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Research article

Using individual-based habitat selection analyses to understand the nuances of habitat use in an anthropogenic landscape: a case study using greater sage-grouse trying to raise young in an oil and gas field

EDITOR'S CHOICE

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Habitat selection analyses conducted at an individual level may reveal patterns in selection not apparent when individuals are pooled in population-level approaches. Using GPS transmitters that gather high-resolution location data, we explored fine-scale habitat selection and space use within home ranges of female greater sage-grouse *Centrocercus urophasianus* that raised young (brood-rearing sage-grouse) in an oil and gas development area. To evaluate fine-scale habitat selection of brood-rearing sage-grouse we used a two-stage approach. First, we developed models for each individual (i.e. individual-level modeling) and evaluated individual-level responses to modified habitats and infrastructure. Second, we averaged individual-level estimates using a bootstrap approach to make population-level inference. The average home range size during brood-rearing in our study, from nest hatch to six weeks, was 0.85 ± 0.21 km^2. Individual and population-level results indicated that brood-rearing females consistently selected for natural vegetation and avoided disturbed surfaces at a fine spatial scale. Our study area included substantial areas of recent ($\leq$ 10 years) habitat reclamation which females also avoided. Visible power lines consistently led to avoidance behavior. In addition to consistent patterns of habitat selection, our individual models demonstrated variability and contrasting behaviors in how brood-rearing females responded to specific infrastructure features and anthropogenic water bodies. At the population-level anthropogenic water bodies were avoided but at the individual-level the intensity of avoidance was variable among individuals. Individual variability was often explained by the age of the brood-rearing female (first year or adult). First year females were more likely than adults to use habitats close to infrastructure and consistently established home ranges in areas with more surface disturbance and infrastructure when compared to adults. Our results provide new insights into fine-scale habitat-selection strategies used by female sage-grouse with broods in an area where oil and gas infrastructure is widespread and cannot be avoided.

Keywords: *Centrocercus urophasianus*, greater sage-grouse, home range, individual variation, individual-level modeling, industrial development, reclamation, transmission lines

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Introduction

Animals can exhibit individual variation in habitat selection and space use (Durell 2000, Hertel et al. 2020, Mitchell et al. 2020). Individuals from the same species and population may adopt different habitat-use strategies and these differences can be influenced by factors such as social status (e.g. exclusion of subdominant individuals from preferred habitats) or by an individual's previous experience (Durell 2000, Freitas 2008, Leclerc et al. 2016). Individual variation has also been observed in response to anthropogenic activities and associated habitat modifications at fine spatial scales (Mitchell et al. 2020). Individual-level modeling can reveal variation in habitat selection and avoidance behavior that may otherwise be obscured when individuals are pooled in population-level analyses (Leclerc et al. 2016, Lesmerises and St-Laurent 2017, Thomas et al. 2021).

The greater sage-grouse *Centrocercus urophasianus* (hereafter sage-grouse) has been the subject of many habitat selection studies across its range throughout the intermountain west of North America. Large portions of the sage-grouse range have been modified by industrial development (Copeland et al. 2011, Allred et al. 2015), which sage-grouse often avoid, resulting in functional habitat loss (Aldridge and Boyce 2007, Naugle et al. 2011, Kirol et al. 2015a). Multiple studies, based on very high-frequency (VHF) tracking locations, have demonstrated the displacement of sage-grouse to the periphery of the oil and gas development fields, but this is only possible when undisturbed habitat is available outside of the impacted area (Aldridge and Boyce 2007, Holloran et al. 2010, Naugle et al. 2011, Kirol et al. 2015a). Much less information is available about habitat selection and avoidance behavior at fine spatial scales that require high-resolution GPS location data. These type of data allow for a finer resolution understanding of how sage-grouse respond within their home ranges (i.e. third-order selection; Johnson 1980) when they encounter disturbed habitat, such as active oil and gas roads; well pads; or infrastructure, such as power lines.

Our study took place in the Powder River Basin (PRB) in northeastern Wyoming, which has undergone extensive oil and gas development, mainly in the form of natural gas extraction. Low densities and declining numbers have led to concerns about the persistence of the PRB sage-grouse population (Garton et al. 2011, Taylor et al. 2013, Fedy et al. 2017, Coates et al. 2021). This population of sage-grouse acts as a critical genetic link between populations in Wyoming and those in North Dakota, South Dakota and Montana, USA (Row et al. 2018, Cross et al. 2023). The majority of the natural gas development in our study area took place between 2000 and 2005; therefore, sage-grouse populations in this area had been exposed to oil and gas infrastructure for over ten years prior to the start of this study. This study area provided a unique opportunity to explore fine-scale selection and avoidance behavior of anthropogenic disturbance because there were few refugia or undisturbed sagebrush habitats available to the sage-grouse in this area, as almost all of the sagebrush habitat in our study area (i.e. within common sage-grouse movement distances) contained at least some oil and gas infrastructure or other anthropogenic disturbances. Furthermore, approximately twenty percent of the oil and gas disturbance in our study site had undergone reclamation prior the study ($\leq$ 10 years), providing a unique opportunity to assess fine-scale habitat selection in relation to reclaimed surfaces (e.g. reclaimed oil and gas pads; Barlow et al. 2020, Kirol and Fedy 2021).

Animals are able to positively affect their survival and reproductive success through habitat selection (Jones 2001, Long et al. 2016). In this study, we wanted to understand maternal decision making by female sage-grouse raising chicks in an industrial landscape to inform management and conservation. Our study focused on female sage-grouse that raised chicks to six weeks. Sage-grouse chicks are precocial and stay in close proximity to their mothers until they can forage independently after approximately six weeks of age when brood break-up begins (Drut et al. 1994, Gregg et al. 2007, Blomberg et al. 2014). Therefore, female sage-grouse with broods are under strong selection pressure to balance predation risk to themselves and their chicks with the need to provide foraging opportunities and high-quality nutrition (Hagen 2011, Smith et al. 2018). Habitat modification associated with industrial development can lead to lower reproductive success (e.g. nest success and chick survival) likely because of chicks and adult females being more vulnerable to predators in these environments (Lyon and Anderson 2003, Aldridge and Boyce 2007, Dzialak et al. 2011, Kirol et al. 2015a).

Our objective in this study was to inform fine-scale resource management in an area that has experienced extensive oil and gas development. We wanted to better understand the habitat selection behavior of maternal sage-grouse in response to anthropogenic features or landcover that has been changed by development within their brood-rearing home ranges. We accomplished this objective using high-resolution and high-frequency GPS location data (e.g. one location every 4 h; Cagnacci et al. 2010) of brood-rearing female sage-grouse. We used generalized linear models fitted for each individual to evaluate individual-level responses and then averaged individual-level model estimates to make population-level inference for the anthropogenic covariates of interest (Prokopenko et al. 2017, Thomas et al. 2021). The specific questions addressed in our study included: 1) what habitat selection and avoidance choices are female sage-grouse making as they try to raise young in an area of widespread oil and gas development? 2) How do females respond to different types of infrastructure (e.g. well or power lines), disturbance features (e.g. anthropogenic water bodies) and surface disturbances, the physical footprint of oil and gas development? 3) What is the extent of individual variability in habitat-use strategies in human-altered habitat and how is this variability related to female experience (i.e. age)?

Material and methods

Study site

Our study area was located in an area dominated by sagebrush landcover in northeastern Wyoming, USA, within the PRB region (44.2603°N, −106.3095W°; Fig. 1). Our study took place between 2017 and 2019 and encompassed an area of 1412 km². Elevations in our study area ranged from 1198 to 1453 m. Monthly average temperatures ranged from 21.6°C in the summer to −5.8°C in the winter. Precipitation averaged 35 cm annually. Precipitation was fairly evenly distributed throughout the year but came as rain in the summer and snow in the winter. Dominant shrubs included Wyoming big sagebrush *Artemisia tridentata wyomingensis* and silver sagebrush *A. cana*, black greasewood *Sarcobatus vermiculatus* and rabbitbrush (*Chrysothamnus* and *Ericameria* spp.). Common native grasses included blue grama *Bouteloua gracilis* and bluebunch wheatgrass *Pseudoroegneria spicata*. Widespread invasive grasses included cheatgrass *Bromus tectorum* and Japanese brome *B. japonicas*.

Primary land uses in our study area were oil and gas development and livestock ranching. Coal-bed natural gas (CBNG) was the prominent type of energy development. CBNG wells were developed at a density of 3.1 well pads per km² (80-acre spacing; Walker et al. 2007). On average, CBNG well pads required the clearing of 0.5 ha of natural vegetation per pad. This estimate does not include access roads of various lengths and other supporting infrastructure (e.g. compressor stations and pipelines). In addition to well pads, CBNG development at this density generally requires 2–7 km of road construction per km² (Walker et al. 2007). CBNG well structures were approximately 3 m tall while supporting infrastructure like compressor stations was much taller (5–8 m). Our study area contained a variety of reclaimed surfaces including reclaimed pipeline corridors, well pads and access roads. Reclamation practices included recontouring (reshaping the disturbed area to the original contour of the surrounding landform), preparation of topsoil surface and broadcasting of authorized mixes of native seeds over the disturbed surfaces (US Bureau of Land Management 2003). Seed mixes were specific to each site but authorized mixes generally included a mix of native forbs (e.g. yarrow *Achillea millefolium*, fringed sagewort *A. frigida*), grasses (e.g. western wheatgrass *Agropyron smithii*, bluebunch wheatgrass) and shrubs (e.g. Wyoming big sagebrush, rubber rabbitbrush *C. nauseosus*; US Bureau of Land Management 2003, Rottler et al. 2018).

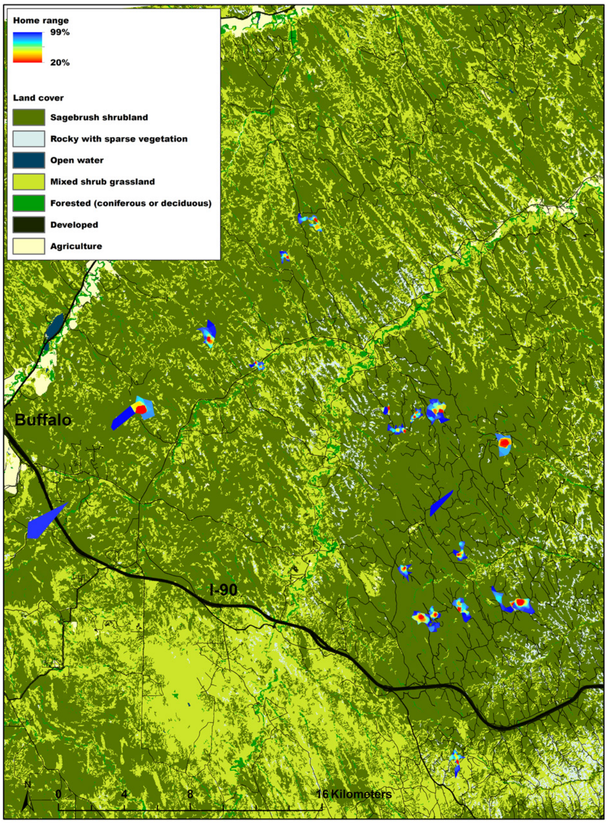

Figure 1. Map of study area land cover and 99% home ranges for brood-rearing greater sage grouse (n = 18; 2017–2019) in northeastern Wyoming, USA. Home ranges estimated using adaptive sphere-of-influence local convex hull nonparametric kernel method (*a*-LoCoH). The red areas are the lower home range percentiles (~ 20%) or 'core areas' within each home range.

Captures and monitoring

We captured female sage-grouse in 2017–2019 using mobile CODA net launchers and night-time spot-lighting with hoop nets (Wakkinen et al. 1992, Sutphin et al. 2018). We targeted capturing at sage-grouse leks in the spring and searched for female sage-grouse along roads in the fall. We fitted females with rump-mounted solar long range download (LRD) GPS-ultra-high frequency (UHF) GPS loggers with independent VHF transmitters attached. With the harness and padding material the entire unit weighed ~ 28 g. Kirol et al. (2020a) provides a detailed description of the tracking devices (hereafter tags) and tracking procedures.

We aged females as first year females (first breeding season) or adults (second breeding season or older) based on the shape and condition of the outermost wing primaries, the outline of the primary tail feathers and coloration of undertail coverts (Eng 1955, Dalke et al. 1963). Habitat selection by birds can be influenced by previous experience of an area or a previous reproductive attempt (Lima 2009, Chalfoun and Schmidt 2012). For our analyses we grouped first year females, termed 'inexperienced' (i.e. no previous experience of the available habitat) and second year or older females, termed 'experienced'.

We only included females that we verified, observationally in the field, to be with a brood (≥ 1 chick) at six weeks' post-hatch (Dahlgren et al. 2010, Kirol et al. 2015a, Lebeau et al. 2019). We used six weeks (e.g. mid to late July) as a cut-off because the majority of chick mortality has occurred by this age; six weeks is before brood break-up begins, when it becomes difficult to assign individual chicks to their mothers; and chicks begin to forage independently and are capable of full independence after this age (Drut et al. 1994, Gregg et al. 2007, Blomberg et al. 2014). We monitored tagged female sage-grouse weekly. At each visit, we tried to determine if the female was still with chicks by observing brooding behavior (e.g. distraction displays, feigning injury and clucking) but we were cautious not to flush the female. Determining if a female has young in the day is often unreliable especially when the observer is trying not to flush the female (Dahlgren et al. 2010). Therefore, we confirmed if a female still had chicks at approximately six weeks' post-hatch by tracking the female at night and using a thermal monocular and spot-lighting techniques to confirm the presence of chicks (Dahlgren et al. 2010).

We estimated the location error of our tags by placing two tags at fixed locations in our study area. These tags were set to gather GPS locations every 30 min for a one-month period. We calculated location error as the median linear distance between tag recorded GPS points and the true tag location as determined by placing a hand-held GPS unit at the tag location and averaging waypoints for 15 min to improve waypoint accuracy. After waypoint averaging the hand-held GPS reported a location error of 3 m.

Location data

Tags were set to collect GPS locations from every 30 min to every 4 h. High-resolution movement data (i.e. frequent relocation intervals) can be highly autocorrelated, resulting in biased models and error terms (Boyce et al. 2010, Calabrese et al. 2016). Prior to modeling our brood-rearing data and estimating home ranges, we assessed autocorrelation with the continuous-time movement modeling ('ctmm') package (Calabrese et al. 2016). This allowed us to inspect the autocorrelation structure of relocation data for each individual using variogram plots. We inspected variograms as described by Calabrese et al. (2016, Supporting information). Based on this assessment we rarified our data to 4 h relocation intervals using the 'amt' package (Signer et al. 2019).

Spatial covariates

Because we were interested in using our high-frequency GPS location data to explore fine-scale habitat selection and avoidance in this study (Johnson 1980, Cagnacci et al. 2010), we used the finest resolution of the available spatial data, 30 m resolution (Yang et al. 2018) or 15 m neighborhood radii, to assess relationships between brood-rearing sage-grouse and their environment. The resolution of the spatial covariates used in our analysis was consistent with the median location error of our tags (median = 14.46 m). Spatial variables were processed using ArcGIS 10.7.0–10.7.1 (www.esri.com) and R statistical software (www.r-project.org).

This research focused on responses of brood-rearing females to anthropogenic disturbances. We included environmental covariates in our models to account for environmental variation in the study area (i.e. statistical control; Hosmer and Lemeshow 2008). The environmental covariates we included in our models were relevant to sage-grouse brood-rearing ecology and supported by previous studies on sage-grouse habitat selection during the brood-rearing period (Table 1). Vegetation cover variables including sagebrush cover, sagebrush height (cm) and herbaceous cover were derived from the 2016 shrubland layers (30 m resolution) available through the US National Land Cover Database (NLCD; Xian et al. 2015, Yang et al. 2018). The importance of sagebrush and herbaceous cover to brood-rearing sage-grouse has been demonstrated by many studies (Cassaza et al. 2011, Kirol et al. 2015a, Aldridge and Boyce 2007). Brood-rearing sage-grouse select for flat areas and against rough terrain at landscape and local scales (Dinkins et al. 2014a, Fedy et al. 2014, Kirol et al. 2015a). We calculated slope and terrain roughness (vector roughness measure, VRM) at a 30 m resolution using a 10 m digital elevation model (Sappington et al. 2007). Low VRM values indicate less rugged terrain, while high values indicate more rugged terrain. The normalized difference vegetation index (NDVI) is a measure of live green vegetation or 'greenness' (Robinson et al. 2017). NDVI has proved predictive of sage-grouse habitat selection in multiple studies (Blomberg et al. 2012, Fedy et al. 2014, Smith et al. 2018); however, in areas of high sagebrush canopy cover NDVI may be less sensitive to forb and grass productivity because of being masked by the sagebrush overstory (Guttery et al. 2013). We calculated time-varying NDVI covariates using dynamic 30 m resolution NDVI products generated every 16 days (Robinson et al. 2017). For each year (2017–2019), we averaged four NDVI composites that overlapped the brood-rearing period in our study, approximately 15 May–31 July.

Habitat modification and infrastructure associated with energy development can influence habitat use patterns during all sage-grouse life stages (Naugle et al. 2011). Development of gas reserves requires the clearing of vegetation for well pads and supporting infrastructure such as roads, wastewater holding ponds, facilities and pipelines (sensu Walker et al. 2007, Finn and Knick 2011, Walker et al. 2020). We created covariates related to natural gas development and general anthropogenic disturbance that fell into two broad categories: 1) natural vegetation removal (i.e. disturbance) and 2) infrastructure features (Table 1).

To assess the response of brood-rearing females to discrete landcover types (Erickson et al. 2001) we used available spatial data that characterized both disturbed and undisturbed landcover at a fine spatial resolution. We obtained disturbance layers that were digitized (head's up digitizing at a min. 1:5000 screen resolution) following the disturbance calculation tool (DDCT) process. DDCT is used to quantify disturbances in the sagebrush ecosystem in Wyoming, USA (State of Wyoming 2019). We used the DDCT disturbance data to create discrete surface disturbance layers, at a 1 m resolution, that represented the disturbance footprint (i.e. removal of natural vegetation). These included both reclaimed and active surfaces. Active surfaces were areas stripped of vegetation that remain devegetated or partially vegetated with interim reclamation seed mixes. Examples of active disturbance in our study area included graveled access roads and well pads. Reclamation surfaces included areas with infrastructure removed that had been revegetated with reclamation seed mixes but were largely

Table 1. Covariates that were assessed in our generalized linear models (GLM) used to model fine-scale habitat selection in brood-rearing female sage-grouse. The environmental covariates that had the most support across individual models formed the base model. The anthropogenic covariates were assessed in conjunction with the base model for each individual. For fractional (e.g. Herb) and discrete landcover covariates (e.g. Landcover factor) we modeled covariates at a 30 m resolution (Yang et al. 2018) or 15 m neighborhood radii, to explore fine-scale responses to landcover.

Covariate	Covariate type	Description
Sage	Environmental	% sagebrush cover (all *Artemisia* spp.; Xian et al. 2015)
Sage + SageQ	Environmental	Quadratic form of % sagebrush cover
Herb	Environmental	% herbaceous cover (Xian et al. 2015)
NDVI	Environmental	Biweekly normalized difference vegetation index (NDVI) representing live green vegetation averaged over study period (15 May–31 July each year; Robinson et al. 2017)
NDVI + NDVIQ	Environmental	Quadratic form of NDVI
Slope	Environmental	Slope in percent
VRM	Environmental	Vector roughness measure (VRM; low values indicate flat terrain; high values indicate rugged terrain; Sappington et al. 2007)
Landcover factor	Anthropogenic	Categorical covariate of undisturbed natural vegetation (coded as 0) or disturbed (active + reclamation; coded as 1). Active surfaces were stripped of natural vegetation and associated with infrastructure or access roads. Reclamation surfaces were formerly active surfaces that have been reclaimed and revegetated with reclamation seed mixes but lacking a sagebrush overstory
Power line viewshed	Anthropogenic	A count of the number of power poles that were visible from any given pixel on the landscape based on a 0.5 km viewshed distance
Structure viewshed	Anthropogenic	A count of the number of infrastructure features – primarily coal-bed natural gas (CBNG) wells – that were visible from any given pixel on the landscape based on a 0.5 km viewshed distance
Infrastructure distance	Anthropogenic	Linear distances to infrastructure features (primarily CBNG wells) transformed using a decay function ($e^{-d/\alpha}$) where *d* was the distance in meters from each pixel to the water body edge. We assessed three decay constants (α): 200 (decays to zero at 600 m), 100 (decays to zero at 300 m) and 50 (decays to zero at 150 m)
Pond distance	Anthropogenic	Linear distances to man-made water bodies transformed using a decay function ($e^{-d/\alpha}$) where *d* was the distance in meters from each pixel to the water body edge. We assessed three decay constants (α): 200 (decays to zero at 600 m), 100 (decays to zero at 300 m) and 50 (decays to zero at 150 m)

devoid of sagebrush. Reclamation surfaces in our study area included recently (≤ 10 years) reclaimed well pads, access roads and pipeline corridors (see Supporting information). We merged the 2016 NLCD landcover (Yang et al. 2018) with the active and reclamation disturbance layers we produced to create a discrete layer that categorized the landscape into classes of undisturbed natural vegetation or disturbed surfaces (active + reclamation) at a 30 m resolution. We termed this categorical covariate Landcover factor.

Infrastructure covariates included power transmission lines (hereafter power lines), infrastructure features (primarily CBNG wells) and anthropogenic ponds (Table 1). Power line data were obtained from the Powder River Energy Corporation; and both active, and plugged and abandoned well data were obtained from the Wyoming Oil and Gas Conservation Commission (wogcc.wyo.gov). Ponds were extracted from the DDCT disturbance layers. All infrastructure was verified, and in some cases corrected, using ESRI World Imagery (https://services.arcgisonline.com/arcgis/rest/services/World_Imagery/MapServer).

Visible structures can be negatively associated with sage-grouse habitat selection and chick survival (Kirol et al. 2015a, Lebeau et al. 2019). We developed viewshed surfaces to determine the number of infrastructure features and power lines that were visible by sage-grouse from any given pixel on the landscape (Table 1). Power lines can uniquely influence habitat selection and fitness rates in sage-grouse (Dinkins et al. 2014b, Gibson et al. 2018, Lebeau et al. 2019). Therefore, we developed a viewshed covariate for power lines and a second viewshed covariate for all other structures in our study area. We calculated how many structures were visible within a 0.5 km viewshed distance (Gillan et al. 2013). Each type of structure received a specific height above ground value. For instance, well structures were given a height of 3 m, compressor or pumping stations a height of 5 or 8 m and power lines a height of 27 m (Supporting information). The height values were based on the average heights of these structures measured in the field.

We used decay distances to understand fine-scale relationships between brood-rearing habitat selection and infrastructure in our study area. Decay distances allowed us to assess selection or avoidance of habitats in close proximity to CBNG wells or anthropogenic water sources (i.e. ponds; Walker et al. 2016). We transformed continuous distance variables using a decay function ($e^{-d/\alpha}$) where *d* was the distance in meters from each pixel to the feature of interest (e.g. infrastructure or pond edge) which allowed the effect to decay as distance from the feature of interest increased (Fedy and Martin 2011, Walker et al. 2016). We assessed three decay constants (α): 200 (decays to zero at 600 m), 100 (decays to zero at 300 m) and 50 (decays to zero at 150 m). Ponds were created for holding CBNG wastewater, livestock watering and agricultural irrigation. Ponds are prevalent in our study area and, in parts of our study area with higher concentrations of CBNG development, ponds reach densities of one pond per 2 km^2.

Home range characteristics

We estimated brood-rearing home ranges using the local convex hull (LoCoH) non-parametric kernel method and, specifically, the adaptive sphere-of-influence LoCoH method (*a*-LoCoH; Getz et al. 2007). We generated 99% *a*-LoCoH home range for each individual.

We used sagebrush landcover and anthropogenic disturbance layers to measure the proportion of sagebrush landcover and anthropogenic disturbance within each brood-rearing home range. Anthropogenic disturbance included any disturbance that replaced natural vegetation (e.g. active disturbance and reclamation) that was derived from the DDCT surface disturbance layers. We used the 2016 NLCD landcover to determine the proportion of sagebrush landcover in each brood-rearing home range (Yang et al. 2018).

For each individual, we calculated two movement metrics, step lengths and net-squared displacement (NSD), to explore movement patterns and detect changes in movement behavior (Edelhoff et al. 2016). We generated step lengths (i.e. the distance between the start-point and end-point of a given step) and NSD using the 'move' package; Kranstauber et al. 2020). NSD calculates the squared distance between each location along an individual's track and its original location. We calculated NSD from each individual's nest.

Research has shown that environmental conditions can lead to use of distinct areas and habitats for rearing chicks that are termed early and late brood-rearing periods (Atamian et al. 2010, Connelly et al. 2011). However, the timeframes describing transitions from early to late brood-rearing vary in sage-grouse literature from 2–3 weeks to 5–6 weeks (Drut et al. 1994, Thompson et al. 2006, Hagen et al. 2007, Atamian et al. 2010). Early and late brood-rearing are often analyzed separately because of movements to different habitat types for late brood-rearing (Hagen et al. 2007, Atamian et al. 2010). To determine if brood-rearing females in our study were moving to new areas at a consistent age post-hatch, suggesting a shift between potential early and late brood-rearing habitats before six weeks (e.g. 2–3 weeks), we plotted NSD against days since the female and chicks left the nest (hatch day) to six weeks for all of the brood-rearing females in our sample. NSD allowed us to visualize change-points that might suggest shifts in habitat use (Edelhoff et al. 2016). We also inspected the shape of home ranges and 'core areas' within home ranges for each female. As described by Getz et al. (2007), core areas are lower home range percentiles (20%) within each home range that represent higher densities of use locations. A bimodal shape or more than one core area would suggest distinct shifts in space use (Moskát et al. 2019).

Statistical analysis

We used a type III design to assess fine-scale habitat selection within brood-rearing home ranges (third-order selection, Johnson 1980) where we used observations of individuals (i.e. individual-level models) to make inferences about the population (Erickson et al. 2001, Thomas and Taylor 2006). We used a two-stage approach were we first fit individual-level models and identified the most parsimonious model for each individual. Second, we averaged and bootstrapped across individual model coefficients to produce population-level estimates (Fieberg et al. 2010, Puth et al. 2015, Prokopenko et al. 2017).

We used weighted generalized linear models (GLM) to compare use locations with pseudo-absence locations for our individual-level models. We generated available points (i.e. pseudo-absence) at a ratio of 20:1 to used points for each individual (Muff et al. 2020). The spatial extent of the area considered as available to the animal should be based on biologically realistic movements of that species or individual (Jones 2001, Meyer and Thuiller 2006). We established available points within a specific availability domain for each individual. The availability domain was based on the maximum linear distance across that individual's home range that corresponds directly to that individual's movements during the brood-rearing period. Therefore, each brood-rearing home range was buffered by this distance, and available points were established within this buffer (e.g. that individual's availability domain). We weighted available locations to account for the uneven ratio of available points (20:1) to used points (Fithian and Hastie 2013, Fieberg et al. 2021).

For our individual-level models, we first modeled environmental covariates to form a base model (Scrafford et al. 2018). We considered both linear and quadratic terms for vegetation covariates to allow us to detect selection for intermediate values of these covariates, such as selection for intermediate sagebrush cover (Doherty et al. 2010). All the environmental covariates were standardized. To assess model support and identify the most informative parameters we relied on Akaike's information criterion (AIC) scores and 95% confidence limits (CIs) at each stage of the model building process (Burnham and Anderson 2002, Arnold 2010). When environmental variables were correlated ($r \geq |0.70|$), we chose the most informative covariate or covariate representation (i.e. linear or quadratic) based on the degree of AIC support across the individual models.

We used the base model to assess the relative contribution of each anthropogenic covariate while accounting for environmental variation (Hosmer and Lemeshow 2008). When assessing support for anthropogenic covariates for each individual model (e.g. the model built for each individual) we used the same base model and combined it with each anthropogenic covariate of interest (base model + anthropogenic covariate). Anthropogenic covariates that had 95% CIs that did not overlap zero were assessed in our final candidate set. Using AIC, the candidate sets were compared to each other and to the base model. The candidate model with the lowest AIC score was identified as the most parsimonious model for that individual (Burnham and Anderson 2002). We used AIC to optimize the decay distance for infrastructure features and ponds (McGarigal et al. 2016). We modeled each decay distance with the base model and the decay distance with the lowest AIC score for each covariate was brought forward to the next modeling step (McGarigal et al. 2016). Note, exposure to anthropogenic covariates was not consistent across individuals and some individuals were not exposed to covariates of interest within their availability domain. For example, several of the brood-rearing females in our study settled in home ranges that did not contain power lines. When the anthropogenic covariate was not within the availability domain of that individual it was not assessed in the candidate set. We considered anthropogenic covariates to not be within the availability domain if > 95% of available locations contained zero values for that covariate.

For our second analysis step, we obtained population-level results by averaging individual-level model coefficients for each covariate of interest (base model + anthropogenic covariate; Prokopenko et al. 2017). We calculated 95% CIs using 5000 bootstrap replicates with the adjusted percentile bootstrap (BCa) method (Efron and Tibshirani 1993, Puth et al. 2015). We only calculated population-level results for the distance decay variables that were present in our most parsimonious individual-level models. All analyses were conducted using R statistical software (www.r-project.org).

Results

We monitored a total of 73 females during the reproductive seasons (n = 15 in 2017, n = 29 in 2018 and n = 29 in 2019). Our analysis focused on brood-rearing females and included 18 female sage-grouse that were alive and were verified to still have chicks at approximately six weeks' post-hatch (n = 4 in 2017, n = 5 in 2018 and n = 9 in 2019). No females in the analysis were in the brood-rearing sample for more than one year. After resampling to 4 h intervals, the mean number of relocations per individual was (± SE) 236.22 ± 2.60 (range = 204–244).

Space use

The average 99% home range size for all individuals was 0.85 ± 0.21 km^2 (range = 0.26–4.02 km^2). Seventy-two percent of home ranges included the female's nest site (Fig. 2). For most individuals, NSD from the nest plotted against time showed little change over the first six weeks after hatch and, across all individuals, NSD plots did not demonstrate any consistent movement or space use shifts at a specific chick age (Fig. 3). Only two individuals (RAP27 and PAR09) had NSD distributions that signaled pronounced movements suggesting shifts in space use. RAP27 moved ~ 3.5 km on day five post-hatch. PAR09 moved ~ 8 km between days 37 and 38 post-hatch (Fig. 3). Inspection of 99% *a*-LoCoH home ranges indicated that most individuals had one distinct core area within their home ranges. Four of the home ranges (22%) were bimodal with two distinct core areas.

Home range characteristics

The proportion of sagebrush landcover was never less than 40% (range = 40.28–98.20%) of an individual's home range and averaged 77.37 ± 3.36% across all individuals. The average proportion of anthropogenic surface disturbance for all home ranges was 3.59 ± 0.75%. The greatest proportion of anthropogenic disturbance for any home range was 14.65%, which was an outlier and twice as high as the second highest proportion of disturbance (6.68%) for any individual. Of the 14.65% disturbance within this individual's home range, 5.33% was reclamation, which was also the highest amount of reclamation surface within any individual's home range. Seventeen out of the 18 brood-rearing females had at least some surface disturbance, such as active or reclaimed roads, well pads or pipeline corridors, within their home ranges (range = 1.38–14.65%). Of these 17 individuals, seven (41%) had reclaimed surfaces (range = 0.21–2.76%), in addition to active disturbance, within their home ranges.

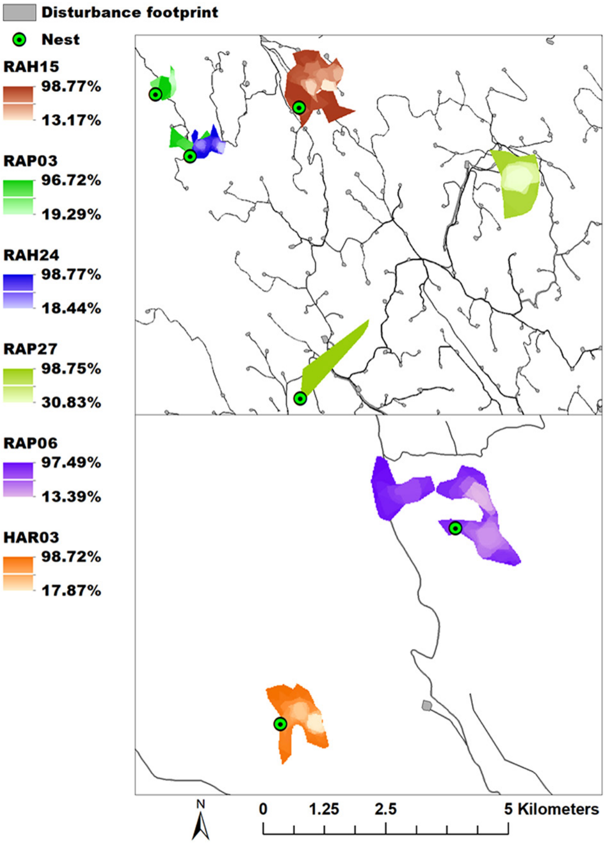

Figure 2. Example of 99% home ranges estimated using adaptive sphere-of-influence local convex hull non-parametric kernel method (*a*-LoCoH) for six brood-rearing greater sage-grouse in northeastern Wyoming, USA. Color gradient for each individual indicates ~ 10 to ~ 99 percentile isopleths. The lightest areas are the lower home range percentiles (≤ 20%) or 'core areas' within each home range.

Experienced females (n = 11) were less likely than inexperienced females (n = 7) to establish home ranges in areas with anthropogenic disturbance or infrastructure. Within brood-rearing home ranges, 82% of experienced females had active disturbance, 27% had reclaimed surfaces, 18% had power lines and 55% had CBNG structures. In contrast, 100% of inexperienced females had active disturbance, 57% had reclaimed surfaces, 43% had power lines and 57% had

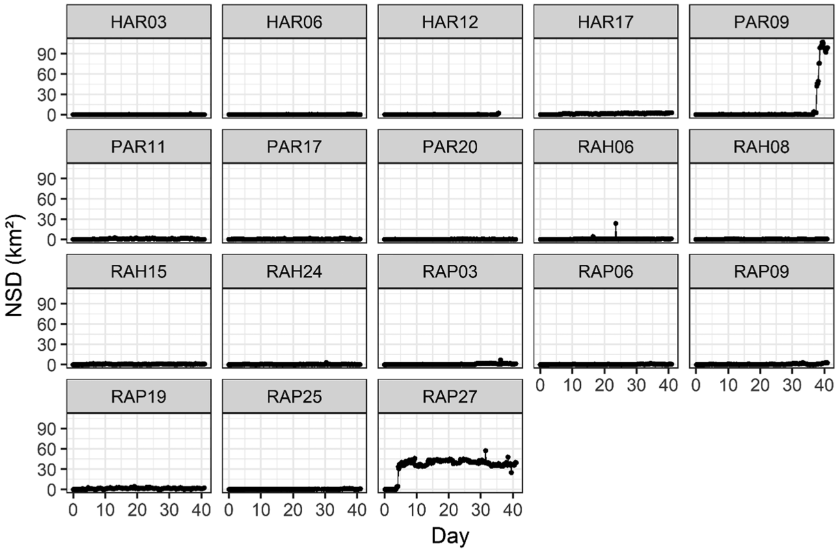

Figure 3. Net-squared displacement (NSD) for each individual from its nest site. We plotted NSD against post-hatch days (days since the female and chicks left the nest) to 40 days. NSD allows for detection of change-points that indicate movement shifts to different areas. Movement data are from brood-rearing greater sage-grouse in northeastern Wyoming, USA.

CBNG structures within their brood-rearing home ranges (Fig. 4).

Habitat selection

The environmental covariates with the most support across models formed the base model and included a quadratic form of sagebrush cover, a measure of terrain roughness (VRM), slope and NDVI. Support for a quadratic form of sagebrush cover across individual models suggests that brood-rearing females consistently showed a selection preference for intermediate values of sagebrush cover. Brood-rearing sage-grouse were also consistently selecting for flatter areas (lower slope values) with less rugged terrain (lower VRM values).

Selection for natural landcover and against disturbed surfaces (Landcover factor), which included both active and reclaimed surfaces, was statistically supported at the population level (Table 2). Landcover factor was present in six of the most parsimonious individual-level models. No individuals indicated a selection preference for disturbed surfaces, which included active disturbance and reclamation (Table 3). Habitat selection for natural landcover and avoidance of disturbed surfaces was similar between experience and inexperienced females.

All of the brood-rearing individuals were exposed to at least one anthropogenic feature covariate (CBNG well, power line or pond) within their availability domain. Population-level results show that brood-rearing females were avoiding habitat within 150 m of CBNG infrastructure (Table 2). Ninety-four percent of the most parsimonious individual-level models included decay distance to infrastructure (primarily CBNG wells) within 150 m (decay constant 50) or 600 m (decay constant 200). Across individual models habitat selection was always negatively associated with CBNG infrastructure within 150 m (decay constant 50; Table 4). But this relationship was not consistently negative or positive within 600 m of infrastructure. Brood-rearing females in areas with higher well densities were more likely to show localized avoidance (150 m). Generally, individuals exposed to well densities > 2 well per km^2 were avoiding infrastructure within 150 m (Fig. 5).

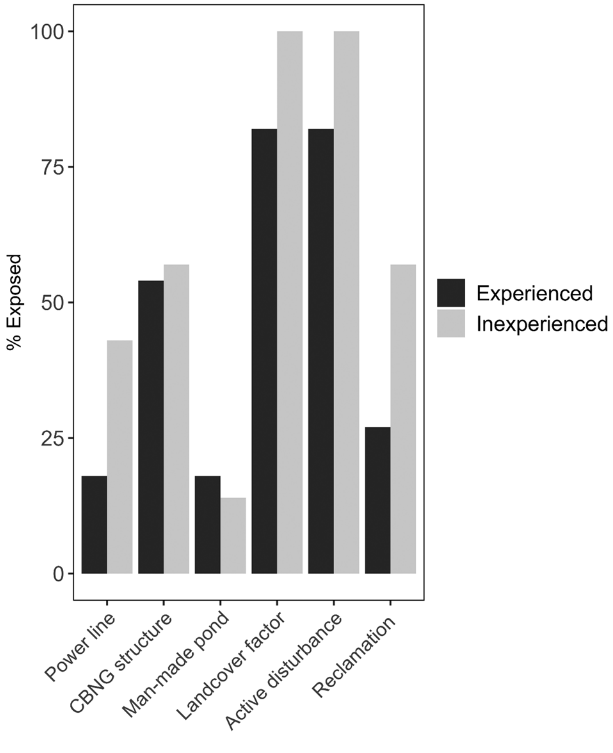

Figure 4. Comparison between the proportion (%) of anthropogenic features that occurred within experienced (adult) and inexperienced (first year) home ranges of brood-rearing females in northeastern Wyoming, USA.

Table 2. Population-level results for brood-rearing female sage-grouse. Coefficients and 95% confidence intervals for anthropogenic covariates of interest derived from averaging and bootstrapping across individual-level models. For comparison, all non-categorical covariates were standardized. We only calculated population-level results for the decay distance variables (200 [decays to zero at 600 m], 100 [decays to zero at 300 m] and 50 [decays to zero at 150 m]) that were supported in individual-level models (Table 3, 4). The Landcover factor covariate represented areas categorized into discrete classes of undisturbed natural vegetation or disturbed (active disturbance + reclamation). Reclamation areas were those revegetated with reclamation seed mixes but largely devoid of sagebrush. Active surfaces were areas stripped of vegetation that were devegetated or partially vegetated with interim reclamation seed mixes and associated with active development. A negative coefficient for Landcover factor indicates selection for undisturbed natural vegetation (coded as 0) and against disturbed areas (coded as 1). Power line viewshed represented the number of power poles that were visible from any given pixel on the landscape. Structure viewshed represented the number of infrastructure features, primarily 3 m tall coal-bed natural gas (CBNG) well structures, that were visible from any given pixel on the landscape. We calculated how many power poles or structures were visible within a 0.5 km viewshed distance. Asterisks (*) indicate coefficients with 95% confidence intervals that do not overlap zero.

Anthropogenic covariate	Females exposed	β (95% CI)
Landcover factor (categorical)	16	−0.411 (−0.669, −0.218)*
Power line viewshed (count)	13	−1.107 (−2.287, −0.505)*
Structure viewshed (count)	15	−0.745 (−2.524, 0.061)
Infrastructure distance (decay^{50})	15	−0.914 (−2.400, −0.253)*
Infrastructure distance (decay^{200})	15	−0.179 (−0.692, 0.134)
Pond distance (decay^{100})	13	−3.494 (−8.262, −0.956)*
Pond distance (decay^{200})	13	−1.297 (−4.036, −0.215)*

Only one brood-rearing female, RAH08, did not follow this pattern. The top model for RAH08 included a positive associated with infrastructure at a 600 m decay distance (Fig. 5). Of the six individuals positively associated with infrastructure within 600 m, four of these were inexperienced females.

Seventy-two percent of brood-rearing females in our study were exposed to power lines within their availability domain. At the population level, we found that the number of visible power line poles within 500 m was negatively associated with habitat selection by brood-rearing sage-grouse (Table 2). Of the brood-rearing females exposed to power lines, a negative relationship between power line visibility and habitat selection was supported 62% of the time in the most parsimonious individual-level models. No individual-level models

Table 3. Coefficients and 95% confidence intervals for anthropogenic covariates that were in the most parsimonious model (top AIC model) for each brood-rearing sage-grouse. For comparison, all non-categorical covariates were standardized. Well density is the density of wells within each individual's availability domain. The Landcover factor covariate represented areas categorized into discrete classes of undisturbed natural vegetation or disturbed (active disturbance + reclamation). Reclamation areas were those revegetated with reclamation seed mixes but largely devoid of sagebrush. Active surfaces were areas stripped of vegetation that were devegetated or partially vegetated with interim reclamation seed mixes and associated with active development. A negative coefficient for Landcover factor indicates selection for undisturbed natural vegetation (coded as 0) and against disturbed areas (coded as 1). Power line viewshed represented the number of power poles that were visible from any given pixel on the landscape. Structure viewshed represented the number of infrastructure features, primarily 3 m tall coal-bed natural gas (CBNG) well structures, that were visible from any given pixel on the landscape. We calculated how many power poles or structures were visible within a 0.5 km viewshed distance. Gray shaded rows indicate inexperienced females (first year). Non-shaded rows indicate experienced females (second year or older females). These covariates were modeled at a 30 × 30 m resolution. An NA indicates that the individual was not exposed to that covariate. A dash (–) indicates that the covariate was within the individual's availability domain but the covariate was not present in the top model.

Grouse Id	Well density (km^2)	Landcover factor (categorical)	Power line viewshed (count)	Structure viewshed (count)
		β (95% CI)	β (95% CI)	β (95% CI)
RAP25	3.2	–	−3.995 (−6.450, −2.400)	0.771 (0.591, 0.948)
HAR17	3.0	–	−0.391 (−0.604, −0.191)	–
RAP19	2.7	−1.013 (−1.626, −0.525)	–	−0.194 (−0.335, −0.525)
RAH24	2.4	–	NA	−0.415 (−0.612, −0.236)
PAR17	2.2	−0.263 (−0.679, 0.101)	–	−0.276 (−0.427, −0.129)
RAH06	2.2	−1.026 (−2.303, −0.209)	−2.073 (−4.130, −0.999)	0.953 (0.784, 1.130)
RAH08	2.1	–	−1.700 (−3.130, −0.851)	–
RAP27	1.8	−0.882 (−1.571, −0.324)	−0.718 (−1.190, −0.387)	0.760 (0.673, 0.845)
RAP03	1.7	–	NA	–
RAH15	1.6	–	−0.777 (−1.400, −0.361)	0.343 (0.219, 0.465)
PAR11	1.2	−0.596 (−1.440, 0.023)	–	0.327 (0.163, 0.485)
HAR06	0.9	–	NA	–
HAR12	0.7	–	–	–
PAR20	0.2	−0.419 (−0.950, 0.017)	–	–
PAR09	0.1	–	–	–
HAR03	0.0	NA	NA	NA
RAP06	0.0	–	NA	NA
RAP09	0.0	NA	−0.382 (−0.665, −0.144)	NA

Table 4. Beta coefficients and 95% confidence intervals for anthropogenic covariates that were in the most parsimonious model (top AIC model) for each brood-rearing sage-grouse. For comparison all non-categorical covariates were standardized. Well density is the density of wells within each individual's availability domain. Infrastructure and pond distance represents linear distances to the feature of interest and transformed using a decay function. The decay distance allows the effect to decay as distance to the feature of interest increased. A negative coefficient for decay indicates avoidance of the feature of interest areas. We assessed three decay constants: 200 (decays to zero at 600 m), 100 (decays to zero at 300 m) and 50 (decays to zero at 150 m). Gray shaded rows indicate inexperienced females (first year). Non-shaded rows indicate experienced females (second year or older females). An NA indicates that the individual was not exposed to that covariate. A dash (–) indicates that the individual was exposed to that covariate but the covariate was not statistically supported.

Grouse Id	Well density (km²)	Infrastructure distance (decay) β (95% CI)	Pond distance (decay) β (95% CI)
RAP25	3.2	−0.316 (−0.679, −0.030)^{50}	–
HAR17	3.0	−0.555 (−0.852, −0.298)^{50}	0.650 (0.545, 0.752)^{200}
RAP19	2.7	−0.408 (−0.660, −0.191)^{50}	−0.108 (−0.272, 0.037)^{100}
RAH24	2.4	−0.481 (−0.842, −0.209)^{50}	NA
PAR17	2.2	−0.146 (−0.302, 0.003)^{200}	–
RAH06	2.2	−0.905 (−1.520, −0.412)^{50}	–
RAH08	2.1	0.632 (0.511, 0.752)^{200}	NA
RAP27	1.8	0.282 (0.083, 0.477)^{200}	−0.530 (−1.320, −0.080)^{100}
RAP03	1.7	−0.341 (−0.506, −0.187)^{200}	NA
RAH15	1.6	0.352 (0.212, 0.490)^{200}	NA
PAR11	1.2	−1.895 (−2.270, −1.550)^{200}	−1.854 (−2.500, −1.320)^{200}
HAR06	0.9	0.548 (0.408, 0.686)^{200}	–
HAR12	0.7	0.623 (0.489, 0.756)^{200}	−1.150 (−1.980, −0.543)^{100}
PAR20	0.2	0.763 (0.633, 0.895)^{200}	NA
PAR09	0.1	−2.24 (−3.280, −1.430)^{200}	0.212 (0.149, 0.266)^{200}
HAR03	0.0	NA	−1.044 (−1.510, −0.658)^{200}
RAP06	0.0	NA	0.208 (0.078, 0.322)^{200}
RAP09	0.0	NA	0.651 (0.591, 0.711)^{200}

demonstrated a positive association with visible power line poles within 500 m and habitat selection (Table 3). Avoidance of visible power lines was similar between experienced and inexperienced females (Table 3).

Eighty-three percent of individuals were exposed to 3 m tall CBNG well structures within their availability domain. Only one individual (RAP27) was exposed to taller CBNG structures such as compressor stations (5–8 m). Visible structures (Structure viewshed) within 500 m was not a statistically supported at the population level but trended negative (Table 2). Responses to Structure viewshed were variable across individual-level models. A positive coefficient for the Structure viewshed covariate in four of the individual models suggested that these females were selecting areas with higher densities of visible CBNG wells (Table 3). Yet, all four of the individuals that had a positive coefficient for CBNG well visibility were avoiding areas with greater power line visibility (Table 3). Of the four individuals that had a positive association with visible structures in their top model, three of these were inexperienced females (Table 3).

At the population level, habitat selection was negatively associated with anthropogenic ponds, suggesting avoidance of habitat within 300 m (decay constant 100) and 600 m (decay constant 200) of pond edge (Table 2). At the individual level there was a large amount of variability between individuals. The most parsimonious individual-level models contained either the covariate pond decay distance 100 or 200. None of the top individual-level models contained the covariate pond distance decay 50 (decays to zero at 150 m). Of the females exposed to ponds within their availability domain (n = 13), 31% had a positive coefficient suggesting selection for habitats within 600 m of pond edge (decay constant 200). No individual-level models indicated a positive association with pond edge within 300 m (Table 4). There was no apparent pattern between pond avoidance or selection

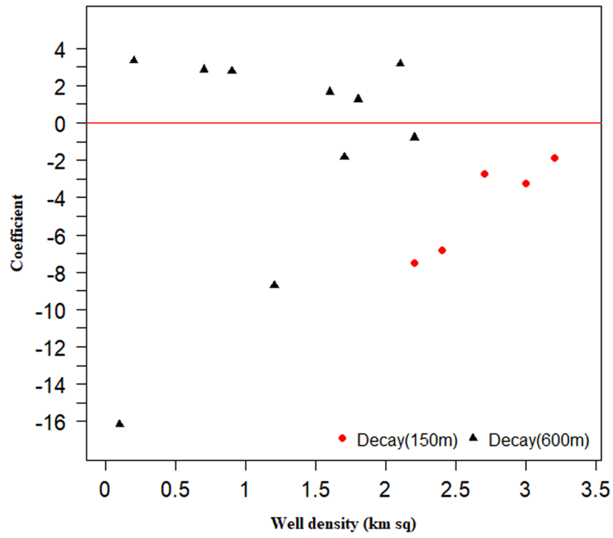

Figure 5. Individual model (n = 15) beta coefficients for the covariate decay distances to coal-bed natural gas (CBNG) infrastructure plotted against well density. Symbols above the red line indicate selection while symbols below indicate avoidance. Avoidance was more likely when brood-rearing females were exposed to higher well densities in northeastern Wyoming, USA.

and female experience. See Supporting information for competitive (≤ 10 AIC) model sets for each individual.

Discussion

We evaluated several interrelated research questions to inform fine-scale resource management in an area that has experienced extensive oil and gas development. We used high-resolution relocation data from female sage-grouse raising young to better understand space use and habitat selection, and avoidance behavior, during the brood-rearing period at fine spatial scales. Our population-level results summarized the consistent patterns in habitat selection within home ranges (third-order selection; Johnson 1980, Erickson et al. 2001). Our individual-level models quantified and highlighted different intensities of avoidance and contrasting behaviors towards some anthropogenic features made by individual females raising young. All of the most parsimonious individual-level models included at least one anthropogenic disturbance or structure covariate. This suggests that selection choices made by maternal sage-grouse that were successful at raising chicks is reliably influenced by anthropogenic habitat change in our study area.

Home range characteristics

The average size of brood-rearing home ranges in our study was 0.85 ± 0.21 km^2. To our knowledge this is the first time that home ranges have been estimated for brood-rearing sage-grouse using high-frequency relocation data. Because of differences in relocation frequency and variation in the definition of brood-rearing periods, it was difficult to directly compare the size of our brood-rearing home ranges with other research. However, most estimates of brood-rearing or breeding home range sizes are much larger than the home ranges in our study. In some areas, female sage-grouse commonly move broods over 5 km between nesting habitats and early summer brood-rearing areas (Atamian et al. 2010, Connelly et al. 2011). Estimates from VHF tracking studies suggest female home range sizes during the breeding season can be 26 times larger than the home ranges in our study (Schroeder et al. 1999). Atamian et al. (2010) reported that areas used by brood-rearing females, to almost six weeks' post-hatch, averaged 7.2 km^2 in Nevada, USA. Conversely, Wallestad (1971) used VHF to track sage-grouse broods twice a day over the brood-rearing period and reported a home range size of 0.86 km^2 in Montana, USA, which is similar to the average brood-rearing home range in our research. It is possible the brood-rearing grouse in our study were obtaining the food resources needed for their chicks in smaller home ranges and, therefore, had no incentive to move larger distances. However, given the relatively small home range sizes in our study, it is likely that the limited amount of undisturbed sagebrush habitat, and the high density of anthropogenic disturbance, are restricting movements of brood-rearing females in this region.

The majority (89%) of brood-rearing females remained in close proximity (mean = 0.59 km, SE = 0.01 km) to their nests over the first six weeks. While the majority of brood-rearing females moved minimal distances, two brood-rearing females underwent large movements. One female moved her chicks approximately 5 km starting five days after hatch. Another female stayed in close proximity to her nest site until day 37 when she moved her chicks approximately 8 km. This female moved up in elevation which corresponded to the sage-grouse literature describing movements to late brood-rearing habitats at upper elevations that are retaining succulent forbs while forbs in lower elevations are desiccating (Connelly et al. 2011). If early brood-rearing habitat is the habitat used in the vicinity of a nest (Connelly et al. 2011), then the majority of females in our sample were not moving to new areas or late brood-rearing habitat before six weeks' post-hatch. However, Atamian et al. (2010) suggest that environment conditions (e.g. drought) and food availability may change brood-rearing periods across years. For instance, one year a shift from early to late brood-rearing may occur at approximately three weeks and the next year it may occur several weeks later (Atamian et al. 2010). It is possible that our study did not overlap a year when shifts to late brood-rearing habitat may have occurred earlier due to low moisture conditions. It is also possible that the movements and brood-rearing space-use patterns we observed were different from those that historically occurred in this population, before widespread energy development occurred in this region, when there was more contiguous sagebrush and fewer obstructions to sage-grouse movements.

The selection of habitats by animals is a hierarchical process (Johnson 1980). In sage-grouse, females select nest sites within larger areas that also provide resources needed to successfully raise chicks (Gibson et al. 2016). We found the majority of brood-rearing home ranges in our study included the individual's nest site, which reiterates that the fine-scale habitat relationships we identified were influenced by decisions made at a higher order of selection, when the female selected an area to nest (Fedy et al. 2015). For instance, female sage-grouse in our study raised chicks in areas that, on average, had 3.5% anthropogenic surface disturbance and 94% of home ranges contained less than 7% disturbance. Yet, disturbance levels measured within the extent of an average home range size far exceeded 7% in our study area (Kirol et al. 2020b, Fedy and Kirol unpubl.). This pattern suggests that brood-rearing females in our study chose to nest in areas with lower levels of disturbance, which consequently reduced exposure during nesting and brood-rearing (Holloran et al. 2010, Aldridge et al. 2012, Fedy et al. 2015, Kirol et al. 2015a).

Habitat selection

At the population level, we found support for fine-scale selection of patches of natural landcover and avoidance of disturbed surfaces (both active oil and gas, and reclaimed surfaces). With regard to selection for natural landcover there was little variability across our individual-level results. When natural landcover (Landcover factor) was supported in the most parsimonious individual-level model it was always a positive relationship, as no females selected for disturbed surfaces. Across all females, 87% of our brood-rearing locations were within sagebrush cover, suggesting that brood-rearing females in our study were spending very little time in areas outside of sagebrush habitat. Combined, these findings demonstrate that at fine scales the brood-rearing females are strongly tied to concealment cover which, in our study was primarily sagebrush cover, but can also be tall grass or tall and dense forbs (Thompson et al. 2006, Hagen et al. 2007, Kirol et al. 2012, Smith et al. 2018). Our results are consistent with foraging theory and concur with the conclusions of Hagen (2011) that described sage-grouse seasonal habitat selection as a balance between selecting concealment cover for predator avoidance while also meeting biological demands (e.g. food and thermoregulation).

At the population level and across the most parsimonious individual-level models, we found support for avoidance of disturbed surfaces, which included reclaimed surfaces. The reclaimed surfaces in our study represent early-stage reclamation ($\leq$ 10 years since the surface was reclaimed) and are dominated by seeded grass and forbs without a sagebrush overstory (Kirol and Fedy 2021). In arid sagebrush ecosystems, such as our study area, it can take sagebrush 80 years to naturally re-establish on disturbed surfaces (Avirmed et al. 2015). Shrub cover is important to brood-rearing females in combination with an understory of diverse forbs and grasses (Connelly et al. 2011). Therefore, it is likely the reclamation surfaces in our study were not selected by females with chicks because of the lack of a shrub overstory that acts as concealment cover (Thompson et al. 2006, Hagen 2011). For example, in a post-fire landscape, Germino et al. (2023) found that sage-grouse use, as measured by the density of scat, was greater near sagebrush seedling outplantings when compared to burned areas without sagebrush. Mitigating the impacts of energy development through reclamation is a long-term strategy, and other approaches to mitigation (e.g. decreased activity, buried powerlines, reduced sagebrush removal) should also be pursued (Fedy et al. 2015, Kirol et al. 2015b).

At a population level, brood-rearing sage-grouse demonstrated localized avoidance (within 150 m) of well structures; however, this avoidance behavior dissipated at greater distances (e.g. 600 m). Decay distance to infrastructure was in the most parsimonious individual-level models 94% of the time, with a large amount of variability in the responses of individual brood-rearing females. No individuals selected habitats within 150 m of well structure. However, contrasting behaviors became apparent at 600 m from well structures, as some individuals selected habitats within 600 m of well structures. Individuals in areas with higher well densities – well densities greater than two wells per km^2 – were more likely to demonstrate localized avoidance of infrastructure than those in areas of lower well densities. Consistent with this finding Fedy et al. (2015) showed that mitigation, such as remote well monitoring to reduce traffic, may lessen some avoidance behavior by sage-grouse, but even with mitigation grouse demonstrate increased avoidance in areas of higher well densities.

CBNG wells in our study area were generally small buildings (~ 2 × 2 m structures) that were approximately 3 m tall. Therefore, unlike power lines, these short structures were not commonly used as perches by raptor species (e.g. golden eagles *Aquila chrysaetos*) that prey on sage-grouse and their chicks (Hagen 2011, Dinkins 2014b). At the population level, CBNG structures within 500 m did not influence habitat selection. Our population-level results were inconsistent with Aldridge and Boyce (2007) and Kirol et al. (2015a) who found that higher densities of visible wells led to avoidance by brood-rearing females. CBNG wells in our study area were developed at densities up to three wells per km^2. At this density, wells were generally spaced 400–600 m from each other. Therefore, there was little sagebrush habitat that did not have a visible well within 500 m. Furthermore, wells were placed in areas with flatter terrain. Sage-grouse in our study also showed a strong preference for habitats with flatter terrain. It is likely that our results were inconsistent with Aldridge and Boyce (2007) and Kirol et al. (2015a) because the brood-rearing females using sagebrush habitats in this area cannot completely avoid visible well structures because of high well densities and the widespread distribution of wells across most of the available habitat. This brings up the important point that habitats identified as selected in a study area may not necessarily be preferred habitats – they may simply be the best of what is available (Erickson et al. 2001). Similar to individual-level findings on distances to well structures, we detected inconsistent behaviors in responses to visible well structures among individuals. Some females were selecting areas with visible wells while others were avoiding areas with visible wells. Yet, all of the females that were avoiding visible wells were in areas with higher well densities ($\geq$ 2 wells per km^2).

Infrastructure other than wells can influence habitat selection. For example, individuals that did not avoid CBNG wells frequently avoided areas of higher power line visibility. The relationships between brood-rearing sage-grouse and visible power lines was universally negative across individual-level models. Our population-level results also demonstrated avoidance of visible power poles within 500 m. This finding suggests a consistent pattern of avoidance exhibited by brood-rearing females as visible power poles increased. Of the individuals exposed to power lines, power line visibility was included in the top model 62% of the time. Power lines are used for perching and nesting by avian predators including various raptor species and common ravens *Corvus corax* (Lammers and Collopy 2007, Coates et al. 2014, Howe et al. 2014, Gibson et al. 2018). While common ravens were not widespread in our study area (Barlow et al. 2020) several species of raptors were common (sensu Tack and Fedy 2015, Dunk et al. 2019). Dinkins et al. (2014b) found the density of power lines within a 1 km^2 area was negatively related to female sage-grouse survival. They concluded that reduced survival was likely a consequence of power lines acting as perching structures for raptors (Dinkins et al. 2014b). Brood-rearing females in our study may have recognized the increased risk for themselves and their chicks of using habitats near power poles. Our study contributes to accumulating evidence suggesting that avoidance of power lines is common in prairie grouse species (Pruett et al. 2009, Hovick et al. 2014, Gibson et al. 2018).

Mesic habitats adjacent to water may provide succulent vegetation for sage-grouse chicks and consequently may be selected by brood-rearing sage-grouse (Connelly et al. 2011). The ponds, also called impoundments, in our study area were generally formed by building earthen dams in ephemeral drainages (Watchhorn et al. 2018). Our population-level finding demonstrates that brood-rearing sage-grouse were avoiding habitats near pond edges (≤ 600 m). Research has demonstrated that areas near water bodies and riparian areas may be riskier for sage-grouse nests and chicks, likely due to increased predation (Kirol et al. 2015b, Gibson et al. 2017, Foster et al. 2019). Gibson et al. (2017) found that broods using habitat closer to water sources had lower survival than broods located further away from water sources. Foster et al. (2019) found that nests farther from riparian areas had higher success in a post-fire environment. Kirol et al. (2015b) found that sage-grouse nests in closer proximity to anthropogenic ponds were more likely to be depredated than nests further away from ponds. Brood-rearing females may recognize the increased predation risk of habitats in closer proximity to ponds. Furthermore, the minimal amount of mesic vegetation associated with these ponds likely makes them less attractive to brood-rearing females compared to mesic resources like natural swales, temporary wetlands, wet meadows and riparian areas, that are spread out over larger areas and generally not associated with standing water (Connelly et al. 2011, Donnelly et al. 2016). Ponds in our study reach densities of one pond per 2 km^2 so avoidance behavior of habitats near ponds could result in a large amount of functional habitat loss. However, individual-level models demonstrated variability in the responses to ponds by brood-rearing females. Some females were selecting habitats within 600 m of ponds. Yet, no brood-rearing females were selecting habitat within 300 m of ponds, which suggests that brood-rearing females were not seeking out habitats along pond edges.

We found more variability in avoidance behavior among individuals than expected. At the population level, females with young were avoiding disturbed surfaces, both reclamation and active; visible power lines; and habitats in close proximity to infrastructure and ponds, but the intensity of this avoidance behavior varied across individuals. For instance, some individuals showed strong avoidance of habitats near ponds, while other individuals avoided habitats near ponds but with less intensity. Furthermore, we found that individual variability in responses to disturbance and infrastructure was often explained by the age of the individual. While selecting brood-rearing habitat, inexperienced females were less likely to avoid CBNG infrastructure than experienced females. Inexperienced females were also more likely than experienced females to establish brood-rearing home ranges in areas with higher amounts and densities of all the anthropogenic features including active and reclamation disturbances, power lines and well structures. Other research has also found that an animal's age and experience can influence habitat selection and space use. Cresswell (1994) showed that juvenile redshank *Tringa tetanus* primarily feed on saltmarshes while adults primarily feed on mussel beds. The saltmarshes were riskier habitats and, consequently, juvenile redshanks experienced more predation than the adults. Based on previous experiences, birds will modify their habitat-selection patterns to avoid predation of themselves, nests or dependent young (Lima 2009). It is possible that inexperienced female sage-grouse (first year) did not recognize the risk to themselves and their offspring of occupying areas with more infrastructure and disturbance (Aldridge and Boyce 2007, Dinkins et al. 2014b, Kirol et al. 2015a), while experienced females avoided these areas because they have learned that they are riskier habitats.

Similar to other recent avian studies using high-resolution GPS transmitters (Moskát et al. 2019, Taubmann et al. 2021), our sample size was robust in regard to location data (n = 3526) but was acquired from a limited number of individuals (n = 18). Given the negative population trend in the PRB (Garton et al. 2011, Fedy et al. 2017) and the many anthropogenic factors contributing to low female survival and reproductive rates in this area (Walker et al. 2007, Kirol et al. 2015b, Kirol et al. 2020b), the low number of individuals that were able to raise young to independence (i.e. brood-rearing females) was not surprising. However, we acknowledge that a larger sample of brood-rearing females would have strengthened the inference drawn from this study.

Conclusions

We found consistencies and differences in maternal decisions in our study area. Brood-rearing females consistently selected for natural landcover and avoided disturbed surfaces, which included reclamation surfaces that did not contain sagebrush. Visible structures elicited different responses. Elevated structures like power lines were avoided, but visibility of shorter CBNG well structures had variable influences on habitat selection across individuals. Females exposed to higher well densities were more likely to demonstrate local avoidance of CBNG wells than those exposed to lower well densities. At the population and individual levels our results show that habitats in close proximity to anthropogenic ponds were avoided by brood-rearing females. Our findings suggest that brood-rearing females with previous experience of available habitats (i.e. second year or older females) were more likely to establish home ranges in areas with less CBNG disturbance, and experienced females were more likely to respond negatively to CBNG structures when compared to inexperienced females. There is limited available habitat that is undisturbed in our study area; therefore, females cannot completely avoid anthropogenic disturbance and are forced to use the best of what is available (e.g. areas with less disturbance). This is supported by our assessment of the proportion of disturbance and landcover within home ranges that demonstrated females established home ranges in areas with lower levels of disturbance when compared to available areas. More research is needed to better understand avoidance and habitat selection occurring at higher orders of selection in industrial landscapes.

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Christopher P. Kirol: Conceptualization (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (supporting); Writing – original draft (lead); Writing – review and editing (equal). **Bradley C. Fedy**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (lead); Writing – original draft (supporting); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.g4f4qrfwb (Kirol and Fedy 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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