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ARTICLE

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Resource selection by greater sage-grouse varies by season and infrastructure type in a Colorado oil and gas field

Brett L. Walker

Colorado Parks and Wildlife, Grand Junction, Colorado, USA

Correspondence
Brett L. Walker
Email: brett.walker@state.co.us

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Abstract

Energy development is one of the most rapidly increasing land uses in North America, so understanding how wildlife respond to different types of energy infrastructure is crucial for informing land-use policies. Effects of energy development on wildlife habitat use and selection can vary depending on infrastructure type, level of industrial activity, and density. I examined seasonal habitat use and selection of greater sage-grouse in relation to energy development in a high-elevation oil and gas field in western Colorado by linking spatially and temporally explicit energy infrastructure layers with telemetry locations of marked females from 2006 to 2014. Objectives were to (1) quantify energy infrastructure around seasonal use locations; (2) examine how seasonal resource selection is affected by energy infrastructure with disturbed versus reclaimed surface and different levels of industrial activity; and (3) assess current surface disturbance and infrastructure density caps. Between 92% and 97% of seasonal use locations had <3% disturbed surface within 1000 m. After accounting for landcover and topography, breeding and wintering females selected locations with less disturbed, reclaimed, and total anthropogenic surface. Breeding females selected locations farther from high-activity well pads and facilities. In contrast, females selected locations with low to intermediate values of disturbed and reclaimed surface and locations closer to pipelines and roads in summer–fall. This is the first evidence that greater sage-grouse select locations with energy infrastructure in any season and suggests that responses to energy development may differ between mesic and arid sagebrush ecosystems. Females avoided locations with >1.1%–2.5% disturbed surface during breeding and winter and selected locations with lower densities of active energy features during breeding and roads in winter. Density caps of one active energy feature and 1.5 mi (2.41 km) of road per section were adequate to prevent avoidance except during the breeding season. Disturbance caps should be set at 1.1% disturbed surface and 1.8% total anthropogenic surface in breeding habitat and 2.5% disturbed surface and 3.5% total anthropogenic surface in winter habitat to minimize negative impacts on female habitat selection in this population. Results also support timing restrictions on construction and drilling during breeding and rapid transitioning of well pads from drilling to production.

KEYWORDS
Centrocercus urophasianus, density caps, energy development, land use, pipeline, reclamation, resource selection, road, sagebrush, surface disturbance, unconventional natural gas, well pad

INTRODUCTION

Understanding how wildlife respond to infrastructure associated with energy development is crucial for informing management and land-use policies. Energy development is one of the most rapidly expanding land uses in North America (Allred et al., 2015; Copeland et al., 2011; Trainor et al., 2016), and current and projected energy demand in the United States is expected to drive additional development through 2050 (U.S. Energy Information Administration, 2020). The increasing rate and distribution of energy development in North America has prompted assessments and projections of its effects on landcover, ecosystem services, biodiversity (e.g., Allred et al., 2015; Jones et al., 2015; McClung & Moran, 2018; Moran et al., 2017), and wildlife habitat (e.g., Nasen et al., 2011; Riley et al., 2012; Sushinsky et al., 2017). Energy development requires a network of different infrastructure components (i.e., well pads, facilities, pipelines, roads, etc.), each of which can have different effects on wildlife habitat suitability (Jones & Pejchar, 2013; Northrup & Wittemyer, 2013; Walston et al., 2009). The combined effects of infrastructure often lead to avoidance by wildlife and declines in wildlife populations within and around developed fields (Hovick et al., 2014; Naugle, 2011; Northrup & Wittemyer, 2013). However, some components of infrastructure may increase suitable habitat for some species or in some seasons (e.g., Barton et al., 2016; Bernath-Plaisted et al., 2017; Farwell et al., 2019; Harju et al., 2018).

Reducing negative impacts of energy development on wildlife populations requires an understanding of how animals respond to different components of energy infrastructure. Some components, such as well pads, facilities, and roads, convert natural landcover to disturbed (i.e., "impervious") surfaces with bare, compacted soil or structures and result in habitat loss for most terrestrial species (Jones & Pejchar, 2013). In contrast, pipelines and inactive (or abandoned) well pads and facilities usually have reclaimed or recovering (i.e., "non-impervious") surface with residual habitat value for wildlife that increases over time as soil and vegetation recover (Avirmed et al., 2015; Gasch et al., 2016; Waller et al., 2018). Energy development also influences the suitability of areas around infrastructure for species with large-scale habitat requirements (e.g., "area-sensitive" and "landscape" species; Brittingham et al., 2014). Industrial activity (e.g., noise, light, dust, emissions, and human presence) can cause wildlife to avoid areas around energy infrastructure (e.g., Blickley, Blackwood, & Patricelli, 2012; Blickley, Word, et al., 2012; Farwell et al., 2019; Sawyer et al., 2009, 2017, 2019; Thompson et al., 2015). Energy infrastructure can also have cascading effects on a species' predators, parasites, pathogens, or prey that influence ecological interactions and responses to development in different ways (e.g., Coates et al., 2020; Gibson et al., 2018; Harju et al., 2018; Hethcoat & Chalfoun, 2015).

How wildlife respond to energy infrastructure can also vary among populations or ecosystems due to variation in the availability of suitable alternative habitat, success of on-site reclamation or mitigation, rate of vegetation recovery following disturbance, the amount and density of infrastructure, and the distribution of infrastructure in relation to important seasonal habitats. For these reasons, understanding population-specific wildlife responses to energy infrastructure is essential for predicting and mitigating impacts of specific development proposals (Doherty et al., 2010; Harju et al., 2010). Understanding variation in responses across populations is also needed to predict effects of energy development at statewide and regional levels (e.g., Doherty et al., 2016; Garman, 2018; Heinrichs et al., 2019; Juliusson & Doherty, 2017).

The Bureau of Land Management (BLM) recently amended resource management plans to include disturbance and density caps to reduce negative impacts of energy infrastructure on wildlife on federal lands (e.g., BLM, 2015a, 2019a). However, due to the potential for population-specific responses, it is important to assess the effectiveness of disturbance and density caps in local populations. This can be done by quantifying wildlife responses to percent surface disturbance and infrastructure density and examining whether animals avoid areas where surface disturbance values exceed recommended caps.

The greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") is a native upland game bird inhabiting sagebrush (*Artemisia* spp.) ecosystems of western North America. Individuals often have large seasonal home ranges and can make long movements within and between seasons (Fedy et al., 2012; Pratt et al., 2019; Tack et al., 2012). Sage-grouse are a major conservation and management concern due to long-term population declines and range contraction (Aldridge et al., 2008; Connelly et al., 2004; Schroeder et al., 2004) as well as ongoing loss and modification of sagebrush ecosystems by expanding energy infrastructure (U.S. Fish and Wildlife Service, 2015). Numerous previous studies have documented negative impacts of energy development on sage-grouse habitat, physiology, habitat use and selection, demographic rates, and abundance (reviewed in Naugle et al., 2011; Appendix S1: Table S1).

Little is known about how sage-grouse respond to energy development in mesic mountain big sagebrush ecosystems. In all, 14 previous studies have documented avoidance of energy infrastructure by sage-grouse (Appendix S1: Table S1), all of which were conducted in relatively arid ecosystems (18–36 cm annual precipitation; Goodrich et al., 1999) with flat, open terrain within largely contiguous sagebrush or sagebrush-grassland in Montana, Wyoming, or Alberta. Avoidance in these studies may be due to low reclamation success and slow recovery of sagebrush following disturbance in arid ecosystems (35–87 years; Avirmed et al., 2015; Gasch et al., 2016; Nauman et al., 2017; Rottler et al., 2018). Effects of industrial activity (e.g., noise, dust) may also radiate farther around infrastructure in open terrain (Blickley, Blackwood, & Patricelli, 2012; Holloran, 2005). In contrast, mountain big sagebrush ecosystems have higher annual precipitation (36–64 cm; Goodrich et al., 1999), so vegetation typically recovers more quickly following disturbance and reclamation (Davies & Bates, 2010; Nelle et al., 2000; Pyke et al., 2015). The presence of more rugged terrain and more diverse landcover around infrastructure in mountainous areas may help buffer effects of industrial activity on surrounding habitat. Responses to energy infrastructure may also be constrained if limited habitat is available for movement or dispersal in geographically isolated mountain populations (Holloran et al., 2010).

Understanding the distance around infrastructure at which industrial activity influences sage-grouse habitat selection is also important to infrastructure siting to minimize impacts (Manier et al., 2014). Well pads and facilities with greater industrial activity (e.g., in the construction and drilling phase) are assumed to be more disruptive to sage-grouse than those with either low levels of activity (e.g., in production phase) or no activity (e.g., abandoned or reclaimed) (BLM, 2015a, 2019a). Managers therefore commonly apply daily or seasonal timing restrictions on construction and drilling to reduce impacts of industrial activity on sensitive life stages. While this assumption is reasonable, it has not been widely tested. Blickley, Blackwood, and Patricelli (2012) experimentally demonstrated that leks with continuous drilling and intermittent road noise had reduced male attendance compared to control leks, and Holloran et al. (2015) found evidence that wintering sage-grouse avoided well pads with greater levels of industrial activity.

Finally, reducing impacts of energy development on local sage-grouse populations requires identification of metrics and thresholds that accurately predict negative impacts (BLM, 2011; Gamo & Beck, 2017). Negative impacts on sage-grouse are most often associated with measures of percent anthropogenic surface disturbance (e.g., Gamo & Beck, 2017; Kirol et al., 2020; Smith et al., 2014) or well-pad density (e.g., Carpenter et al., 2010; Dinkins et al., 2014; Doherty et al., 2008, 2010; Fedy et al., 2015; Green et al., 2017; Gregory & Beck, 2014; Holloran et al., 2015; Spence et al., 2017). For that reason, resource management plan amendments in Colorado have incorporated caps on anthropogenic surface disturbance (3%) and disruptive energy feature density (one feature per section) for development projects in priority sage-grouse habitat management areas (BLM, 2011, 2015a, 2019a). Road density caps of 1.5 mi (2.41 km) of improved road/section within sage-grouse habitat have also been proposed (BLM, 2019b). It is important to assess whether current disturbance and density caps are adequate to prevent avoidance by sage-grouse. Determining which components of infrastructure result in avoidance, and which do not, also helps managers determine which components should be included in surface disturbance calculations.

In this study, I use telemetry locations of marked females and time-stamped, spatial data on energy and other anthropogenic infrastructure to answer questions about how sage-grouse use and select seasonal habitat in relation to energy development. Specifically, my work aimed to determine (1) how much infrastructure occurs around locations used by sage-grouse, (2) how females select habitat in relation to energy infrastructure with different surface status (i.e., disturbed vs. reclaimed) and different levels of industrial activity, and (3) whether current disturbance and density caps are adequate to prevent avoidance. To do this, I first modeled third-order resource selection in relation to landcover and topography in each season and then examined whether the performance of landcover and topography models was improved by the addition of relevant infrastructure metrics.

METHODS

Study area

The study area encompassed Colorado Parks and Wildlife's 1413.3-km^2 occupied range boundary for the Parachute-Piceance-Roan (PPR) sage-grouse population in Rio Blanco and Garfield counties in western Colorado (Figure 1). Birds in this population occupy shrub-dominated habitats

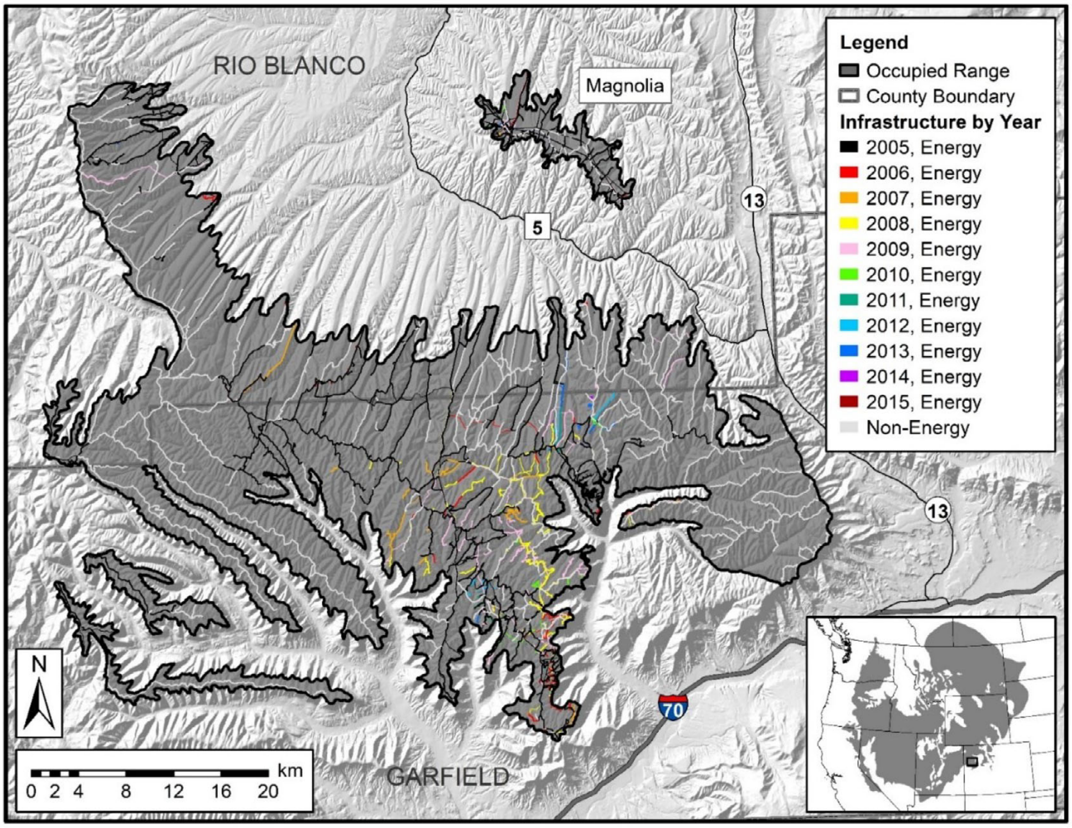

FIGURE 1 Study area showing the distribution of anthropogenic (primarily energy) infrastructure as of mid-summer 2015 within occupied range for the Parachute-Piceance-Roan greater sage-grouse population in Rio Blanco and Garfield counties, Colorado, USA (from Walker et al., 2020). Colors denote estimated most recent year of infrastructure construction or modification. Inset shows the study area in relation to greater sage-grouse range (from Schroeder et al., 2004) and US state and Canadian provincial boundaries

on ridges and plateaus between 2150 and 2750 m in elevation (Hagen, 1999; Walker et al., 2016). Average annual precipitation increases with elevation from 41 to 64 cm (Colorado Greater Sage-grouse Steering Committee [CGSSC], 2008). Vegetation in occupied habitats is dominated by mountain big sagebrush (*Artemisia tridentata vaseyana*), sagebrush-grassland, and sagebrush mixed with mountain shrubs, such as serviceberry (*Amelanchier* sp.), Gambel oak (*Quercus gambelii*), yellow rabbitbrush (*Chrysothamnus viscidiflorus*), snowberry (*Symphoricarpos* sp.), bitterbrush (*Purshia tridentata*), and mountain mahogany (*Cercocarpus* sp.) (Cottrell & Bonham, 1992). Occupied habitat occurs on ridges, upper slopes, and in the top ends of valleys and is naturally fragmented by cliffs and deep drainages. At higher elevations, sagebrush is interspersed with patches of quaking aspen (*Populus tremuloides*), conifers, and mountain shrubs. At lower elevations, sagebrush transitions to two-needle pinyon (*Pinus edulis*) and juniper (*Juniperus* spp.) woodland. Major land uses included year-round natural gas development and spring–fall livestock grazing. Most energy development in the study area was concentrated in the south-central portion of the main population and in the disjunct Magnolia portion (Figure 1). Land and mineral ownership in the study area was approximately 61% private surface with private mineral rights, 4% private surface with federal minerals, 33% federal surface and minerals (Bureau of Land Management), and 2% state surface with mostly federal minerals (CGSSC, 2008). Some private landowners (including energy companies) worked with CPW to voluntarily protect or enhance sage-grouse habitat on private land during the study from 2006 to 2014. From 1997 to 2014, new energy development was prohibited on federal surface and federal mineral leases within 3.2 km (2 mi) of active leks during the breeding season, within concentration areas in winter (if designated), and within 0.4 km (0.25 mi) of active leks year-round (BLM, 1997).

Capture and telemetry

Field crews captured and marked female sage-grouse with unique, numbered, aluminum leg bands and VHF necklace collars from April 2006 to November 2009 and again from July 2012 to November 2013 (Walker et al., 2016). Birds were captured using long-handled hoop nets and spotlighting with binoculars (Wakkinen et al., 1992), throw nets, drop nets, CODA net launchers (CODA Enterprises, Mesa, AZ), and SuperTalon (Advanced Weapons Technology, La Quinta, CA) and MagNet (Wildlife Capture Services, Flagstaff, AZ) compressed air net-guns. The Colorado Parks and Wildlife (CPW) Animal Care and Use Committee (#01-2006 and #08-2012, plus addenda) approved all capture and marking methods.

Crews tracked marked birds primarily during the day using three-element directional Yagi antennas and hand-held VHF receivers (Communication Specialists, Orange, CA). Crews located birds visually or by close-range triangulation (5–100 m) and recorded their locations with global positioning system units (Garmin International, Olathe, KS). Crews located birds 4–10 times per month in spring–summer (March–July) and two to four times per month in fall–winter from 2006 to 2010, then two to four times per month in spring 2013 and 2014 (Walker et al., 2016).

Study design

The objective was to investigate how sage-grouse select habitat within seasonal use areas (i.e., third-order or "within home-range" selection; Mayor et al., 2009; Meyer & Thuiller, 2006) in relation to different components of energy infrastructure after accounting for the effects of surrounding landcover and topography. To do this, I defined seasonal use areas for each individual, modeled relative probability of selection in each season based on used-available data within those areas in relation to landcover and topography, and tested whether the addition of infrastructure variables to the best-supported landcover + topography model in each season improved model fit (Aarts et al., 2008; Beyer et al., 2010; Manly et al., 2002). Used and available locations were matched by individual and, within each individual, stratified by year, a modified type III design (Erickson et al., 2001; Thomas & Taylor, 2006). Stratifying used and available locations by year was necessary because the distribution of energy infrastructure, and therefore, infrastructure cover, distance, and density values measured at each used and available location, changed over time.

Data analysis

Used and available locations

I included each nest and relocation of a live, marked bird as a used location and assumed that locations of different individuals were independent. I analyzed used-available data during breeding, summer–fall, and winter separately. I divided used locations by season following Walker et al. (2016): (1) breeding (14 March–end of early brood-rearing [22 June–9 July, depending on the year]), (2) summer–fall (late brood-rearing–14 November), and (3) winter (15 November–13 March), except that the start of winter was moved to 15 November to better coincide with breakpoints in snow depth and temperature at local weather stations (Western Regional Climate Center, Reno, NV). I defined seasonal use areas by creating a dissolved 1-km radius (3.14 km^2) buffer around used locations for each individual in each year in each season. This approach facilitates defining availability for individuals with sparse data and for individuals that make long-distance within-season movements for which estimating a seasonal home range is difficult. A 1-km radius corresponds closely with the maximum daily movement distances of marked birds across seasons (927–1091 m). I generated a systematic-random grid of available locations 100 m apart across the study area and selected available locations from within each individual's seasonal use area in each year. I clipped available locations to occupied range (Figure 1; defined as areas of suitable habitat with known use or adjacent to areas of known use [CGSSC, 2008]) to appropriately constrain the extent of available points for third-order selection and to minimize inclusion of obviously unsuitable habitat in the available distribution. This resulted in used-to-available location ratios of 1:114–1:121. I ran final models with fewer available points to confirm the stability of coefficient and SE estimates and ensure the number of available locations was adequate to estimate the integral in the denominator of the used distribution (Northrup et al., 2013).

Analyses

I estimated resource selection function (RSF) coefficients using conditional logistic regression in R (version 3.6.3; R Core Development Team, www.r-project.org, accessed 30 March 2020), with a response variable of 1 for used locations and 0 for available locations. When estimating RSFs using logistic regression software, the intercept term is discarded and raw RSF scores are calculated as $\hat{w}(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k)$, where β_1–β_k are regression coefficients for k predictor variables, x_1–x_k (Johnson et al., 2006; McDonald, 2013; Warton & Shepherd, 2010). I fit models using the *glmmTMB* function in package *glmmTMB* (Muff et al., 2019). I weighted available locations by 1000 as recommended by Muff et al. (2019). I included a random intercept for stratum (i.e., for individual j in year h) with a large, fixed variance value (10^6) in all models to avoid shrinkage of stratum-specific intercepts to the overall mean that can bias estimates of fixed-effect parameters and variances (Muff et al., 2019). I also included either a random intercept term or random slope term(s) for individual in all models to induce correlation among repeated, potentially non-independent, observations from the same individual. I fit null models with nested random intercepts for stratum and individual (with stratum nested within individual). I fit models with fixed effects with a random slope term for each fixed-effect variable to reduce bias in fixed-effects coefficients and to account for differences in availability among individuals (Duchesne et al., 2010; Gillies et al., 2006; Muff et al., 2019). If one or more models in a set failed to converge, I fit infrastructure models in that set with a random slope term for the infrastructure variable and the landcover + topography model with nested random intercepts for stratum and individual. If models with random slope terms failed to converge, I reverted to fitting all models in that set with nested random intercepts for stratum and individual. When testing the effects of distance from infrastructure, I used subsets of data from used-available locations ≤1 km from each type of infrastructure. This assumes that infrastructure features >1 km do not influence selection within seasonal use areas. I assessed relative support among models in the same set using the Akaike information criterion for finite samples (AIC_c; Burnham & Anderson, 2002) because my focus was estimating population-level (i.e., marginal) responses to infrastructure. In the penalty term for AIC_c, *K* is the number of estimated fixed parameters plus the number of estimated random effects terms (Vaida & Blanchard, 2005). However, because the overall intercept is ignored when using logistic regression to estimate RSF coefficients (McDonald, 2013) and the random intercept term for stratum was set to a fixed value (Muff et al., 2019), neither counted toward *K*.

Variables

I calculated proportion landcover and proportion infrastructure cover around used and available locations in each year from a classified landcover layer modified to reflect both natural and anthropogenic changes to the landscape over time. I used a 25-m resolution, classified Colorado Vegetation Classification Project (CVCP) layer derived from Landsat Thematic Mapper imagery from 1993 to 1995 as the base landcover layer. I grouped CVCP vegetation cover types into 11 cover classes using Spatial Analyst in ArcGIS 10.2 (Walker et al., 2016). Of those 11 classes, seven were sufficiently represented within the study area (Table 1). Of those seven, two classes, xeric shrub cover and barren cover, co-occurred on steep slopes, so I combined them into a single class, xeric-barren. I then modified this base layer to reflect major changes in landcover due to habitat treatments and wildfires that occurred from 1995 to 2015. I identified and mapped the boundaries of treatments and wildfires from shapefiles provided by CPW, BLM, and Encana Oil and Gas, and by visually comparing ortho-rectified National Agricultural Inventory Program (NAIP) imagery across years from 1995 to 2015 against original CVCP cover types. I determined when changes occurred based on reported treatment dates or when changes first appeared in imagery. I assigned raster cells within treatment or wildfire polygons to one of the six cover classes analyzed based on visual assessment of vegetation in the field, from NAIP imagery, or both. I used this modified layer to generate separate landcover layers for each year from 2005 to 2015. Finally, I modified each annual landcover layer to also reflect anthropogenic (primarily energy) infrastructure present each year (Walker et al., 2020). To do this, I first re-sampled each annual layer to 12.5 12.5-m resolution to allow more accurate representation of narrow, linear features such as pipelines and roads. I then assigned raster cells within infrastructure polygons to infrastructure cover classes following Walker et al. (2020). Each energy infrastructure feature (or portion thereof) was assigned a type (well pad or facility, road, or pipeline) and a surface status (disturbed or reclaimed), and each well pad or facility was assigned a level of industrial activity (high, low, or inactive) in each year. All roads were classified as disturbed surface and all pipelines and abandoned well pads and facilities where vegetation was recovering were classified as reclaimed surface. See Walker et al. (2020) for additional details of infrastructure mapping. I combined energy and non-energy features when estimating proportion infrastructure cover because most infrastructure (73%–86%) was from energy development (Walker et al., 2020) and sage-grouse should respond similarly to disturbed or reclaimed surface regardless of why a feature was built.

I buffered all used and available locations for each individual in each season in each year by 100, 400, and 1000-m radius circles and intersected buffers with final, corrected, modified annual cover class layers using ArcPro 2.1.2. I calculated proportion landcover and proportion infrastructure cover around each location at each radius. I used 100 m as the smallest radius to minimize potential bias from location error. Previous analyses found the strongest support for selection in relation to landcover at 100 and 400-m radii in this population (Walker et al., 2016). However, I also tested landcover and infrastructure cover within 1000 m because it matches maximum observed daily movement distances and the distance at which birds realistically

TABLE 1 Variables tested in analysis of greater sage-grouse third-order seasonal habitat selection in the Parachute-Piceance-Roan population, Colorado, USA, 2006–2014

Variable	Description
Vegetation (proportion cover within a 100, 400, or 1000-m radius)	
SD	Proportion sagebrush-dominated cover
SDG	Proportion sagebrush-dominated + sagebrush-grassland cover
SDM	Proportion sagebrush-dominated + sagebrush-mountain shrub cover
SDMG	Proportion sagebrush-dominated + sagebrush-mountain shrub + sagebrush-grassland cover
FOR	Proportion forest cover
MTNS	Proportion mountain shrub cover
XB	Proportion xeric shrub and barren cover combined
Topographic	
TRI_Z	Terrain roughness index (100-m radius; standardized)
CTI_Z	Compound topographic index (100-m radius; standardized)
TPI_Z	Topographic position index (2000-m radius; standardized)
Infrastructure (proportion cover within a 100, 400, or 1000-m radius)	
WPF-Disturbed	Well pad or energy facility cover with disturbed surface
WPF-Reclaimed	Well pad or energy facility cover with reclaimed surface
PIPELINE	Pipeline cover (reclaimed surface)
ROAD	Road cover (disturbed surface)
DISTURBED	Total disturbed surface cover
RECLAIMED	Total reclaimed surface cover
ANTHRO	Total anthropogenic (disturbed + reclaimed) surface cover
Infrastructure (density)	
AEF DENSITY	Active energy feature density—no. active well pads and energy facilities per square mile[a]
ROAD DENSITY	Road density—mile of roads per square mile (excluding two-tracks)[a]
Infrastructure (Euclidean distance from infrastructure in kilometers)	
DistHIGH	Distance from nearest high-activity well pad or energy facility
DistLOW	Distance from nearest low-activity well pad or energy facility
DistINAC	Distance from nearest inactive well pad or energy facility
DistROAD	Distance from nearest road
DistPIPE	Distance from nearest pipeline
Infrastructure (exponential decay functions for Euclidean distance from infrastructure)	
DistHIGHα	$e^{\ d/\alpha}$, where d = DistHIGH in meters and α = 100, 250, 500, 1000
DistLOWα	$e^{\ d/\alpha}$, where d = DistLOW in meters and α = 100, 250, 500, 1000
DistINACα	$e^{\ d/\alpha}$, where d = DistINAC in meters and α = 100, 250, 500, 1000
DistPIPEα	$e^{\ d/\alpha}$, where d = DistPIPE in meters and α = 100, 250, 500, 1000
DistROADα	$e^{\ d/\alpha}$, where d = DistROAD in meters and α = 100, 250, 500, 1000

[a] 1 mi = 1.61 km; 1 mi^2 = 2.59 km^2.

perceive and respond to changes in landcover caused by energy infrastructure when selecting habitat within seasonal use areas is likely greater than 400 m (Dinkins et al., 2014; Kirol et al., 2020). Some infrastructure cover variables were standardized to a *z*-scale to facilitate model convergence.

I tested three scale-dependent topographic variables derived from a 10-m resolution USGS digital elevation model in all analyses: a small-scale terrain roughness index (TRI), a small-scale compound topographic index (CTI), and a large-scale topographic position index (TPI). I calculated TRI as the standard deviation of elevation of pixels within a 100-m radius (Doherty et al., 2008). I calculated mean CTI within a 100-m radius based on slope and upstream area (Gessler et al., 1995). I calculated TPI as the difference between elevation at the center point and mean elevation of pixels within a 2000-m radius divided by the standard deviation of elevation of pixels within that radius (De Reu et al., 2013). I calculated TRI and TPI using Spatial Analyst in ArcGIS 10.6, and I standardized values of TRI, CTI, and TPI to a z-scale prior to analyses.

I tested distance from five different types of infrastructure to assess whether industrial activity level influences selection in areas around infrastructure. I estimated distance from infrastructure as Euclidean distance to the nearest feature of each type. Distance-from-infrastructure variables were tested as linear functions (in kilometers) and as exponential decay functions of the form $e^{d/\alpha}$, where d was distance in meters to the feature and α was set at 100, 250, 500, or 1000 m to allow for the possibility of different response curves (Aldridge et al., 2012; Smith et al., 2014).

I used moving-window analyses to calculate active energy feature density as the number of active energy feature center points within a 2.59-km^2 (1-mi^2) circular buffer and road density as miles of improved road within a 2.59-km^2 circular buffer. The BLM's resource management plan amendments included a feature density cap of one "disruptive" energy feature (e.g., active oil and gas well pads or facilities, coal mines, wind towers, solar fields, or geothermal plants) per 2.59 km^2 (1 mi^2) (BLM, 2015a, 2019a). However, BLM guidelines for implementing density caps (appendix E in BLM, 2015a) lack specific criteria for defining which well pads and facilities are "disruptive" and which are not. After consultation with BLM, I defined "disruptive" energy features in each year as active (i.e., low-activity or high-activity) well pads and energy facilities with $\geq$0.17 ha of disturbed surface, the size of the smallest producing well pad in the study area (Walker et al., 2020). This definition captured all well pads with wells in the construction, drilling, completion, injection (i.e., fracturing), workover, and production phases and most energy facilities but excluded inactive well pads and small facilities associated with pipelines (e.g., sheds, risers).

Predictions

I allowed models with sagebrush-dominated cover to compete against sagebrush-dominated + sagebrush-grassland cover, sagebrush-dominated + sagebrush-mountain shrub cover, and all three classes combined in univariate analyses to identify a best-supported overall sagebrush cover variable. I predicted positive linear effects of sagebrush cover classes and negative linear effects of non-sagebrush classes in all seasons based on previous research (Hagen, 1999; Walker et al., 2016) and the year-round dependence of sage-grouse on sagebrush canopy cover and sagebrush landscapes (Connelly et al., 2011; Crawford et al., 2004; Hagen et al., 2007). I tested linear and quadratic effects of TRI, a quadratic effect of CTI, and linear and quadratic effects of TPI based on previous research suggesting selection for areas with less rugged topography, intermediate levels of soil moisture, and certain landforms (LeBeau et al., 2017; Smith et al., 2014; Walker et al., 2016; Walker et al., 2020).

Previous studies in oil and gas fields (Appendix S1: Table S1) suggest that sage-grouse generally avoid areas converted to disturbed surface. I therefore tested linear effects of disturbed infrastructure cover and predicted that proportion disturbed surface would negatively affect selection in all seasons. Infrastructure with reclaimed or recovering surface, such as pipelines and reclaimed portions of well pads and facilities, typically have substantially reduced sagebrush cover and height and generally do not meet sage-grouse nesting and winter micro-habitat requirements for several decades following disturbance (Arkle et al., 2014; Avirmed et al., 2015; Gasch et al., 2016). I therefore predicted that reclaimed infrastructure would also have a negative linear effect on selection during breeding and winter. However, sage-grouse commonly use a greater diversity of vegetation types and take advantage of forb- and insect-rich mesic habitats for foraging in summer–fall (CGSSC, 2008; Connelly et al., 2011; Crawford et al., 2004). Because reclaimed areas often support new sagebrush and forb growth (Johnston, 2019), and reclaimed and disturbed infrastructure often co-occur, sage-grouse may select locations with intermediate values of reclaimed or disturbed energy infrastructure cover in summer–fall. Therefore, I tested both linear and quadratic effects of reclaimed and disturbed infrastructure in summer–fall.

I predicted that females would select areas farther from infrastructure (i.e., distance should have a positive effect on selection) and that effects of infrastructure would be strongest for high-activity features (i.e., well pads and facilities in the construction and drilling stage or large, permanent facilities), intermediate for low-activity features (i.e., well pads in production and small facilities, roads), and weakest for inactive features (i.e., inactive or abandoned well pads and facilities, pipelines). I was unable to assign roads different activity levels, so I assumed responses to roads would be similar, on average, to responses to low-activity features. Although power lines are often a major component of energy infrastructure in other oil and gas fields (e.g., Doherty et al., 2008), few power lines occurred in the study area (Walker et al., 2020).

I tested the effects of active energy feature density and road density to assess the adequacy of disruptive feature and road density caps proposed or included in recent amendments to BLM resource management plans. I predicted that feature density and road density would have a negative effect on selection in all seasons.

Model development and selection

I used a sequential model-fitting process. In each season, I first conducted univariate screening to identify the best-supported landcover and topography variables (Table 1), to examine the direction and magnitude of those effects, and to screen and cull uninformative variables to reduce potential for over-fitting (Arnold, 2010; Burnham & Anderson, 2002). I ranked models based on ΔAIC_c units from the best-supported model (Burnham & Anderson, 2002). I excluded from further consideration variables for which the univariate model ranked ≥ 2 ΔAIC_c units above the best-supported model in each subset or for which 95% CIs of the coefficient estimate overlapped zero. I then tested all combinations of best-supported landcover and topography variables to find the best-supported multivariate landcover + topography model. I avoided fitting models with highly correlated variables ($|r| \geq 0.7$), with moderately correlated variables ($0.4 < |r| < 0.7$) if coefficients switched sign or had inflated SEs, or for which the tolerance statistic (t) was ≤ 0.4 to avoid problems with multicollinearity. I also excluded models with additional uninformative parameters relative to higher-ranked models with the same approximate likelihood (Arnold, 2010). I considered models comprising $\geq 90\%$ of summed model weights competitive.

I then added infrastructure variables (Table 1) to the best-supported landcover + topography model in each season to test whether the addition of that variable improved model performance. I interpreted infrastructure variables as having a statistically significant effect on selection if the model was ranked ≥ 2 ΔAIC_c units above the landcover + topography model and 95% CIs for the infrastructure coefficient did not overlap zero.

I used parametric bootstrapping to illustrate the effects of infrastructure variables on selection. I generated a bootstrap data set of 1 million sets of regression coefficients for fixed effects with the same variance–covariance structure as the model with the infrastructure variable over the observed range of values for that variable. I set all other variables at their means for used locations to represent selection responses within typical used habitat. However, because proportion cover values summed over all cover classes cannot exceed 1, with each incremental increase in infrastructure cover, I incrementally reduced cover of natural landcover classes by the same amount in proportion to their initial mean values. I used 2.5% and 97.5% cutoffs for the distribution of bootstrapped values to generate 95% CIs for RSF scores. I rescaled all RSF scores and CIs to a [0, 1] interval using a linear stretch (Johnson et al., 2004), $RSF_{rescaled} = (\hat{w}[x] \quad \hat{w}[x]_{min})/(\hat{w}[x]_{max} \quad \hat{w}[x]_{min})$, where $\hat{w}(x)_{min}$ and $\hat{w}(x)_{max}$ were the minimum and maximum predicted 95% confidence limits for RSF scores for that model.

RESULTS

Infrastructure around seasonal used locations

Locations used by female sage-grouse had the least surrounding infrastructure during the breeding and winter seasons and the most in summer–fall (Table 2). Total anthropogenic surface within 1000 m around used locations averaged 2.3% (median 1.5%), 3.1% (median 2.5%), and 1.7% (median 1.2%) and active energy feature density averaged 0.12 (median 0.00), 0.17 (median 0.00), and 0.09 (median 0.00) during breeding, summer–fall, and winter, respectively. A large majority of seasonal use locations (96.6% during breeding, 92.4% in summer–fall, and 97.2% in winter) had <3% disturbed surface within 1000 m, and most (73.2%, 66.7%, and 84.2%) had <3% total anthropogenic surface within 1000 m.

Selection in relation to landcover and topography

Univariate analyses

I included 1157 locations from 169 individual-years (i.e., strata) and 108 individuals in breeding-season analyses (Appendix S1: Table S2), 1334 locations from 179 individual-years and 109 individuals in summer–fall analyses (Appendix S1: Table S3), and 862 locations from 91 individual-years and 69 individuals in the winter analyses (Appendix S1: Table S4). Best-supported univariate models in all seasons included positive effects of sagebrush cover, negative effects of forest, mountain shrub, and xeric-barren cover, either negative or quadratic effects of TRI and TPI, and quadratic effects of CTI (Appendix S1: Tables S2–S4).

TABLE 2 Summary statistics for mean infrastructure cover and density variables around used locations by season for female greater sage-grouse in the Parachute-Piceance-Roan population, Colorado, USA, 2006–2014

Variable[a]	Breeding (n = 108)		Summer–fall (n = 109)		Winter (n = 69)	
WPF-Disturbed 100	0.3	0.9, 0.0 (0.0–6.0)	0.7	1.8, 0.0 (0.0–9.3)	0.2	0.8, 0.0 (0.0–5.2)
WPF-Disturbed 400	0.2	0.6, 0.0 (0.0–2.6)	0.5	1.1, 0.0 (0.0–7.7)	0.2	0.6, 0.0 (0.0–2.8)
WPF-Disturbed 1000	0.3	0.5, 0.0 (0.0–2.8)	0.4	0.8, 0.1 (0.0–3.6)	0.2	0.5, 0.0 (0.0–2.0)
WPF-Reclaimed 100	0.2	1.0, 0.0 (0.0–9.4)	0.3	1.3, 0.0 (0.0–12.6)	0.2	1.0, 0.0 (0.0–8.0)
WPF-Reclaimed 400	0.2	0.4, 0.0 (0.0–2.9)	0.2	0.4, 0.0 (0.0–3.4)	0.1	0.3, 0.0 (0.0–1.7)
WPF-Reclaimed 1000	0.1	0.2, 0.0 (0.0–1.5)	0.1	0.2, 0.1 (0.0–1.3)	0.1	0.2, 0.0 (0.0–0.9)
PIPELINE 100	3.4	7.1, 0.0 (0.0–48.7)	5.7	9.4, 1.9 (0.0–47.1)	2.4	8.2, 0.0 (0.0–54.9)
PIPELINE 400	1.6	2.9, 0.3 (0.0–14.2)	2.3	3.1, 0.8 (0.0–13.9)	0.9	2.1, 0.2 (0.0–13.6)
PIPELINE 1000	1.1	1.6, 0.2 (0.0–7.1)	1.4	1.6, 0.9 (0.0–6.0)	0.7	1.0, 0.1 (0.0–5.1)
ROAD 100	1.7	1.3, 1.6 (0.0–7.2)	2.8	2.3, 2.5 (0.0–12.7)	1.1	1.2, 0.7 (0.0–5.3)
ROAD 400	1.1	0.6, 1.1 (0.0–3.2)	1.4	0.6, 1.3 (0.0–3.7)	0.9	0.4, 0.8 (0.0–1.7)
ROAD 1000	0.9	0.4, 0.8 (0.1–1.8)	1.1	0.4, 1.1 (0.0–1.9)	0.8	0.3, 0.7 (0.3–1.3)
DISTURBED 100	1.9	1.7, 1.8 (0.0–9.9)	3.5	2.9, 2.7 (0.0–13.6)	1.3	1.5, 1.0 (0.0–6.6)
DISTURBED 400	1.3	0.8, 1.1 (0.0–4.1)	1.9	1.4, 1.5 (0.0–10.1)	1.1	0.7, 0.9 (0.0–3.8)
DISTURBED 1000	1.2	0.7, 0.9 (0.1–3.5)	1.5	1.0, 1.3 (0.0–5.0)	0.9	0.6, 0.8 (0.3–3.0)
RECLAIMED 100	3.6	7.1, 0.0 (0.0–48.7)	6.0	9.6, 2.0 (0.0–47.1)	2.7	8.2, 0.1 (0.0–54.9)
RECLAIMED 400	1.8	2.9, 0.4 (0.0–14.2)	2.4	3.2, 1.0 (0.0–13.9)	1.1	2.2, 0.4 (0.0–13.6)
RECLAIMED 1000	1.2	1.6, 0.4 (0.0–8.0)	1.6	1.6, 1.1 (0.0–7.3)	0.8	1.0, 0.4 (0.0–5.1)
ANTHRO 100	5.5	7.6, 2.6 (0.0–53.0)	9.5	10.4, 5.9 (0.0–52.2)	4.0	9.0, 1.5 (0.0–59.7)
ANTHRO 400	3.1	3.1, 1.9 (0.0–15.3)	4.3	3.7, 2.8 (0.0–15.4)	2.1	2.5, 1.3 (0.0–14.7)
ANTHRO 1000	2.3	2.0, 1.5 (0.1–9.6)	3.1	2.2, 2.5 (0.0–8.9)	1.7	1.4, 1.2 (0.4–5.9)
AEF DENSITY	0.12	0.26, 0.00 (0.00–1.16)	0.17	0.29, 0.00 (0.00–1.35)	0.09	0.22, 0.00 (0.00–1.26)
ROAD DENSITY	1.85	0.83, 1.75 (0.20–3.81)	2.17	0.76, 2.20 (0.03–4.14)	1.57	0.64, 1.44 (0.00–3.02)

Note: Proportion cover values are presented as percentages. Values are presented as mean SD, median (range).
[a]See Table 1 for variable definitions. Numbers following proportion cover variables refer to the radius (in meters) of the circular buffer around locations within which variables were measured.

Multivariate analyses

Multivariate analyses produced a final set of one competitive landcover + topography model for the breeding season, one competitive landcover + topography model for summer–fall, and two competitive landcover + topography models in winter (Table 3). All multivariate winter models were run with nested random intercepts to facilitate convergence. The three best-supported models with landcover + topography in all seasons included positive effects of sagebrush cover, negative effects of forest, either negative linear or quadratic effects of TRI, and quadratic effects of TPI (Table 3, Appendix S1: Table S5). Breeding and summer–fall models also included negative effects of mountain shrub and xeric-barren cover. Summer–fall and winter models also included quadratic effects of CTI.

Selection in relation to proportion infrastructure cover

Breeding

Best-supported breeding models indicated that females selected locations with less disturbed well pad + facility cover, less pipeline cover, and less road cover within 1000 m, but there was no effect of reclaimed well pad + facility cover (Figure 2a–d, Appendix S1: Table S6). Breeding females selected locations with less disturbed surface, less reclaimed surface, and less total anthropogenic surface within 1000 m (Figure 3a–c, Appendix S1: Table S6). Breeding RSF scores dropped below those in undeveloped areas when disturbed surface within 1000 m exceeded ~1.1% or total anthropogenic surface within 1000 m exceeded ~1.8% (Figure 4a,b).

TABLE 3 Final set of competitive multivariate breeding, summer–fall, and winter resource selection models based on landcover and topography for female greater sage-grouse in the Parachute-Piceance-Roan, Colorado, USA, 2006–2014

Model[a]	LL	K	n	AIC_c	ΔAIC_c	w_i
Breeding						
SD 100 + FOR 100 + MTNS 100 + XB 400 + TRI_Z + TPI_Z + TPI_Z^2	14,819.3	14	108	29,671.1	0.0	0.99
Summer–fall						
SDM 400 + FOR 100 + MTNS 100 + XB 100 + TRI_Z + TRI_Z^2 + TPI_Z + TPI_Z^2 + CTI_Z + CTI_Z^2	17,179.5	20	109	34,408.5	0.0	0.96
Winter[b]						
SDM 400 + FOR 100 + TRI_Z + TRI_Z^2 + TPI_Z + TPI_Z^2 + CTI_Z + CTI_Z^2	11,122.3	9	69	22,265.7	0.0	0.51
SDM 400 + FOR 100 + TRI_Z + TRI_Z^2 + CTI_Z + CTI_Z^2	11,125.0	7	69	22,265.8	0.1	0.49

Abbreviations: ΔAIC_c, difference in AIC_c units from the best-supported model; AIC_c, Akaike information criterion; K, number of model parameters; LL, log-likelihood; n, number individuals; w_i, Akaike model weight. Z refers to variables standardized to a z-score.

[a]See Table 1 for variable definitions.

[b]Models were fit with nested random intercepts for stratum within individual.

Summer–fall

Best-supported summer–fall models indicated that females selected locations with intermediate values of disturbed well pad + facility cover (0%–43%) within 100 m, pipeline cover (0%–60%) within 100 m, and road cover (0%–3%) within 400 m (Figure 2e,g,h, Appendix S1: Table S7). Females selected locations with intermediate values of disturbed surface (0%–28%), reclaimed surface (0%–60%), and total anthropogenic surface (0%–78%) within 100 m (Figure 3d–f, Appendix S1: Table S8). There was more support for a quadratic, rather than linear, effect of disturbed surface within 1000 m in summer–fall, with females selecting areas with an intermediate amount of disturbed surface (0%–5.5%) (Figure 4c), but the model was poorly supported relative to the model with disturbed surface within 100 m (Appendix S1: Table S8). Total anthropogenic surface within 1000 m (up to ~18%) had no effect on selection in summer–fall (Figure 4d).

Winter

Best-supported winter models indicated that females selected locations with less disturbed well pad + facility cover, less pipeline cover, and less road cover within 1000 m (Figure 2i,k,l) and less disturbed surface, less reclaimed surface, and less total anthropogenic surface within 1000 m (Figure 3g–i, Appendix S1: Table S9). Winter RSF scores dropped below those in undeveloped areas when disturbed surface within 1000 m exceeded ~2.5% or total anthropogenic surface within 1000 m exceeded ~3.5% (Figure 4e,f).

Selection in relation to distance from infrastructure

Breeding

Of the 108 females tracked during the breeding season, only 33 (31%) and 29 (27%) had a high-activity or a low-activity feature, respectively, within their breeding use area. After accounting for landcover and topography, these females selected locations farther from high-activity well pads and facilities (Figure 5a) and closer to pipelines (Figure 5b), but distance from road had no effect (Appendix S1: Table S10). In the subset of data used to test for effects of distance from high-activity features, only 3.9% of 153 breeding-season locations were ≤100 m from a high-activity well pad or facility.

Summer–fall

Of the 109 females tracked in summer–fall, only 39 (36%) and 46 (42%) had a high-activity or low-activity feature, respectively, within their summer–fall use area. Models with effects of distance from high-activity features did not converge, and there was no effect of distance from low-activity features on selection in summer–fall (Appendix S1: Table S11). Females selected locations farther from inactive well pads and facilities (Figure 5c) but

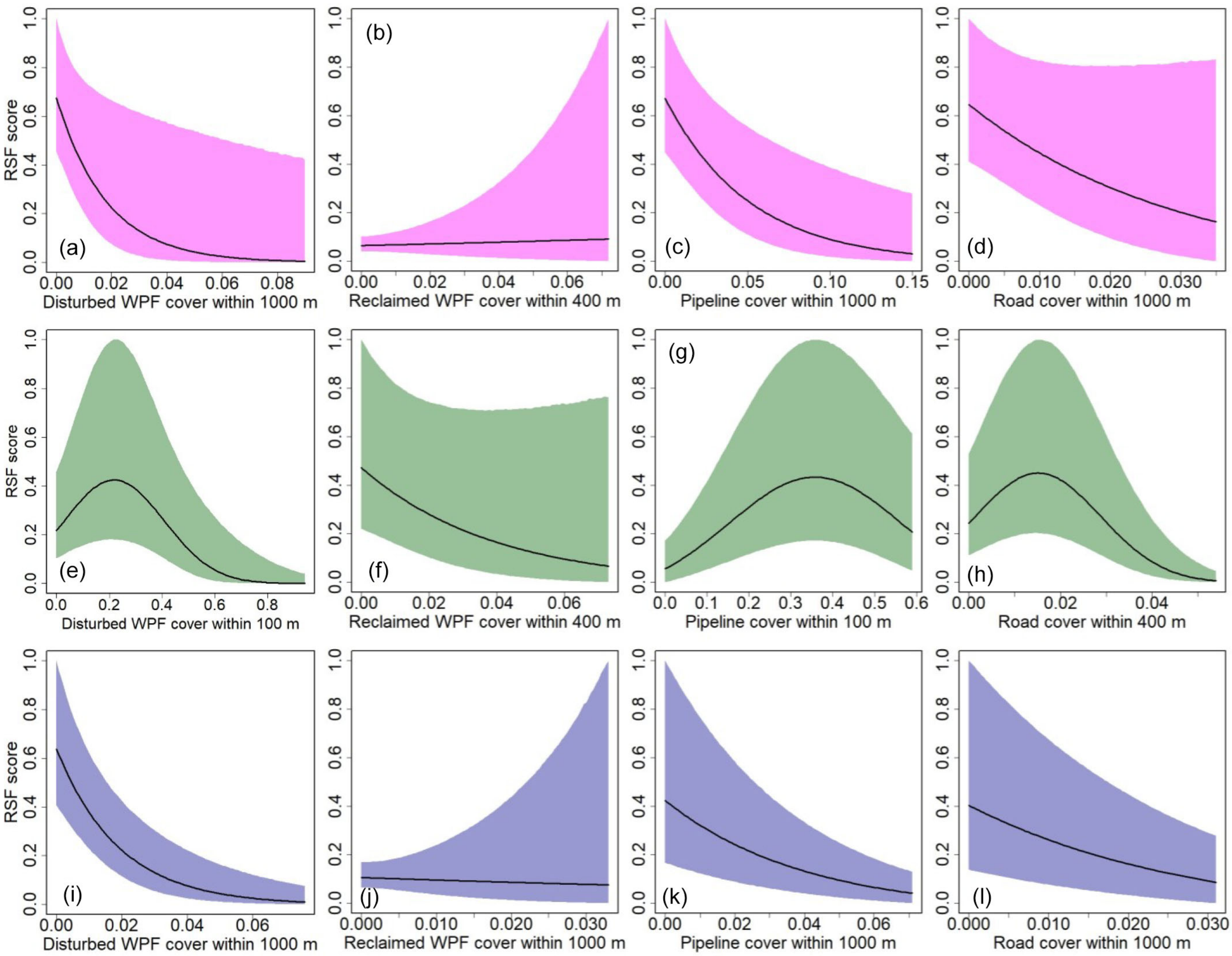

FIGURE 2 Best-supported relationships between female resource selection within seasonal use areas (rescaled resource selection function scores with color-shaded 95% CIs) and proportion cover of four different components of infrastructure during breeding (pink), summer–fall (green), and winter (blue) in the Parachute-Piceance-Roan greater sage-grouse population, Colorado, USA, 2006–2014. Estimates are based on mean landcover and topography values around used locations and account for loss of natural landcover as infrastructure cover increases. WPF, well pad or facility

closer to pipelines and roads in summer–fall (Figure 5d,e, Appendix S1: Table S11). In the subset of summer–fall data used to test pipeline effects, 29% of 680 used locations were ≤10 m from a pipeline and 54% were ≤100 m. In the subset of summer–fall data used to test road effects, 13% of 1280 used locations were ≤10 m from a road and 51% were ≤100 m.

Winter

Of the 69 females tracked in winter, only 18 (26%) and 13 (19%) had a high-activity feature or a low-activity feature, respectively, within their winter use area. Effects of distance from high-activity, low-activity, and inactive well pads and facilities on selection in winter were not supported (Appendix S1: Table S12). Females selected locations farther from pipelines in winter (Figure 5f), but distance from road had no effect (Appendix S1: Table S12).

Selection in relation to infrastructure density

Breeding

Breeding females selected locations with lower active energy feature density, and a model with a negative effect of road density was also supported (Figure 6a,b; Appendix S1:

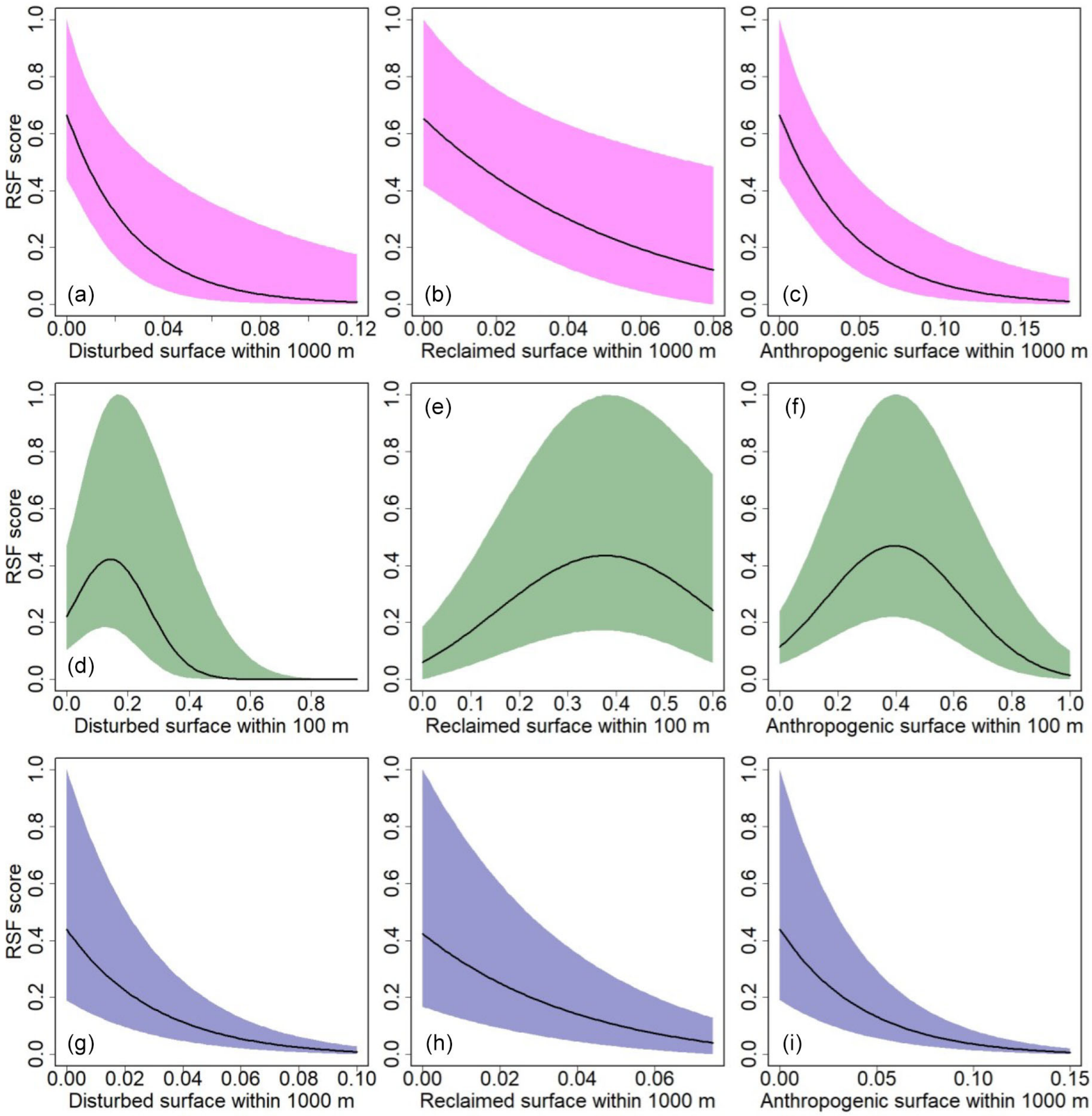

FIGURE 3 Best-supported relationships between female resource selection within seasonal use areas (rescaled resource selection function scores with color-shaded 95% CIs) and proportion cover of total disturbed surface, total reclaimed surface, and total anthropogenic surface during breeding (pink), summer–fall (green), and winter (blue) in the Parachute-Piceance-Roan greater sage-grouse population, Colorado, USA, 2006–2014. Estimates are based on mean landcover and topography values around used locations and account for loss of natural landcover as infrastructure cover increases

Table S13). Avoidance was detectable once active energy feature density exceeded ~0.50 (Figure 6a) and once road density exceeded ~2.7 (Figure 6b).

Summer–fall

There was little support for an effect of active energy feature density (up to 3.0) or road density (up to 6.0) on selection by females in summer–fall (Figure 6c,d, Appendix S1: Table S13).

Winter

There was little support for an effect of active energy feature density on selection within winter use areas, but females selected locations with lower road density

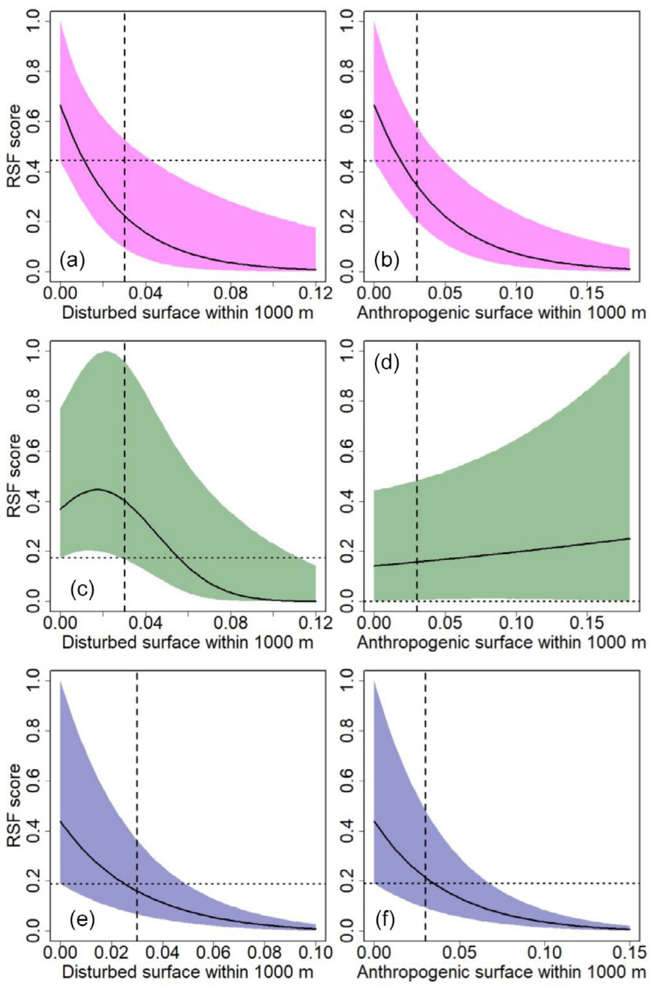

FIGURE 4 Relationships between female resource selection within seasonal use areas (rescaled resource selection function [RSF] scores with color-shaded 95% CIs) and proportion cover of total disturbed surface, and total anthropogenic surface during breeding (pink), summer–fall (green), and winter (blue) in the Parachute-Piceance-Roan greater sage-grouse population, Colorado, USA, 2006–2014. Estimates are based on mean landcover and topography values around used locations and account for loss of natural landcover as infrastructure cover increases. Vertical dashed lines represent the 3% surface disturbance threshold implemented in recent Bureau of Land Management resource management plan amendments. Horizontal dashed lines show the 95% lower confidence limit of the RSF score at proportion cover values of 0.0

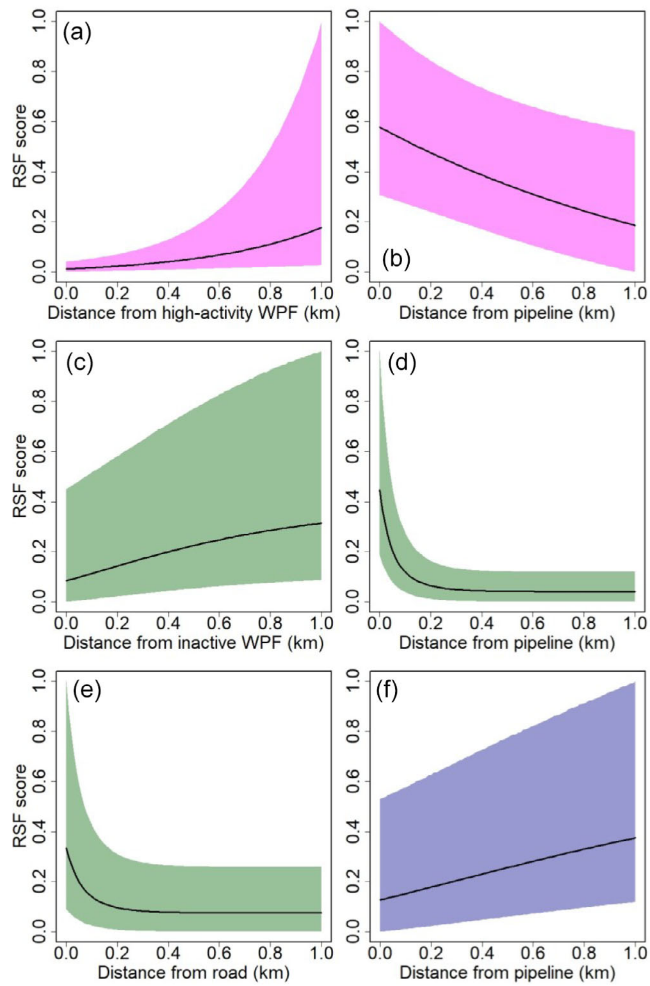

FIGURE 5 Best-supported relationships between female resource selection within seasonal use areas (rescaled resource selection function scores with color-shaded 95% CIs) and distance from different components of infrastructure during breeding (pink), summer–fall (green), and winter (blue) in the Parachute-Piceance-Roan greater sage-grouse population, Colorado, USA, 2006–2014. Estimates are based on mean landcover and topography values around used locations. WPF, well pad or facility

(Figure 6e, f, Appendix S1: Table S13). Avoidance in winter was detectable once road density exceeded ~2.8 (Figure 6f).

DISCUSSION

Consistent avoidance of infrastructure features with disturbed surface by female sage-grouse during breeding and winter supports the conclusion that habitat loss from energy development causes females to avoid developed areas during those seasons when they are most dependent on sagebrush, even when the footprint of anthropogenic infrastructure is relatively small (1.1%–2.5% disturbed surface within 1000 m). These findings are consistent with numerous previous studies that have demonstrated negative relationships between disturbed surface from energy infrastructure and habitat use and selection in sage-grouse (Appendix S1: Table S1) as well as in other avian species (e.g., Nenninger & Koper, 2018). Similarities in selection responses during breeding and winter could also be related to extensive spatial overlap in sage-grouse breeding and winter habitats in the PPR (Walker et al., 2016).

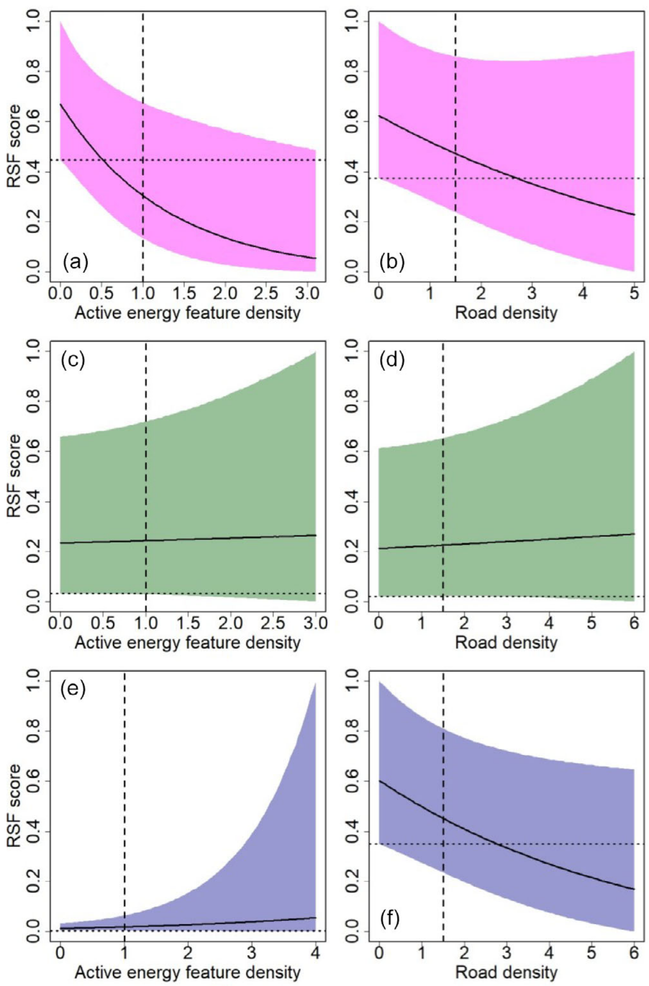

FIGURE 6 Relationships between female resource selection within seasonal use areas (rescaled resource selection function [RSF] scores with color-shaded 95% CIs) and active energy feature density and road density during breeding (pink), summer–fall (green), and winter (blue) in the Parachute-Piceance-Roan greater sage-grouse population, Colorado, USA, 2006–2014. Estimates and 95% CIs (shaded areas) are based on mean landcover and topography values around used locations. Vertical dashed lines represent density thresholds implemented or proposed in recent Bureau of Land Management resource management plan amendments. Horizontal dashed lines show the 95% lower confidence limit of the RSF score at active energy feature or road density values of 0.0

In contrast, use and selection of locations with intermediate values of disturbed and reclaimed infrastructure cover in summer–fall were unexpected and are novel in the greater sage-grouse and energy literature. To my knowledge, this is the first study to document selection for low levels of any type of energy infrastructure by sage-grouse in any season. The only similar finding comes from Baxter et al. (2017), who documented a preference for mechanically altered sagebrush by brood-rearing females in summer in a high-elevation, mountain big sagebrush community (2300–2600 m). Differences in the shape of selection curves for disturbed versus reclaimed infrastructure in summer–fall are also informative. Females started to avoid locations once disturbed surface within 100 m exceeded ~28% (Figure 3d) but continued to select locations with as much as 60% reclaimed surface (primarily pipelines) within 100 m (Figure 3e). Selection for intermediate values of pipeline cover supports the idea that the presence of some pipeline cover within sagebrush landscapes actually increased suitable summer–fall habitat for sage-grouse in the PPR.

Strong selection for locations with intermediate amounts of reclaimed infrastructure in summer–fall raises questions about the ecological mechanisms driving such phenomena. Females may select locations near reclaimed infrastructure if reclaimed areas are used at certain times of day, for example, for foraging on forbs and invertebrates in the morning and evening. The abundance of grasses, annual forbs, and herbaceous vegetation typically increases, and sagebrush cover decreases, following mechanical disturbance in mountain big sagebrush ecosystems (Baxter et al., 2017; Dahlgren et al., 2006; Davies et al., 2012). In a concurrent reclamation study in the PPR, reclaimed seeded areas had double the forb cover, similar grass cover, and approximately one-third the sagebrush cover compared to adjacent, undisturbed controls after 5 years (Johnston, 2019). Access to abundant forbs and invertebrates for nutrition is important for pre-nesting and brood-rearing females and dependent chicks (Dahlgren et al., 2015; Gregg et al., 2008; Huwer et al., 2008), and sufficient grass height is important as cover for nesting hens (Hagen et al., 2007). Mesic conditions in the PPR may allow reclaimed areas to recover vegetation structure and composition suitable for early brood-rearing more quickly after disturbance than in arid regions (Johnston, 2019). Although sage-grouse use and consume sagebrush year-round, they increase use of other, more mesic, landcover classes that provide forbs and invertebrates for foraging in summer–fall. This includes natural landcover types such as wet meadows and greasewood bottoms as well as some atypical, anthropogenically altered mesic habitats, such as lawns and agricultural fields (Connelly et al., 2000, 2003). Summer–fall results for females in the PPR suggest that reclaimed pipelines (and possibly also reclaimed well pads) may perform a similar ecological function in high-elevation, mountain big sagebrush ecosystems.

Selection for locations with intermediate amounts of road cover, disturbed well pad + facility cover, and disturbed surface, as well as locations closer to roads and without regard to active energy feature or road density in summer–fall demonstrates that greater sage-grouse in the PPR do not always avoid areas with low levels of habitat loss. However, it remains unclear why females selected such locations. Similar to the hypothesized mechanism for pipelines, there may be a flush of foraging resources in narrow strips of disturbed soil or drainage ditches along roadsides or along well pad edges that were not captured by infrastructure mapping. Roads or well pads may also be used for roosting at night, so females may have simply been found nearby during the day. Field crews in the PPR commonly reported seeing sage-grouse feeding along roadsides in the mornings and evenings and occasionally encountered birds roosting on roads or well pads at night, so field observations are consistent with both explanations. Alternatively, apparent selection for features with disturbed surface could be driven, at least in part, by strong selection for pipeline cover because roads and active well pads often occur adjacent to pipelines along ridgetops (Figure 1). These patterns could also be an artifact of upslope movement of birds to higher-elevation, summer–fall habitats that simply happen to have greater energy development (Walker et al., 2016; Figure 1).

Overall, results from distance-from-infrastructure models did not reveal an obvious pattern of greater avoidance of well pads and facilities with more industrial activity. Females only selected locations farther from high-activity features during the breeding season, rather than in all three seasons as expected. Apparent avoidance of high-activity features during the breeding season could also arise if protective measures centered on leks meant that fewer high-activity features were built in nesting and early brood-rearing habitat around active leks. There was no clear evidence of avoidance of low-activity features in any season. Although there was some evidence that females avoided inactive well pads in summer–fall, that pattern may be a consequence of other phenomena (e.g., selection for pipelines and areas with low levels of active energy development in summer–fall). However, power to estimate effects of industrial activity was relatively low because only 13–46 females had one or more active energy features within their seasonal use areas. Selection for locations closer to pipelines during breeding and in summer–fall may be due to foraging or roosting resources provided by pipelines as discussed above. But breeding females also selected areas with less pipeline cover within 1000 m, which suggests that females take advantage of pipelines that occur within largely sagebrush-dominated landscapes. In contrast, selection for locations farther from pipelines in winter may be because recent pipeline cuts have substantially lower sagebrush shrub cover that reduces winter foraging and roosting resources for sage-grouse (Gasch et al., 2016).

My results suggest four strategies that land-use managers, landowners, and operators could employ to reduce avoidance of areas with energy development by female sage-grouse in the PPR. First, avoid exceeding 1.1% and 2.5% disturbed surface and 1.8% and 3.5% total anthropogenic surface within 1000 m in breeding and winter habitat, respectively. Second, avoid exceeding an active energy feature density threshold of 0.5 (i.e., one feature per 2 mi^2) or a road density threshold of 2.7 in breeding habitat and a road density of 2.8 in winter habitat. Third, implement timing restrictions on construction and drilling during the breeding season and avoid situating large, permanent facilities in or near breeding habitat. Fourth, speed the transition of well pads and facilities from the construction and drilling phase to either production or reclamation. Although eliminating timing restrictions during the breeding season may allow more rapid transition of individual well pads from construction and drilling to production, it would likely also result in a faster overall rate of energy development and more rapid conversion of sagebrush to disturbed surface.

My results also inform which features BLM should include when quantifying surface disturbance. First, all four of the infrastructure cover components I examined (well pads + facilities with disturbed or reclaimed surface, pipelines, and roads) had negative effects on selection in one or more seasons and should be included as anthropogenic surface disturbance in BLM's annual disturbance cap calculations. Results also support implementation of a 3% or lower surface disturbance cap in breeding and winter habitat. A large majority of female use locations in the PPR had <3% disturbed surface within 1000 m, and mean and median values for disturbed and total anthropogenic surface around sage-grouse used locations in all three seasons were also below or only slightly above BLM's 3% recommended surface disturbance cap, even in summer–fall, when females actively selected locations near pipelines and roads. These results are similar to those from six studies in Wyoming, where >90% of marked sage-grouse locations occurred in areas with <3% disturbed surface (i.e., "press disturbance"; Kirol et al., 2020). Based on selection relationships during breeding and winter, disturbance caps should be set between 1.1% and 2.5% disturbed surface (see Figure 3a,e) or 1.8% and 3.5% total anthropogenic surface (see Figure 3b,f), to prevent detectable levels of avoidance in the PPR.

Differences in how surface disturbance is measured by BLM and how it was measured in this study suggests that avoidance may occur during breeding and winter at surface disturbance values even lower than presented here. The BLM defines anthropogenic disturbance as "physical removal of habitat, including, but not limited to, paved highways, graded gravel roads, transmission lines, substations, wind turbines, oil and gas wells, pipelines, and mines" and calculates disturbance within each priority habitat management zone (and project boundary) using a surface disturbance analysis and reclamation tracking tool (SDARTT). However, BLM excludes numerous anthropogenic features with disturbed surface from SDARTT calculations, including those on private land, those that lack a federal nexus, those defined as "temporary" features (e.g., oil and gas access roads), and those that have undergone reclamation and are expected to meet (but have not yet met) sage-grouse habitat requirements (BLM, 2007, 2015a, 2019a). In contrast, disturbed surface in this study included all infrastructure with disturbed surface visible in imagery, regardless of land ownership, mineral ownership, temporary status, or the likelihood of successful reclamation. For that reason, in any given area, values of surface disturbance estimated using SDARTT will typically be lower, suggesting that impacts may occur at SDARTT surface disturbance values lower than the 1.1%–2.5% estimated in this study.

If current density caps are adequate to prevent avoidance by sage-grouse, estimated RSF scores at cap values should be statistically indistinguishable from those in areas with no infrastructure. Energy feature and road density caps of 1.0 and 1.5 per section, respectively, appeared adequate to prevent measurable levels of avoidance by sage-grouse during summer–fall and winter, but not during the breeding season. Females showed a detectable negative response once active energy feature density exceeded 0.5 during breeding, but RSF scores at an active energy feature density threshold of 1 were statistically indistinguishable from those at an active energy feature density of 0 in the other two seasons. A similar relationship was found with road density during the breeding season, but RSF scores at a road density threshold of 1.5 were statistically indistinguishable from those at a road density of 0.0 in all seasons. Exclusion of oil and gas access roads from BLM's route density calculations (BLM, 2019b) precludes direct comparison between estimates of road density in this study and those calculated by BLM, but it suggests that estimates in this study would be higher. Two studies along the North Dakota–Montana border documented negative relationships between road density and sage-grouse use. Areas that nesting birds avoided had 2.6 times higher road densities than those areas they selected (Fritz, 2011). Birds selected locations with lower road density within 560 m (1 km^2) in winter and lower road density within 3.2 km (32 km^2) during nesting (Parsons, 2019).

Low levels of disturbed infrastructure and low densities of active energy features within seasonal use areas in the PPR also hint that sage-grouse may avoid energy development at a higher order of selection (e.g., second order) than I investigated. Several previous studies have suggested that sage-grouse avoid active energy development when selecting seasonal use areas (Doherty et al., 2008; Holloran et al., 2010; Kirol et al., 2020; Pratt & Beck, 2019; Smith et al., 2014). Holloran et al. (2010) most clearly demonstrated this phenomenon by showing that yearling males and females recruited into the breeding population preferentially selected seasonal use areas outside a major natural gas field in southwestern Wyoming. Therefore, energy development within winter use areas may have been too low find strong evidence of negative effects of active energy feature density on third-order selection. I did not analyze energy effects on second-order selection because the sampling scheme for marked birds in this study was not designed to assess such effects.

This study illustrates that the overall response of sage-grouse to energy development is the outcome of season-specific responses to different components of infrastructure that vary both in magnitude and in direction. Responses in any given population will also depend on the extent and distribution of specific infrastructure components and their juxtaposition with important seasonal habitats. In the PPR, topography constrains both where energy infrastructure is built and where sage-grouse occur, so the potential for future overlap between energy infrastructure and greater sage-grouse habitat is high (Walker et al., 2020). In light of previous studies that consistently showed negative effects of energy infrastructure on seasonal habitat selection in arid sagebrush ecosystems (Appendix S1: Table S1), my findings suggest that sage-grouse response to energy development may differ in mesic, high-elevation, sagebrush ecosystems.

Positive responses to low to intermediate levels of reclaimed infrastructure in summer–fall suggests that rapid reclamation may help ameliorate otherwise negative impacts of energy development. Indeed, substantial use and selection of locations with reclaimed infrastructure in summer–fall in the PPR is encouraging, considering this population overlays massive unconventional natural gas and oil shale reserves and will continue to be developed (BLM, 2015b). However, the positive response to low levels of infrastructure observed in the PPR is anomalous and cannot be extrapolated to other Colorado populations or to populations in arid sagebrush ecosystems. Furthermore, it is unclear how use and selection of certain components of infrastructure during summer–fall affects demographic rates, so population-level impacts of energy development on the PPR population remain unknown. Future studies should investigate the ecological mechanisms and demographic consequences of sage-grouse selecting locations near energy infrastructure in summer–fall.

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CONFLICT OF INTEREST

The author declares no conflict of interest.

ORCID

Brett L. Walker https://orcid.org/0000-0003-1183-3449

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

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