots show the area (km²) of wind power classes within more-selected habitat for each raptor species.

nesting on cliffs (Kochert et al. 2002) and on taller substrates than ferruginous hawks (MacLaren et al. 1988). For example, 44% of golden eagle nests in our sample were on cliffs compared to 0% for ferruginous hawks. Although both species nest on erosional features, trees, and human-made structures, our results showed that ferruginous hawks selected relatively flat landscapes across home ranges, possibly to facilitate hunting or to reduce niche overlap and/or predation from golden eagles and other raptors. Golden eagles are also known to select locally elevated nesting substrates within broader landscapes of relatively smooth terrain (Tack and Fedy 2015, Dunk et al. 2019). However, our results suggest strong selection for rougher terrain in the immediate vicinity of nest sites, which may provide an axis of habitat separation between the overall rougher terrain selected by golden eagles compared to

ferruginous hawks. The avoidance of topographically rough areas by ferruginous hawks that we documented was also predicted by Keinath et al. (2010). An important caveat with our RSF models is the topographic roughness based on a 30-m digital elevation model was our inability to identify fine-scale habitat features used by ferruginous hawks as nest substrates (i.e., isolated trees, small erosional features). Rather, we evaluated a general index to topographic roughness that ranged from flat landscapes to areas of higher topographical complexity associated with cliffs, foothills, and low mountains.

We also demonstrated that resource selection of ferruginous hawks and golden eagles included predictive covariates associated with energy infrastructure, but in a manner inconsistent with our a priori predictions. Given that ferruginous hawks (White and Thurow 1985, Lehman et al.

2007, Ng et al. 2017) and golden eagles (Kaisanlahti-Jokimäki et al. 2008, Spaul and Heath 2016) exhibit sensitivity to human disturbance, we expected that energy development could alter resource selection similar to other species confronted with human disturbance. However, we found that energy infrastructure at current development densities (~2014–2015) did not predict patterns of nest-site selection for ferruginous hawks or golden eagles at the home-range scale. Ferruginous hawks nesting on natural substrates selected sites that were closer to roads compared to random expectation. Most gravel roads present in home ranges were associated with oil/gas infrastructure, and we recognize that ferruginous hawks can habituate to vehicular traffic (MacLaren et al. 1988, Nordell et al. 2017). The observed linear response of ferruginous hawks to roads (see Fig. 2) was consistent with preferential use of some energy-related infrastructure (e.g., roads, power poles) for perching or as nest substrates as documented by Tigner et al. (1996) and Zelenak and Rotella (1997). In contrast, Smith et al. (2010) found that ferruginous hawks in Wyoming, USA, exhibited greater nest-cluster use in areas with less oil and gas development and proportionately more non-energy roads within 0.8 km, but the relationship diminished at larger scales (>2.0 km). The study area of Smith et al. (2010) included more areas of high-density energy development, compared to our representative sample from across the distribution of ferruginous hawks in Wyoming, USA. Fifty-five percent of ferruginous hawk pairs in our study nested within 5 km of an oil/gas well and 20% nested within 1 km. Consistent with our observed patterns of resource selection, Wallace et al. (2016a, b) found this same population showed no correlation of nest-site occupancy, daily nest survival rate, or fledgling production with oil/gas infrastructure at the current development density.

Although we found that ferruginous hawks appeared relatively insensitive to energy-related infrastructure in their nest-site selection, we believe there are anecdotal observations that suggest an upper threshold exists where human disturbance influences nest-site occupancy. For example, the Pinedale Anticline and the Jonah Drilling Project Areas, near Pinedale, Wyoming, USA, had an approximate density of 21 and 27 producing gas and oil wells per km², respectively

(Wyoming Oil and Gas Conservation Commission). The Jonah field supported 6 pairs in 1997 and 1998 (i.e., pre-development; Bureau of Land Management 1999) compared to no pairs in the core oil field and two active pairs immediately adjacent in 2012 (U.S. Bureau of Land Management 2012). Ferruginous hawks ceased to nest on the ground concurrent with the sharp increase in energy development (R. Yanish, *personal communication*). Thus, there may be a disturbance threshold where high levels of energy development may reduce nest-site occupancy for ferruginous hawks, as well as golden eagles. Therefore, future research is justified to empirically identify these species-specific thresholds and use them as siting criteria.

We predicted that ferruginous hawks nesting on artificial nest structures would differ in their patterns of resource selection compared to ferruginous hawk pairs selecting natural substrates (i.e., rock outcrops, hill sides, trees, erosional spires), since human placement of nests may not mimic the nest selection process of ferruginous hawks. Artificial nest structures are often used to lure raptors away from nesting on energy infrastructure (e.g., wells, tanks, power poles), so they are often placed in areas of high energy development (Howard and Hilliard 1980, Neal et al. 2010, Smith et al. 2010). These nest structures are also used as mitigation for loss of natural nests. The environmental characteristics around artificial nest platforms differed in some ways to ferruginous hawks nesting on natural substrates. Compared to pairs on natural substrates, ferruginous hawks nesting on artificial nest structures were in areas of low topographic roughness, and areas of moderate amounts (non-linear relationship) of spring precipitation (weaker for birds on natural substrates) and spring temperatures. Hawks nested on both classes of substrates used areas close to energy-haul roads; however, pairs nesting on artificial nest structures used sites close to oil/gas wells in areas of moderate shrub height, and there was no signal that croplands factored into nest selection. Thus, the placement of artificial nest structures and other energy infrastructure used as nesting substrates altered patterns of resource selection for ferruginous hawks. Wallace et al. (2016b) found this same population of ferruginous hawks on artificial nest structures had a higher daily nest survival rate compared to pairs

on natural substrates. The altered pattern of nest-site selection that we documented apparently did not result in an ecological sink or trap. However, we offer this conclusion with the important caveat that we did not monitor population vital rates such as survival to detect increased adult mortality (e.g., electrocution, shooting) or reduced nestling survivorship based on proximity to energy infrastructure.

Ferruginous hawks and golden eagles are morphologically similar species in their ability to kill relatively large-bodied prey (rabbits, hares, prairie dogs, and ground squirrels) when nesting (Kochert et al. 2002, Bedrosian et al. 2017, Ng et al. 2017); ferruginous hawks are the largest Buteo in North America (Ng et al. 2017). Keough and Conover (2012) found that habitat selection by ferruginous hawks in Utah, USA, was driven by biotic interactions including high abundance of favored prey species, such as rabbits, ground squirrels, and prairie dogs coupled with a low abundance of competing raptor species. A strength of our study was the ability to incorporate models of prey abundance that were developed on our study area so these relationships could be considered in relation to raptor resource selection. Our a priori prediction that sagebrush cover would influence patterns of resource selection for ferruginous hawks and golden eagles due to a potential influence on prey populations was generally unsubstantiated based on our modeling. Although sagebrush height was a significant predictor for ferruginous hawks nesting on artificial nest structures, the remotely sensed sagebrush indexes added little predictive ability to models of resource selection for ferruginous hawks or golden eagles. Olson et al. (2017) modeled and spatially mapped potential mammalian prey species at a landscape scale across our inference area using similar remotely sensed covariates, including the same measures of sagebrush height and cover. This study found the density of white-tailed prairie dogs (*Cynomys leucurus*), Wyoming ground squirrels (*Urocitellus elegans*), and leporids was negatively correlated with the proportion of shrub/sagebrush cover and positively associated with herbaceous cover or bare ground. Olson et al. (2017) used the same remotely sensed sagebrush and vegetation layers created by the USGS (Homer et al. 2012) as we did in the present study to index the environmental heterogeneity

associated with this covariate. A limitation of these data layers was a low correlation between modeled sagebrush abundance and actual vegetation quantified in the field (Homer et al. 2009, 2012). Thus, while the USGS sagebrush data product provided the best available index of shrub attributes for modeling that were available, it may not necessarily reflect with high accuracy the actual density or shrub cover present.

Raptor resource selection and energy siting potential

Effective conservation actions that convey the greatest benefit to sympatric raptors such as ferruginous hawks and golden eagles require a spatially explicit understanding of how potential energy development relates to predicted habitat quality (Tack and Fedy 2015, Juliusson and Doherty 2017). They also require a knowledge of how actual patterns of development conform to modeled predictions. Tack and Fedy (2015) documented low overlap between high-quality golden eagle habitat and areas of high wind power potential, such that most nests occurred in areas of low wind power development potential. However, they cautioned that potential bias from their non-random sampling design could limit their ability to draw definitive conclusions of potential energy development risk. Although we also found that more-selected habitat for ferruginous hawks and golden eagles was generally separated spatially from regions modeled as highest for wind energy potential, both species were present disproportionately in the wind power bins that corresponded to areas of actual wind turbine deployment ($N = 1004$ turbines; Hoen et al. 2018), resulting in a high overall spatial exposure to risk.

Our evaluation of energy overlap was based on a random sampling design, resulting in a representative sample of occupied nests that allowed for valid conclusions on the potential risk of habitat fragmentation associated with current and modeled energy development. However, we highlight the caution expressed by Tack and Fedy (2015) that it was also beyond the scope of our research to evaluate long-term demographic responses of ferruginous hawks and golden eagles to overlap with current and projected energy development such as adult survivorship, nest turnover rates, productivity, and patterns of mortality. Risk assessments based on patterns of

species abundance provided no clear pattern of actual mortality (Ferrer et al. 2012), nor account for the vulnerability component of risk (Bedrosian et al., *unpublished manuscript*), which is a function of bird behavior relative to the fine-scale siting of development infrastructure and hazards (Watson et al. 2018). Our results are not intended to inform the fine-scale decisions on the configuration of energy development infrastructure, such as the placement of wind turbines and oil/gas infrastructure. Rather, our findings are intended to inform the broad-scale planning of conservation and development by providing a quantitative evaluation of potential risk from fragmentation and habitat loss from development at a regional scale. We also acknowledge that cumulative impacts associated with multiple sources of additive mortality from anthropogenic sources can result in increased vulnerability of avian populations (Schultz 2010, Loss et al. 2015). Assessing how the cumulative impact of increased energy development may alter patterns of mortality for ferruginous hawks and golden eagles was beyond the scope of our research. However, while our results support the conclusion that ferruginous hawks and golden eagles may be vulnerable to increased habitat fragmentation from both oil/gas and wind energy development based on documented overlap, we could not address actual population-level responses for the long term.

CONCLUSIONS

Although ferruginous hawks and golden eagles differed in their selection for some measures of environmental heterogeneity, neither species exhibited a strong avoidance of energy infrastructure at current levels as evidenced by preferential inclusion of some energy infrastructure (e.g., roads, powerlines) at occupied nests similar to other studies (Zelenak and Rotella 1997, Wallace et al. 2016a). We offer this result with the important caveat that we did not assess impacts to demography, such as survival or productivity, or population persistence. However, we also demonstrated that high-quality habitat for ferruginous hawks and golden eagles in sagebrush and prairie ecosystems is at risk of further loss and fragmentation based on predicted patterns of spatial overlap with oil/gas and wind energy development. Spatial-use predictions for ferruginous hawks and golden eagles provided by

this research provide a means for regional planning to reduce fragmentation from increased energy infrastructure. These results also justify the long-term monitoring plans for ferruginous hawks and golden eagles nesting in sagebrush and prairie ecosystems. Ideally, monitoring efforts would not only document trends in occupancy (Mackenzie and Royle 2005, Ellis et al. 2014, Wallace et al. 2016a), but would also evaluate demographic responses in terms of adult survivorship, pair turnover rates, and productivity across a gradient of energy development intensity. Monitoring plans would need to be long term ($\approx 20\text{--}30$ yr) because changes in territory occupancy can take decades to be expressed given philopatric behaviors of nesting, long-lived raptors (Millsap et al. 2015).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3204/full>