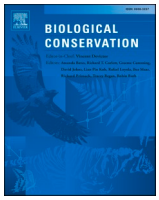
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Geothermal energy production adversely affects a sensitive indicator species within sagebrush ecosystems in western North America

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ABSTRACT

Growing demand for renewable energy has resulted in expansion of energy infrastructure across sagebrush ecosystems of western North America. Geothermal power is an increasingly popular renewable energy source, especially within remote areas, but little is known about the impacts it may have on local wildlife populations. Investigations are warranted given similarities to more conventional surface disturbance activities with well-documented impacts. Using a novel 2-pronged analytical approach, we estimated effects of geothermal energy production activities (hereafter, geothermal) on populations of greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse), a species of high conservation concern. First, we applied a before-after-control-impact paired series design at two geothermal sites in Nevada, USA, to estimate absence rates of male sage-grouse from lek sites (breeding grounds) and changes in predicted apparent abundance ($\widehat{\lambda}$) in relation to geothermal energy infrastructure. We then estimated effects of geothermal energy infrastructure and other environmental covariates on demographic rates. We found $\widehat{\lambda}$ declined ~24 % within 5 km of geothermal sites, while lek absence rates (e.g., indicating local extirpation) increased by ~730 % within 2 km. Our demographic models revealed decreased nest survival in association with proximity to geothermal infrastructure, reduced topographic impedance surface (TIS; a proxy for sound and light dispersion emanating from geothermal infrastructure), and increased density of common ravens (*Corvus corax*), an effective nest predator. Models also estimated decreases in adult survival in relation to TIS. Finally, we applied population matrix models within a quantitative decision support framework to help guide locations for future geothermal development that balance the need for domestic energy production while minimizing adverse effects on wildlife populations.

1. Introduction

Human population growth worldwide has created a prodigious demand for energy production in recent decades (Masson-Delmotte et al., 2018), which is projected to increase ~28 % over the next 2 decades (IEA, 2017). Conventional sources of energy production such as fossil fuels comprised 85 % of worldwide energy generation despite their creation of atmospheric pollutants that contribute to climatic changes (Masson-Delmotte et al., 2018; Dudley, 2018). Low carbon emitting, renewable energy sources (e.g., wind, solar, and geothermal) are viewed as alternative forms of energy production (Amponsah et al., 2014), in part due to growing concern over anthropogenic-driven climate change (Schuur et al., 2015). Within the U.S., renewable sources are the fastest growing energy technologies (IEA, 2017) but the potential impacts to ecosystems and species from dramatically increasing renewable energy footprints remain relatively under-studied (Northrup and Wittemyer, 2013).

Energy production typically occurs in remote environments and involves anthropogenic activities and infrastructures that can alter ecosystem processes, including the sustainability of sensitive wildlife and their habitats (Noss et al., 1995; Sawyer et al., 2006). Numerous species have been adversely affected by conventional forms of energy

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development like fossil fuels (Naugle et al., 2011). However, considerably less is known about the effects of renewable energy production (Northrup and Wittemyer, 2013), and most of those studies have focused on the effects of wind power production on migratory birds and bats (Katzner et al., 2013; Winder et al., 2019). The catalog of solar energy development studies continues to grow, particularly in areas of the southwestern U.S., where impacts to Mojave desert tortoise (*Gopherus agassizii*) and pollinator-dependent cacti species have been documented (Lovich and Ennen, 2011; Brand et al., 2016; Sadoti et al., 2017; Grodsky et al., 2021). However, few studies have evaluated both direct and indirect influences of renewable energy production (Northrup and Wittemyer, 2013). To our knowledge, the effects of geothermal energy on wildlife have not been rigorously examined prior to this study.

Geothermal power production is expected to grow rapidly in the coming years (Copeland et al., 2011; REN21, 2019), as energy availability from geothermal sources does not fluctuate with meteorological conditions (e.g., variation in wind or sun availability) and represents a low-carbon emissions source (Amponsah et al., 2014). Geothermal sources are abundant within shrubland ecosystems of the western U.S. where geothermal-related infrastructure (e.g., roads, buildings, pipelines, well pads) currently occupies approximately 330,000 ha (Copeland et al., 2011). The physical footprint of geothermal energy infrastructure is small relative to other renewable energy sources (Bošnjaković et al., 2019), but noise and light pollution emanating from these power plants likely cause larger adverse direct impacts to wildlife populations than infrastructure alone (DiPippo, 1991; Longcore and Rich, 2004; Copeland et al., 2011; Blickley et al., 2012a,b), increasing the overall footprint. Furthermore, indirect effects from anthropogenic infrastructure (e.g., roads, buildings, powerlines) can occur if these structures attract generalist mesopredators, which can negatively impact nearby prey species (Soulé et al., 1988). For example, common ravens (*Corvus corax*; hereafter, ravens) have garnered substantial management concern in southwestern semi-arid environments because they are an effective predator of multiple species (Coates et al., 2021b) and anthropogenic structures provide resource subsidies that contribute to increased raven abundance (Boarman, 1992, 2003; Dinkins, 2013). Assessing both direct and indirect influences of geothermal energy production on sensitive species is a critical step to informing current and future ecological impacts from this rapidly expanding industry within shrubland ecosystems of the western U.S.

A major challenge in estimating ecological effects from energy production is collecting demographic data, which are often necessary to understand underlying processes that explain broad patterns in species abundance. To date, nearly all previous studies have been observational by design (i.e., correlative analyses), only elucidating general patterns of impacts to population dynamics and distributions with few attempts to identify underlying mechanisms (Northrup and Wittemyer, 2013). Studies that link observed patterns in population dynamics to the underlying mechanistic processes could greatly improve management decisions aimed at protecting sensitive species.

We investigated direct and indirect effects of geothermal production on Greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) populations in north-central and central Nevada, USA. Sage-grouse are considered an ecological indicator species for sagebrush (*Artemisia* spp.) ecosystems because they use a variety of vegetation communities as seasonal habitat to meet their different life history requirements (e.g., nesting habitat). Their large geographic range (~62 million ha; Schroeder et al., 2004) encompasses numerous other sagebrush obligate and semi-obligate species (Rowland et al., 2006; Runge et al., 2019). Sage-grouse populations are experiencing long term declines (Coates et al., 2021a), largely as a result of natural and anthropogenic stressors occurring throughout their range (Connelly et al., 2004). Despite substantial overlap in areas for potential development of geothermal plants and sage-grouse distribution, the effects of geothermal energy are currently unknown.

Here, our objectives were to fill this information gap with a 2-pronged analytical approach. First, we collected lek (traditional breeding area) survey data to estimate changes in population abundance and breeding activity of male sage-grouse in relation to geothermal development using a before-after-control-impact paired series (BACIPS) study design. Changes in males counted at lek sites provide a reliable proxy for changes in population abundance (Connelly et al., 2003, 2004). After elucidating patterns of disturbance at varying distances from geothermal infrastructure, we used intensive telemetry data collected post-development to identify which specific demographic processes were affected by geothermal energy production. To do this, we built a population matrix model and fit geothermal-related effects to each life stage (e.g., nesting, brood-rearing), while accounting for background sources of variation (i.e., non-geothermal effects) in demographic rates. Lastly, we demonstrated how the population-matrix model can be linked to a spatially explicit decision support tool that predicts potential impacts to sage-grouse population growth, abundance, and space use at 135 candidate sites for geothermal development. The tool helps balance the goal of maintaining viable ecosystems with increasing demand for renewable energy production by ranking candidate sites based on their predicted impacts to sage-grouse populations.

2. Methods

2.1. Study area

We counted males on sage-grouse leks and monitored female sage-grouse using radio-telemetry methods to collect data on survival and reproduction at two geothermal study locations, Tuscarora Mountains (TS) and McGinness Hills (MC), where geothermal energy development occurred between 2012 and 2018 (Prochazka et al., 2023). We also monitored female sage-grouse at 17 additional independent study sites without geothermal activities within Nevada and California, U.S.A. (Appendix S1, Fig. S1–1) as part of our demographic study design. Surface disturbance from infrastructure at the geothermal sites (facilities, production wells, etc.) covered ~25 and ~28 ha at TS and MC, respectively, and resulted in a loss of sage-grouse foraging and nesting habitat (Department of Energy, 2011). Infrastructure at MC was more spread out, with substantially more undeveloped area occurring between surface disturbances (Appendix S1, Fig. S1–1). Power transmission lines and access roads also occurred at each facility. Vegetation communities at both sites were sagebrush dominant and typical of sagebrush steppe ecoregions and the semi-arid climate of the Great Basin. For complete descriptions of site characteristics, see Prochazka et al. (2023).

2.2. Analysis 1 – before-after-control-impact paired series design

We used lek survey data collected within a 50-km radius of either geothermal site during 2005–2018 to develop a BACIPS study design. We sought to conduct 3–4, 10-min surveys per lek site during the lekking period (March – late April) each year in collaboration with state and federal agencies using published, standardized lek survey protocols (Connelly et al., 2003). During each survey we recorded a lek count, which represented the maximum number of male sage-grouse observed at that location on that day. We inferred rate of change ($\widehat{\lambda}$) in population abundance and lek absence rate for intervals of 6 years before and 6 years after geothermal operations had been established at each site and assigned lek counts to period (before vs. after onset of geothermal development) categories. Period attributions were fixed for all analyses. Designation of impact and control leks relied on a distance-based approach, where we measured Euclidean distance from each lek to the nearest infrastructure (e.g., powerlines, roads, facilities) and assigned leks as inside (impact) or outside (control) a candidate impact zone. We chose to investigate 6 different candidate impact zones which were 0–2, 0–5, 0–10, 0–15, 0–20, and 0–30 km (Appendix S2, Table S2–1) to

compare model evidence for the distance effect. Specifically, we performed leave-one-out cross-validation using 'loo' in R (R Core Team, 2019; Vehtari et al., 2017) to evaluate statistical support for each candidate impact zone (see Prochazka et al., 2023). This method was useful in understanding to what spatial extent geothermal activities impacted our study populations.

We used Bayesian hierarchical state-space models (SSM; Kéry and Schaub, 2012), which account for imperfect detection, to obtain $\widehat{\lambda}$ for each BACI comparison (Prochazka et al., 2023). The hierarchical nature of the SSM refers to the decomposition of an observed time series (here, counts) into a pair of linked likelihoods that estimate process variation and observation error, respectively. Specific to sage-grouse, observation error represents the contribution of intra-annual under- and over-counting of individuals that attend leks (Coates et al., 2019) as well as variability in lek visitation (Blomberg et al., 2013; Wann et al., 2019). Because these error sources cancel out on average (Coates et al., 2019; Wann et al., 2019), the SSM produces unbiased estimates of $\widehat{\lambda}$ and apparent abundance (Kéry and Schaub, 2012). After obtaining posterior distributions of $\widehat{\lambda}$, we applied BACI ratios (Conner et al., 2016) to estimate the magnitude of geothermal infrastructure effects (Prochazka et al., 2023) for each candidate impact zone. We also measured degree of change between time periods for each control-impact (CI) zone, as well as dissimilarity, using measures of CI-contribution and CI-divergence (Chevalier et al., 2019; Eqs. (6) & (7) in Prochazka et al., 2023). To supplement BACIPS analysis of $\widehat{\lambda}$, we also explored changes in the probability of lek absence, where leks characterized by consecutive counts of 0 were contrasted before and after geothermal development in each of the proposed impact zones. Complete details are provided in Prochazka et al. (2023).

2.3. Analysis 2 – demographic analyses and population matrix model

2.3.1. Sage-grouse monitoring

Concurrent to geothermal operations (2012–2018), we monitored female sage-grouse at both geothermal sites and the 17 additional independent study sites using radio-telemetry methods to collect data on survival and reproduction. Capture and data collection protocol are described in Prochazka et al. (2023). For each monitored female, we determined age, nest identification/location, nest fate, clutch size, number of eggs hatched, brood fate, number of chicks, female survival across all seasons, and raptor/raven point count surveys to index abundance of common predators. These data were used to model demographic and vital rates that collectively drive changes in abundance through time.

2.3.2. Two-stage models for vital rates at geothermal and independent sites

We carried out demographic modeling in two stages. For detailed description of this analytical technique see Prochazka et al. (2023). First, we estimated effects of different environmental variables (e.g., land cover, topography, water sources) at the independent sites for each demographic model (e.g., annual survival; see Sections 2.2.1–2.2.8 of Prochazka et al., 2023). By developing a baseline model used to predict environmental effects at geothermal sites, assuming normal background conditions based on land cover covariates calculated during pre-energy development stages, we were able to ascertain unbiased estimates of geothermal infrastructure effects after accounting for confounder effects. We evaluated evidence of each variable at different spatial scales (radii = 30, 75, 167.9, 439.5, and 1451.7 m, respectively) that had been previously identified as important determinants of sage-grouse space-use and selection (Coates et al., 2016; Dudko et al., 2019). Variable selection was performed to identify spatial scale and to remove non-meaningful variables from consideration and a final 'baseline' model was developed for each vital rate to incorporate all selected variables (Section 2.2.1 of Prochazka et al., 2023).

For the second stage, covariates representing distance to geothermal plant (DGP) and topographic impedance surface (TIS; Fig. 2 of Prochazka et al., 2023) were incorporated into models of vital rates (conditioned on relevant background environmental effects) at geothermal sites. Lacking direct measurements of sound and light levels in relation to geothermal operations at our study site, we generated a spatially explicit TIS index to use as a covariate for each demographic rate. TIS was based on factors responsible for variation in the absorption and dispersion of sound waves emanating from geothermal activities. We included TIS in the models given reported evidence of decreased lek attendance (Blickley et al., 2012a) and increased stress (Blickley et al., 2012b) among sage-grouse populations exposed to experimental chronic noises often associated with energy production (e.g., drilling, road traffic). For full detail in development of TIS see Prochazka et al. (2023). For the nest survival model, we also incorporated a raven density index (RDI), as ravens have negatively impacted sage-grouse nest survival in this study region (Coates et al., 2020). Furthermore, we hypothesized that the magnitude of RDI predation pressure on sage-grouse nests would be modulated, in an interactive manner, according to the presence of geothermal infrastructure. We implemented the Bayesian Lasso (Park and Casella, 2008) combined with indicator variable selection to determine support for geothermal and nest predator effects, which included various 2- and 3-way interactions between covariates (Kuo and Mallick, 2016). Importance of final geothermal covariates were assessed using Bayes Factors where values >3 were considered significant. Further details are provided in Prochazka et al. (2023).

2.3.3. Population matrix model and geothermal application tool

We used an age-structured, stage-based stochastic population matrix model to derive total population abundance for each year at the geothermal sites (Section 2.2.8 of Prochazka et al., 2023). Based on the population matrix model, we developed spatial model predictions for all demographic rates to derive estimates of population growth rate (Prochazka et al., 2023) at potential geothermal point sources (n = 135, hereafter 'candidate sites', Fig. 1). We generated these predictions 'before' and 'after' hypothetical geothermal development to explore overall impact at candidate sites, as indicated by change in $\widehat{\lambda}$ ($\Delta\widehat{\lambda}$). We then incorporated information about sage-grouse relative abundance, by multiplying the $\Delta\widehat{\lambda}$ results by a sage-grouse abundance and space use index surface (AUI) derived from Coates et al. (2016). The product of the $\Delta\widehat{\lambda}$ and AUI surfaces represented the predicted relative impact of potential geothermal infrastructure on sage-grouse population performance for all candidate sites. Full method details are provided in Prochazka et al. (2023).

3. Results

3.1. Analysis 1 – before-after-control-impact paired series design

We compiled 103 lek sites (TS = 65, MC = 38) within 50 km of geothermal infrastructure at both geothermal sites to inform estimation of $\widehat{\lambda}$. Of these, 7, 11, 14, 21, 25, and 50 were within the distance treatment zones of 2, 5, 10, 15, 20, and 30 km, respectively. Based on BACI ratios (and 95 % credible intervals, CRIs), models predicted that geothermal operations substantially impacted sage-grouse $\widehat{\lambda}$ across all candidate distance zones. Meaning, before geothermal operations, our estimates of $\widehat{\lambda}$ at the impact sites outperformed those at controls under each of the candidate distance zones, but then decreased after the onset of geothermal operations relative to controls. All parameters in the SSMs converged (R-hat < 1.1), indicating reliable predictions of $\widehat{\lambda}$ across leks designated as impact and control. Estimates from all distance-treatment demarcations are available in Appendix S2, Table S2–2.

The model with distance zone of 0–5 km was most supported by the data when estimating the effect of geothermal activity on $\widehat{\lambda}$ [Appendix S2, Table S2–1; 95 % highest posterior density (HPD) interval was <1.0;

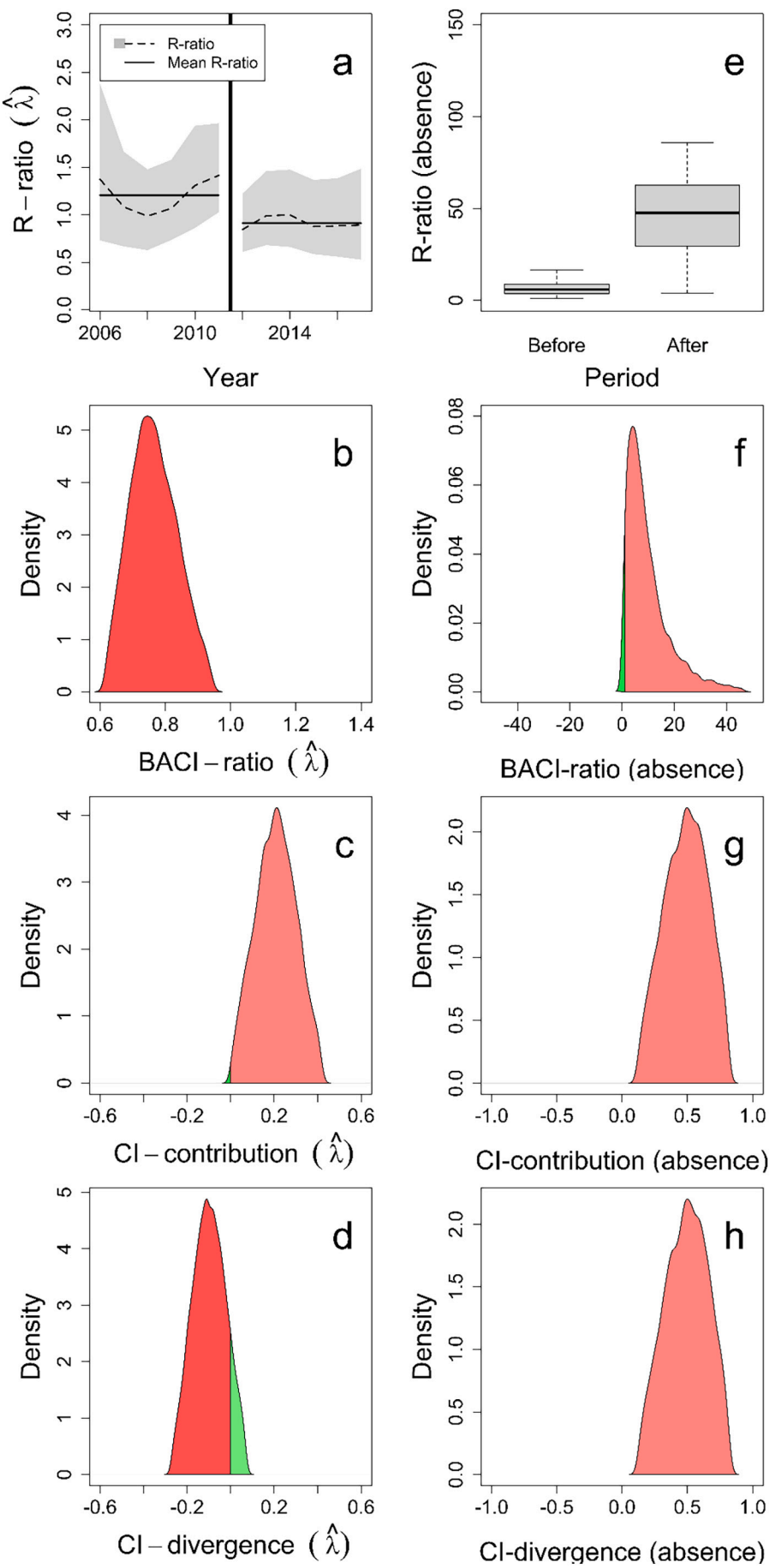


Fig. 1. R-ratios (change in treatment area relative to control), posterior probability distributions of change, CI-contributions (change in treatment area vs change in control), and CI-divergences (change in after period vs change in before) for before-after-control-impact paired series analysis of population growth rates (a–d) and lek absence rates (e–h). Solid vertical line indicates onset of geothermal operations (a). Red shaded regions of posterior distributions provide evidence for negative relationships corresponding to geothermal energy activities (i.e., decreased growth rates, increased absence rates), whereas green shaded regions represent evidence for positive relationships corresponding to geothermal activities. Evidence of positive effects were considered marginal (c, d, f) or absent (b, g, h). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 3a, b; Appendix S2]. Within 5 km of the geothermal footprint, abundance increased annually by ~15 % before geothermal activity ($\widehat{\lambda}$ = 1.15; CRI = 0.73–1.70) but then declined by 10 % annually ($\widehat{\lambda}$ = 0.90; CRI = 0.60–1.36) after geothermal operations began. Meanwhile, controls declined annually before ($\widehat{\lambda}$ = 0.96; CRI = 0.82–1.12) and after ($\widehat{\lambda}$ = 0.98; CRI = 0.85–1.17; Appendix S2, Table S2–2). The average ratio of impact to control was higher before geothermal operations ($R(\widehat{\lambda})_{t:c,b}$ = 1.21 (CRI = 0.77–1.83)) than afterwards ($R(\widehat{\lambda})_{t:c,a}$ = 0.91 (CRI = 0.60–1.41)). These ratios resulted in a median effect $R(\widehat{\lambda})_{BACI}$ of 0.76 (CRI = 0.61–0.95), meaning that $\widehat{\lambda}$ decreased within the 5-km impact area by ~24 % (CRI = 5–39 %) relative to control areas after geothermal infrastructure was installed.

For lek absence analysis, we compiled 37 leks (TS = 18, MC = 19) within 50 km of the infrastructure from both geothermal sites. Of these, 7, 8, 9, 11, 12, and 25 were within distance-treatments of 2, 5, 10, 15, 20, and 30 km, respectively. Estimated lek absence rates increased near geothermal infrastructure (within 2, 5, and 10 km treatment demarcations) relative to controls following geothermal operations (Appendix S2, Table S2–3). BACI ratios and cross-validation scores (Prochazka et al., 2023) indicated that the largest impacts occurred within the 0–2 km treatment zone. Within 2 km of geothermal operations, average absence rate was 6.14 % (CRI = 0.96–18.89 %) prior to onset of geothermal operations, on average, and 49.84 % (CRI = 18.77–81.57 %) after the onset of geothermal operations, while controls were 0.01 % (CRI = 0.00–3.45 %) before and 0.02 % (CRI = 0.00–10.91 %) after. Average ratio of impact to control was higher after geothermal operations [$R(P(Absent))_{t:c,\ a}$ = 47.70 (CRI = 3.92–85.77)] than it was before [$R(P(Absent))_{t:c,\ b}$ = 5.80 (CRI = 1.12–17.97)], which resulted in a median effect $R(P(Absent))_{BACI}$ of 7.31 (CRI = 0.55–49.52) (Fig. 4e and f). Thus, lek absence rates within 2 km of geothermal operations increased by ~730 % relative to control areas, an approximately 7:1 ratio of leks becoming inactive at impact areas relative to leks at unimpacted areas.

3.2. Analysis 2 – demographic analysis at active geothermal developments

We monitored 1049 female sage-grouse across all study sites to estimate demographic parameters for confounder and geothermal effects. Of those, 819 individuals (78.1 %) were used to estimate confounder effects across control sites, while 230 (21.9 %) were used to investigate additional covariates related to geothermal infrastructure at impact sites on each demographic parameter. The number of field sites used to model confounder effects varied across different demographic rates based on sampling limitations, such that sites were excluded with insufficient number of samples, which are reported in Appendix S3, Table S3–1. Below, we provide results of confounder and geothermal effects for nest survival (first and second attempts), and yearling and adult survival (Appendix S3, Table S3–2). Results for hatchability, second nest propensity, and chick survival are reported in Appendix S4.

3.2.1. Nest survival

We estimated effects of confounder covariates from 504 female sage-grouse at 14 control sites that contained enough data to estimate this parameter (Appendix S3, Table S3–1). Nest survival responded strongly to percent tree canopy cover (439-m extent) with a log-hazard ratio of −0.19 (CRI = −0.35 to −0.05). The remaining confounder covariates had log-hazard ratios that overlapped 0 (Appendix S3, Table S3–3). We found substantial variation in the baseline hazard across the nests at control sites (median = −3.35, CRI = −5.04 to −1.72), which corresponded to a 38-day survival estimate of 0.26 (CRI = 0.00–0.78). Nest fates were determined from 191 first nests and 13 second nests at the geothermal sites across the 7 study years. For first nests, 75 survived and 116 failed (10 abandoned; 61 depredated; 11 female mortality; 34 unknown fate). For second nests, 6 survived and 7 failed (5 depredated; 2 unknown fate). After accounting for confounder effects, our models supported a three-way interaction of RDI (log transformed), DGP (exponential decay), and TIS (exponential decay; Bayes Factor value = 4.03) indicating that the relationship between DGP and TIS varied across different levels of RDI (Fig. 2). Under a low RDI and TIS held at its mean, nest survival increased substantially as DGP increased (Fig. 2a).

We further found that when RDI was held at its median value (0.78 ravens km^{-2}; Appendix S5), TIS was held at a relatively low value (25th percentile of the distribution), and DGP was evaluated from 0 to 6 km, modeled nest survival increased from 0.04 (CRI = 0.00–0.23) to 0.36 [CRI = 0.21–0.49, an 83.81 % (CRI = 54.48–99.87 %) increase per 1-km increase in DGP]. Conversely, when TIS was held at a relatively high value (75th percentile), modeled nest survival increased from 0.19 (CRI = 0.06–0.32) to 0.31 (0.21–0.40), a 36.97 % (CRI = 18.62–71.78 %) increase per 1-km increase in DGP. Nest survival probabilities with larger DGP were comparable across low and high TIS.

3.2.2. Adult survival

We estimated effects of multiple confounder covariates from 656 female sage-grouse at 14 control sites (Appendix S3, Table S3–1). Adult survival was most strongly influenced by percent shrub cover (439 m extent) with a log-hazard ratio of −0.14 (95 % CRI = −0.29–0.01). When shrub cover increased by one standard deviation (~26.4 % shrub cover) the monthly risk to survival was predicted, on average, to decrease 13 % relative to baseline hazard (risk = 0.87, CRI = 0.75–1.01). Of the 196 yearling and adult sage-grouse that were monitored at geothermal sites across the 7 study years, 118 died, 22 were recorded as alive in the last interval, and 56 were right-censored (i.e., unknown fates in the last monthly interval). We found substantial variation in the survival model's predicted baseline hazard across individual sage-grouse and monthly intervals (median = −3.47, CRI = −19.81 to −2.16), which equated to an annual survival of 0.69 (CRI = 0.25–1.00). After accounting for confounder effects, we observed support for an additive positive effect of TIS (exponential decay) on yearling and adult survival (Bayes Factor = 5.49). Models estimated that an initial increase of 100 m in TIS corresponded to an increase in annual survival of 54.47 % (CRI = 37.94–78.22 %; Fig. 3), while every 100 m increase in TIS beyond the initial 100 m resulted in an average increase in survival of just 3.24 % (CRI = 0.95–5.55 %).

3.3. Geothermal application tool

We investigated 135 candidate sites for potential impacts of simulated geothermal energy production (section 3.4. of Prochazka et al., 2023) on sage-grouse population performance (Fig. 4). Of these, 105 predicted a negative effect on local population performance within 2 km, 103 within 5 km, and 102 within 10 km (Fig. 4b). Full listing of ranked outputs at thresholds 2, 5, and 10 km are listed in Appendix S6, Table S5–1. The average change (averaged across all pixels) within 2, 5, and 10 km was −1.77 %, −1.20 %, and −0.57 %. Once we removed sites that had a net 0 impact on population performance (i.e., AUI = 0) those values dropped to −2.32 %, −1.54 %, and −0.76 %. The largest decreases in population performance were located predominantly in northeast Nevada (Fig. 4b), corresponding to the highest densities of sage-grouse abundance and space use. We also identified candidate sites that produced relatively low decreases in population performance despite being in proximity to areas of high AUI.

4. Discussion

Although geothermal offers a relatively clean, renewable source of electricity generation (Barbier, 2002), we found evidence of adverse effects from geothermal energy infrastructure on sage-grouse population dynamics immediately following development. To our knowledge, this is the first reported evidence of ecological effects of geothermal energy

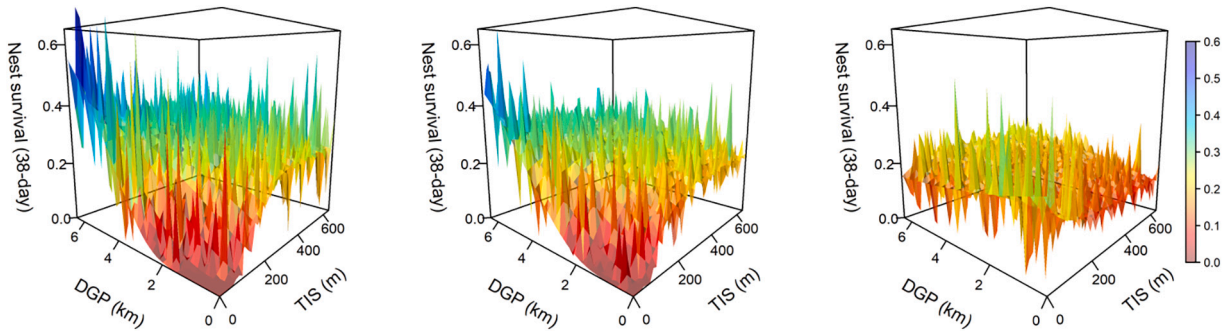


Fig. 2. Illustration of the three-way interaction of distance to geothermal plant (DGP), topographic impedance surface (TIS), and raven density index (RDI) on sage-grouse nest survival. The X and Y axes correspond to TIS and DGP, the Z-axis corresponds to nest survival. Panels a – c corresponds to increasing RDI effects, with RDI held at the 25th (a), 50th (b), and 75th percentile (c) of the distribution of observed values. The color bar on the right side of the three-figure panel represents nest survival values across all three panels (cool = high, warm = low). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

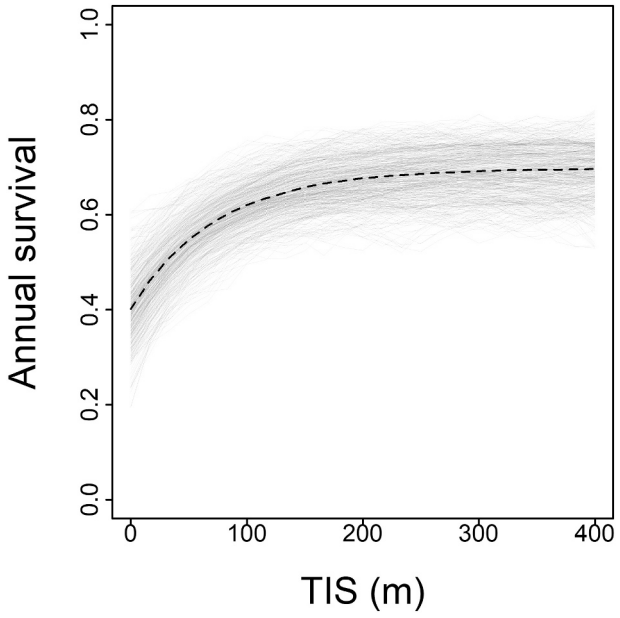


Fig. 3. Non-linear relationship between distances for topographic impedance surface and adult sage-grouse annual survival.

production on a sensitive wildlife species. The effects on $\widehat{\lambda}$ (up to ~5 km) and rate of lek absence (up to ~2 km) were generally consistent with studies that investigated other energy-related effects using distance-based approaches (0.95–12.5 km; Gibson et al., 2018; Holloran et al., 2010; Walker et al., 2007). The wide range of reported distances across studies is likely a result of variation in types of energy infrastructure (e.g., towers, facilities, access roads) or types of energy activities (e.g., road use, noise, and light), as well as variation among site-level environmental characteristics. Importantly, we found strongest evidence of adverse effects at 5- and 2-km distances for changes in $\widehat{\lambda}$ and lek absences, respectively, which support lek buffer distances guidelines of 5–8 km reported in a comprehensive review of surface disturbance effects on sage-grouse populations (Manier et al., 2014).

Our study indicates that site-specific placement of geothermal infrastructure in sagebrush ecosystems can have significant impacts beyond the physical footprint given source-sink dynamics of sage-grouse populations (Kirol et al., 2015). For example, BACIPS results indicate that sites where infrastructure was placed (within 5 km) had supported consistent population growth prior to infrastructure placement, with models estimating 15 % average annual increases in abundance. Thus, these sites may have acted as source populations within a meta-population structure. Evaluations of control areas during the same pre-operational period revealed 4 % average annual declines by comparison. Environmental characteristics at the geothermal sites prior to energy production were conducive to growing sage-grouse populations. During plant operation, these populations reversed their growth trends and subsequently experienced 10 % losses annually, averaging a change of −25 % across periods. Although control sites also expressed rates of decline during the operational period ($\widehat{\lambda} = 0.98$), they increased their rate of change by 2 % over pre-operational values. Geothermal production is typically associated with areas that consist of water resources (e.g., surface or subsurface) and riparian vegetation communities. Such primary productivity often supports relatively higher biodiversity compared to surrounding environments (Calvin et al., 2015) and serve as important habitats for sage-grouse in the Great Basin, particularly during the late brood rearing season (Casazza et al., 2011). Thus, geothermal energy production may have relatively more profound adverse effects on sage-grouse populations than other forms of energy-related development because of its likely placement within sparsely distributed, resource-abundant mesic habitats that are often centers of productivity for sage-grouse (Donnelly et al., 2018). For example, adverse impacts of geothermal on one or more population vital rates (e.g., nest survival) can offset the positive influences to brood rearing within these otherwise high quality habitat sites. Because geothermal resources remain fixed within the landscape, spatial overlap of sage-grouse populations and potential geothermal energy generation warrants careful evaluation prior to new infrastructure developments.

Generally speaking, continued declines in population abundance inevitably leads to local extirpations. In addition to estimated declines in abundance, we observed a ~730 % increase in rate of lek absence within 2 km of geothermal infrastructure relative to controls. Distances associated with absent rates closer to geothermal (0–2 km) versus those associated with declining abundance (0–5 km) suggests that the zone of lek inactivity may continue to expand away from the geothermal infrastructure through time. Similar time lags on impacts to sage-grouse demographic rates were shown in relation to a transmission line in north-central Nevada that also occurred in high-quality habitat, with effects reported up to 12.5 km after 10 years (Gibson et al., 2018). Anthropogenic-related conversion of source populations to sink populations can result in a broadening footprint of extirpation, reducing the capacity of the landscape to sustain metapopulations (Huang et al., 2020).

Importantly, our two-stage analytical approach allowed us to identify underlying demographic processes (i.e., reduced female survival and nest survival) that deterministically influence $\widehat{\lambda}$ and lek absence. The estimated reduction in nest and female survival in proximity to geothermal infrastructure is highly concerning for the species because

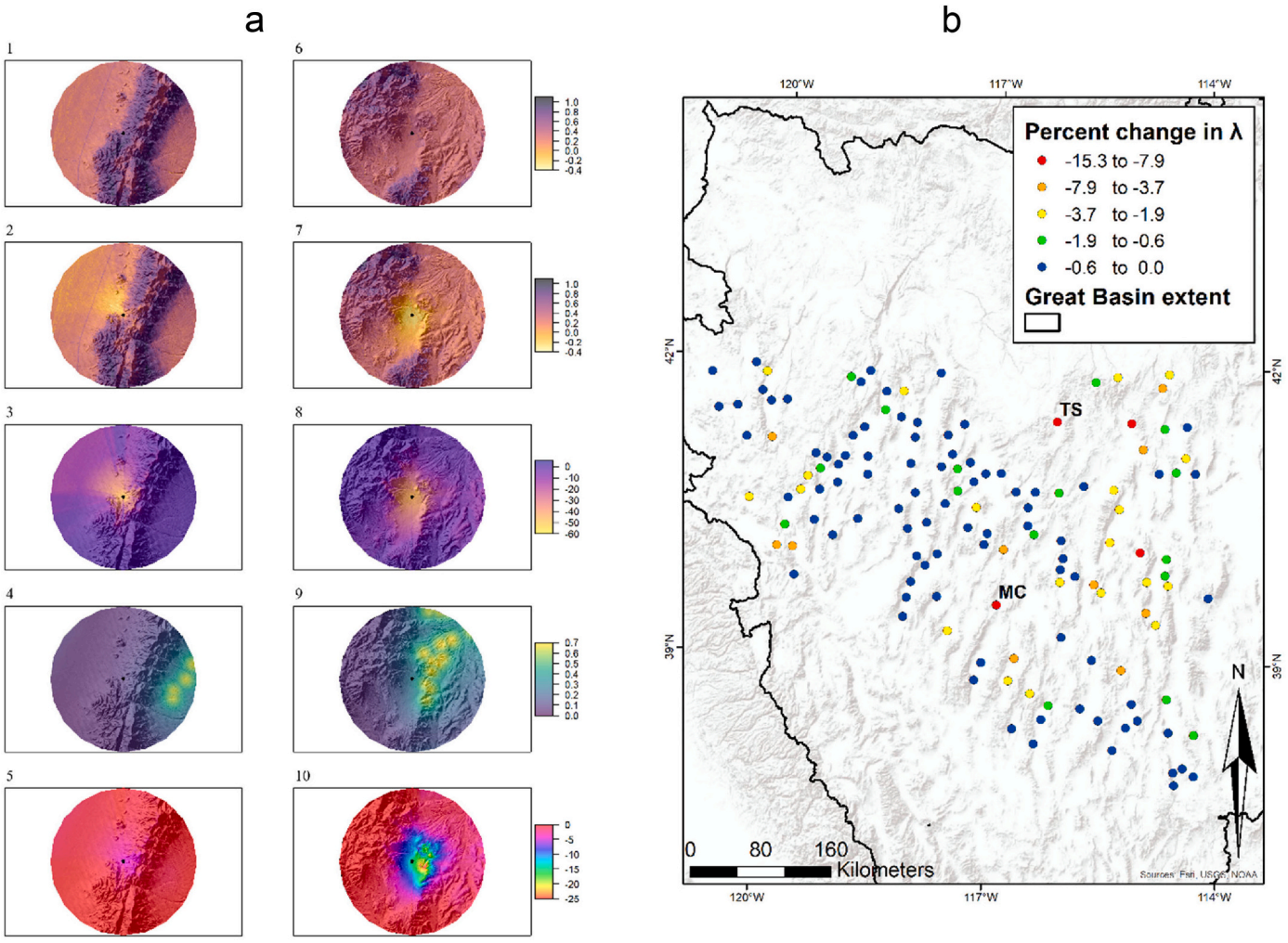


Fig. 4. a) Example model output from the geothermal application tool for two sites with simulated geothermal energy production (SGEP). Column 1 (panels 1–5) illustrates the effect of topographic impedance, where sites with moderate sage-grouse abundance and space use index (AUI) have diminished impacts provided topographic features are present to dampen negative sound and light effects. Column 2 (panels 6–10) illustrates effects of low to absent distance or topographic impedance between geothermal infrastructure and sites with high AUI. Rows represent the intrinsic growth rate before SGEP (panels 1, 6), intrinsic growth rates following SGEP (panels 2, 7), percent change in lambda following SGEP (panels 3, 8), sage-grouse AUI (panels 4, 9), and the product of AUI and the percent change in lambda (panels 5, 10). Both example sites portray direct effects of SGEP on sage-grouse population performance, which does not consider changes in predator communities (e.g., raven abundance) following the introduction of anthropogenic infrastructure to the region. b) Spatially explicit depiction of modeled impacts of potential geothermal development (n = 135 candidate sites) on sage-grouse population performance using a geothermal application tool. Values in the legend represent the long-term average percent change in lambda following simulation of geothermal energy production. Abbreviations MC (McGinness Hills) and TS (Tuscarora Mountains) mark the location of the geothermal study sites where survey and demographic data were collected.

both these vital rates were shown to have substantial influences on population growth compared to other demographic rates based on a range-wide meta-analysis (Taylor et al., 2012). Our model revealed a complex relationship between distance and topography on nest survival probabilities. For example, nest survival was predicted to be reduced by ~25 % where few topographic barriers existed between female locations and energy infrastructure. This decrease in survival likely occurred because noise pollution (continuous and intermittent forms), typically emitted from drilling and power generation equipment (e.g., generators and compressors) or vehicular activity, was not obstructed by physical barriers created by topographic landforms. Topography likely had similar effects on the dispersion of artificial light emitted from power plants during nighttime. Thus, under low topographic impedance, noise and light pollution are more likely to permeate into surrounding habitat even at relatively long distances. We also found that topographic impedance between location of sage-grouse and geothermal infrastructure substantially influenced female survival. Although direct sound and light measurements were beyond the scope of our study, we hypothesize that topography reduced permeation of noise and light pollution that can otherwise interfere with the ability of sage-grouse to avoid predators (Blickley et al., 2012a,b). Noise pollution has been shown to negatively impact sage-grouse populations in Wyoming, where simulations of drilling (continuous) and road use (intermittent) reduced sage-grouse lek attendance by 29–73 %, respectively (Blickley et al., 2012a).

Support for this hypothesis was demonstrated with our three-way interaction (i.e., RDI × DGP × TIS) that included a predator variable, such that the influence of topography and distance to geothermal infrastructure on sage-grouse nest survival was largely dependent on raven densities. Ravens are an effective nest predator of sage-grouse (Lockyer et al., 2013; Coates et al., 2008) and increases in raven densities have been found to substantially impact sage-grouse nest survival (Coates et al., 2020). While development of geothermal infrastructure may directly influence the density of ravens, which readily utilize anthropogenic structures for nesting/perching (Howe et al., 2014), the supported three-way interaction suggests noise and light pollution from geothermal operations also influence predator-prey interactions

(Blickley et al., 2012a,b). For example, sage-grouse typically exhibit regular patterns in recessing from incubation during crepuscular periods, which strategically reduces exposure to visually-cued predators, like ravens, as they move to and from their nests (Coates and Delehanty, 2010). Increased noise and light pollution from geothermal plants may disrupt recess patterns and increase predation rates by ravens, even if raven densities are low. Nests closer to geothermal plants that had low topographic impedance were predicted to have reduced survival, even at relatively low raven densities, indicating ravens may be more efficient at depredating nests due to alterations in sage-grouse incubation behavior under these conditions.

When raven density increased beyond the regional mean (e.g., 3rd quartile), the interactive effect of distance and impedance was nullified, and nest survival was significantly and ubiquitously reduced. A similar study in Nevada found that the geographical extent to which the development of a transmission line adversely affected sage-grouse vital rates was also contingent on local raven abundance (Gibson et al., 2018), and another recent study that included numerous sites across the Great Basin found sage-grouse nest survival was substantially reduced at >0.4 ravens km^{-2} (Coates et al., 2020). These observations are concerning because raven populations are increasing dramatically across their range, particularly within sagebrush steppe and desert ecosystems of the Great Basin (Harju et al., 2021). Although investigation of relationships between geothermal infrastructure and raven density was beyond the scope of this study, other studies have concluded that tall, energy-related infrastructure in remote environments provide anthropogenic subsidies that contribute to raven population expansion and growth (Howe et al., 2014; Coates et al., 2014; O'Neil et al., 2018). Thus, as development of geothermal (and other energy and mineral development in the Great Basin) infrastructure continues, raven densities will likely increase at these sites, further impacting sage-grouse populations over time. When these impacts are considered along with the interactive effects of permeating noise and light pollution, geothermal infrastructure development, especially near sites with low TIS, make the surrounding sage-grouse populations particularly vulnerable to predation and population decline over time.

Although no previous studies have evaluated geothermal activities on sage-grouse survival, other studies reported negative effects from transmission lines (Gibson et al., 2018; LeBeau et al., 2019) and oil and gas development (Holloran et al., 2010). In contrast, wind energy infrastructure has been associated with increased sage-grouse survival (LeBeau et al., 2017). This can be explained by differences in how tall structures are utilized by raptor populations, a primary predator of sage-grouse (Hagen et al., 2011). For example, large raptors avoid wind turbines and new wind farms (Cabrera-Cruz and Villegas-Patraca, 2016) likely because these species experience relatively high mortality rates due to moving rotor blades on turbines (De Lucas et al., 2008), perhaps leading to reduced predation on nearby sage-grouse. Although some anthropogenic features are typically similar among different energy sources, it appears infrastructure unique to specific types of energy generation (e.g., turbines associated with wind) can have substantially different effects on demographic rates. Our study indicates that additional research that investigates differences among energy-related anthropogenic features is needed.

Our study demonstrated clear and predictable effects of geothermal energy generation on sage-grouse population abundance. Although measuring individual dispersal rates away from infrastructure was beyond the scope of this study, we do not entirely dismiss this as a mechanism contributing to population declines. However, our analysis concluded that such declines were primarily manifested through complex relationships between distance to infrastructure, topography, and raven density that reduced demographic rates of female and nest survival. We provide other study caveats and limitations in Appendix S7. Nevertheless, it is important to recognize that placement of geothermal infrastructure in areas also conducive to source populations of sage-grouse appears to have impacts on metapopulation performance which function at much broader spatial scales. However, some variation in distance of these geothermal effects should be expected among different local areas and impacts could be potentially mitigated by topography, configuration of geothermal footprint, and management of ravens. Because effects will vary based on site level environmental characteristics, the spatially explicit application of the model as a decision support tool provides resource managers a means of predicting site-specific impacts to sage-grouse populations and comparing among candidate geothermal sites. This tool can also be used for site planning such as placement of roads, power lines, facilities, piping and wells. Conservation planning that incorporates such tools may be critical in conserving sage-grouse under the continued development of western landscapes (Heinrichs et al., 2019), especially for development of geothermal plants and other anthropogenic features considering increased demand for domestically-generated, clean renewable energy and continued conservation concerns surrounding sage-grouse. While the needs of other native, sensitive species warrant consideration (Germaine et al., 2020), the capacity of sage-grouse to serve as an indicator of sagebrush ecosystem health suggests that mitigation measures enacted for the benefit of sage-grouse populations can benefit sagebrush communities as a whole (Rowland et al., 2006). This conclusion is supported by the expansive distributional overlap of sage-grouse with other sagebrush obligate species of conservation concern (e.g., pygmy rabbit; *Brachylagus idahoensis*), and evidence of negative relationships that those populations have with similarly structured energy development activities (Germaine et al., 2020).

CRediT authorship contribution statement

Peter S. Coates: Conceptualization, Methodology, Investigation, Resources, Writing – Original Draft, Visualization, Supervision, Project administration, Funding acquisition.: **Brian G. Prochazka**: Conceptualization, Methodology, Software, Formal Analysis, Data Curation, Writing – Original Draft, Visualization.: **Shawn T. O'Neil**: Methodology, Software, Formal Analysis, Writing – Review & Editing.: **Sarah C. Webster**: Writing – Original Draft.: **Shawn Espinosa**: Conceptualization, Writing – Reviewing & Editing, Project Administration.: **Mark A. Ricca**: Conceptualization, Methodology, Investigation, Writing – Reviewing & Editing, Planning administration.: **Steven R. Mathews**: Data Curation, Writing – Review & Editing.: **Michael L. Casazza**: Conceptualization, Methodology, Investigation, Writing – Review & Editing, Supervision, Project Administration, Funding acquisition.: **David J. Delehanty**: Conceptualization, Writing – Review & Editing, Supervision, Project Administration.

Declaration of competing interest

The work is all original research carried out by the authors. All authors agree with the contents of the manuscript and its submission to the journal.

No part of the research has been published in any form elsewhere, unless it is fully acknowledged in the manuscript. However, the methodology has been submitted to the journal MethodsX as a companion paper simultaneous to this submission, as requested by guidelines in Biological Conservation. Authors provided this submitted manuscript as supporting information within the submission to Biological Conservation.

Authors should disclose how the research featured in the manuscript relates to any other manuscript of a similar nature that they have published, in press, submitted or will soon submit to Biological Conservation or elsewhere.

The manuscript is not being considered for publication elsewhere while it is being considered for publication in this journal.

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authors have declared any direct financial benefits that could result from publication.

All appropriate ethics and other approvals were obtained for the research. Where appropriate, authors should state that their research protocols have been approved by an authorized animal care or ethics committee, and include a reference to the code of practice adopted for the reported experimentation or methodology. The Editor will take account of animal welfare issues and reserves the right not to publish, especially if the research involves protocols that are inconsistent with commonly accepted norms of animal research.

Data availability

Full Data Available: https://doi.org/10.5066/P9OLC725.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109889.

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