




Research Article

Effects of Rotational Grazing Management on Nesting Greater Sage-Grouse

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ABSTRACT Grazing by domestic livestock is a ubiquitous land use in the sagebrush (*Artemisia* spp.) biome of western North America. Widespread, long-term population declines in greater sage-grouse (*Centrocercus urophasianus*) have elicited concern about potential negative effects of livestock management practices on sage-grouse populations. We evaluated how recently implemented rotational grazing systems affected sage-grouse nesting habitat quality as part of a large-scale, replicated, natural experiment in central Montana, USA. We used Bayesian methods to assess support for effects of rotational grazing management and rest from grazing on daily survival rates of nearly 500 sage-grouse nests monitored over 6 years, and mixed effects models to test for effects of rotational grazing and rest on vegetation structure. Though nests on rotationally grazed ranches displayed a trend toward greater daily survival rates, the evidence for an effect was weak. There was no evidence that rest from grazing (≥ 12 months) increased daily survival rates. Furthermore, rotational grazing systems and rest had negligible effects on herbaceous vegetation height and cover relative to other grazing strategies used in the study area. Results do not support the hypothesis that rotational grazing systems or rest from grazing increase nest success in the northern Great Plains. Estimated nest success, however, was comparable to range-wide averages, suggesting concealing cover for nests is unlikely to be limiting growth of this population regardless of grazing strategy. In light of these results and recent research questioning reported relationships between grass height and nest survival, maximization of hiding cover may be overemphasized in grazing management guidelines and policies. Rather, our findings suggest a variety of locally appropriate grazing strategies focused on fundamental range health principles may provide adequate habitat quality for nesting sage-grouse. © 2017 The Wildlife Society.

KEY WORDS *Centrocercus urophasianus*, greater sage-grouse, livestock, nest survival, Northern Great Plains, rotational grazing.

Once occupying >62 million ha (Küchler 1970), nearly half the sagebrush (*Artemisia* spp.) biome of western North America has been eliminated by sagebrush eradication, conversion to cropland, replacement by exotic annual grasslands, conifer encroachment, and expanding human settlements (Knick et al. 2003, Schroeder et al. 2004). Loss and fragmentation of sagebrush steppe has resulted in concomitant effects on an array of sagebrush-dependent wildlife (Rich et al. 2005, Suring et al. 2005). Strategic, science-based management of land practices in remaining sagebrush grasslands is thus a top conservation priority (Davies et al. 2011). Grazing by domestic livestock is ubiquitous across sagebrush ecosystems (Knick et al. 2003). Management of livestock grazing therefore has potentially

widespread implications for the integrity of the sagebrush ecosystem and its associated wildlife.

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) are a species of conservation concern embodying the challenges of conserving sagebrush ecosystems. Population declines since the mid twentieth century are attributed to widespread habitat loss and degradation (Connelly and Braun 1997, Knick and Connelly 2011). Following several petitions for Endangered Species Act (ESA) protection, the United States Fish and Wildlife Service (USFWS) recently deemed ongoing conservation efforts sufficient to preclude the need for a listing. Livestock grazing, predominantly by cattle and sheep, has been suggested as a contributing factor in historical population declines (Connelly and Braun 1997, Beck and Mitchell 2000, Wisdom et al. 2002, Crawford et al. 2004) and remains a contentious management issue.

Numerous relationships between livestock grazing and sage-grouse have been hypothesized (Beck and Mitchell 2000), with a consensus that nest success, among the most

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influential vital rates contributing to sage-grouse population growth (Taylor et al. 2012, Dahlgren et al. 2016), is likely affected by grazing (Beck and Mitchell 2000, Boyd et al. 2014). The primary mechanisms through which grazing is thought to affect nest success include increased nest abandonment from trampling or disturbance by livestock and reduced concealment by herbaceous understory vegetation facilitating nest detection by predators (Beck and Mitchell 2000, Connelly et al. 2000, Boyd et al. 2014). The latter mechanism is supported by studies reporting a positive relationship between cover or height of herbaceous vegetation, primarily grasses, and nest success (Gregg et al. 1994, Doherty et al. 2014) coupled with livestock consuming herbaceous vegetation. It has been proposed that livestock grazing has played a role in contemporary population declines (Connelly and Braun 1997) and increasing herbaceous cover or height through altered or reduced grazing may help bolster populations (Wisdom et al. 2002, Taylor et al. 2012, Doherty et al. 2014). As a result, habitat management guidelines for sage-grouse have emphasized maintaining tall (e.g., >18 cm) herbaceous vegetation in areas used by nesting females (Connelly et al. 2000, Stiver et al. 2015).

In 2010, the United States Department of Agriculture Natural Resources Conservation Service (NRCS) began implementation of their Sage Grouse Initiative (SGI) to reduce threats to sage-grouse while supporting sustainable agricultural use of sagebrush rangelands. Among other practices, NRCS has encouraged adoption of grazing strategies, including rotational grazing systems with extended periods of rest, to provide additional hiding cover to conceal sage-grouse nests. Participation in NRCS practices is voluntary, but technical and financial assistance are made available to incentivize participation, and payments are contingent upon contract compliance, which is monitored annually. Rotational grazing systems involve moving livestock herds through several pastures throughout the grazing season, shortening duration of use, and altering the timing of use of each pasture from year to year (Hormay 1956, 1970). Additionally, ≥ 1 pastures may be rested (i.e., no livestock grazing for ≥ 12 months) on a rotating basis to allow for plant recovery and accumulation of senesced plant matter and litter. Though frequently recommended to foster conservation goals, evidence for benefits of rotational grazing systems over alternative grazing management strategies is mixed at best (Briske et al. 2008), though few studies have explicitly measured outcomes of rotational grazing systems on species of conservation concern.

We present findings from the first 6 years of a 10-year, natural grazing experiment in central Montana where rotational grazing systems were simultaneously implemented on several ranches participating in SGI. We had 2 primary objectives. First, we tested whether sage-grouse nesting on SGI rotational grazing system (SGI-RGS) ranches experienced greater nest survival than those nesting on neighboring, non-participating (non-SGI) ranches. Second, we directly quantified the difference in herbaceous vegetation height and cover and other range health-related metrics

(vegetation structure) between SGI-RGS and non-SGI ranches. Because resting pastures involves opportunity costs to livestock operations and therefore requires additional financial incentives, we also tested specifically for effects of resting pastures ≥ 12 months on nest survival and vegetation structure.

STUDY AREA

Our study area, near the town of Roundup, Montana (46.448° N, 108.543° W; Fig. 1), was characterized by rolling topography ranging in elevation from 975 m to 1,250 m. Vegetation was typical of inter-mountain basins big sagebrush steppe (NatureServe 2016), with Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and silver sagebrush (*A. cana*) both common and co-dominant with a mix of rhizomatous and caespitose perennial grasses. Climate in the region was cold semi-arid, with average maximum daily temperature in Roundup (1981–2010) ranging from 2.8°C in December to 30.8°C in July and annual precipitation averaging 359 mm (National Climatic Data Center 2017). Annual precipitation during the study ranged from 265 mm in 2012 to 485 mm in 2014. Dominant land uses included livestock grazing and dryland farming; approximately 10% of the study area was occupied by crops. The study area encompassed 30 sage-grouse leks with >1 displaying male recorded in ≥ 1 year between 2011 and 2016. Median high male counts on these leks ranged from 7 in 2014 to 25 in 2016. Common nest predators included badgers (*Taxidea taxus*), common ravens (*Corvus corax*), coyotes (*Canis latrans*), foxes (*Vulpes vulpes*), and bobcats (*Lynx rufus*).

Rotational Grazing Systems

The NRCS began enrolling landowners in SGI-RGS in 2010, targeting ranches in state-designated core areas of high sage-grouse abundance. From 2010 to 2012, 10 landowners

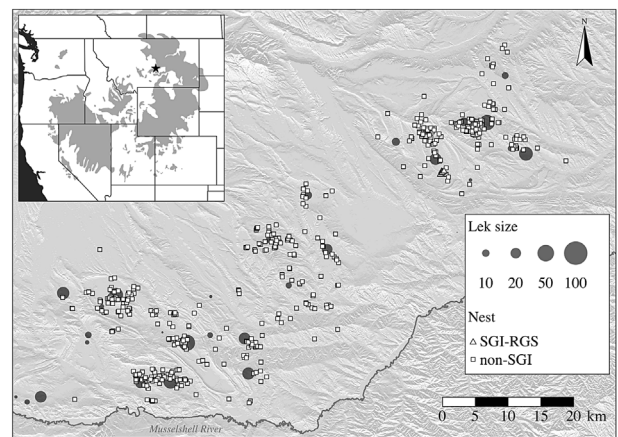


Figure 1. Golden Valley, Musselshell, and Petroleum counties, central Montana, USA. Greater sage-grouse leks are indicated by dark gray circles, with size of circles proportional to the highest male count recorded from 2011 to 2016. Nests monitored from 2011 to 2016 are indicated by triangles (Sage Grouse Initiative rotational grazing systems; SGI-RGS) and squares (non-SGI). Inset shows location of the study area (star) within the contemporary range of sage-grouse (gray shading).

in one core area in central Montana elected to participate in SGI-RGS contracts, with enrolled land peaking in 2012 at approximately 50,585 ha, 67% of which were inside core area boundaries. Ranches enrolled in SGI-RGS comprised a variety of configurations (i.e., ranch size, no. herds, existing infrastructure); therefore, grazing plans were individually customized to accommodate ranch configuration and landowner needs. However, all plans adhered to the NRCS Montana Prescribed Grazing conservation practice standards (NRCS 2012) and implemented a consistent set of minimum criteria designed to positively influence features of sage-grouse habitat. These criteria included 1) utilization rates of $\leq 50\%$ of current year's growth of key forage species, 2) duration of grazing ≤ 45 days, 3) timing of grazing changed by at least 20 days each year, and 4) a contingency plan for exceptional circumstances such as drought or fire. Infrastructure such as cross fencing and supplemental water were added where necessary to facilitate implementation. Landowners could optionally elect to rest 20% of the identified sage-grouse nesting habitat (defined as areas with $\geq 5\%$ sagebrush cover) on their ranches from grazing on an annually rotating basis. The rest period was designed to provide pastures 2 full sage-grouse nesting seasons without livestock use and was generally ≥ 15 months in duration. We use the term rest throughout to refer to pastures left ungrazed for ≥ 12 months as part of the grazing system (Heady 1970). Nine of the 10 landowners enrolled during the study elected to incorporate rest. The SGI-RGS contracted ranches ranged in size from approximately 1,660 ha to 7,690 ha. Nine of the 10 enrolled landowners grazed cattle exclusively, whereas 1 grazed a mix of cattle and sheep. We secured permission to access all 10 ranches enrolled in SGI-RGS, which constituted our treatment group (Fig. 1).

We also secured permission to access land owned or managed by >20 non-enrolled area ranchers, which constituted our control group. We were unable to gather complete data regarding grazing management on all non-SGI lands, which encompassed a variety of grazing systems, but most were managed less intensively (i.e., with a season-long grazing strategy or slower rotations through larger pastures, usually without annual changes in season of use). Two non-enrolled landowners grazed a mix of cattle and sheep; the rest grazed cattle exclusively. Non-SGI ranches were distributed broadly throughout the study area (Fig. 1).

METHODS

Sage-Grouse Capture and Nest Monitoring

We captured female sage-grouse during the early breeding season (Mar–Apr) in 2011–2016, and during late summer (Aug–Sep) in 2012–2015 using spotlights and hoop netting techniques from all-terrain vehicles (Wakkinen et al. 1992). We affixed 25-g necklace-style very high frequency (VHF) transmitters (Advanced Telemetry Systems, Isanti, MN, USA) to all captured females. We tracked females at least twice weekly until they began to make localized movements indicative of nesting behavior, at which point we reduced our monitoring interval to daily if possible. When we detected a

female in the same location on successive relocations, we attempted to identify the female on a nest while maintaining a distance of ≥ 10 m to avoid flushing. We marked nests from a distance of approximately 10 m with natural materials, and established listening points ≥ 100 m from the nest for monitoring nest status remotely via telemetry. We monitored nests from the listening point every 2–3 days until the female moved from the nest, at which point we confirmed nest fate as successful (≥ 1 hatched egg with membrane detached) or failed. Predation is the primary cause of nest failure in sage-grouse, but we recorded failed nests without evidence of predation (i.e., without broken or missing eggs) as abandoned. All animal handling was approved under University of Montana's Institutional Animal Care and Use Committee (Protocol 011-14DNWB-031914).

Model Covariates

We recorded whether each nest was located in an SGI-RGS or non-SGI pasture and whether the pasture was rested from grazing for use as treatment factors. We only classified pastures as SGI-RGS if they had been certified as using SGI prescribed grazing practices for ≥ 1 year before the nesting season. We considered a pasture rested only if it had been ungrazed for ≥ 12 months before the onset of the nesting season (~ 15 Apr) and remained ungrazed throughout the nesting season.

Daily survival rates of nests may vary across the nesting season because of seasonal variation in predator community composition or alternate prey availability, predators developing a search image for nests, or changing weather throughout the nesting season (Klett and Johnson 1982, Burhans et al. 2002, Fisher and Wiebe 2006). Survival may vary by nest age if easily detected nests are depredated earlier because of unmodeled heterogeneity in nest site quality or if females alter incubation behavior throughout the incubation period (Klett and Johnson 1982). We therefore included linear effects of ordinal date (date; days since 1 Jan) and nest age (age; days since estimated onset of incubation). To aid in model convergence and facilitate parameter interpretation, we centered date and age by subtracting the median ordinal date of nest observation (137, corresponding to 16 May) from the date matrix and subtracting the median observed nest age (14 days) from the nest age matrix before model fitting.

Daily Nest Survival Model

Nest encounter histories consisted of observed nest states (y) for each day (t) of observation, where $y_{i,t} = 1$ if we observed nest i alive on day t , $y_{i,t} = 0$ if we determined nest i to have failed (F absent and some or all eggs destroyed), and $y_{i,t} = \text{NA}$ on days when we did not observe the nest state. Beginning on the first day after we detected the nest,

$$y_{i,t} \sim \begin{cases} 0 & \text{if } y_{i,t-1} = 0 \\ \text{Bern}(\phi_{i,t}) & \text{if } y_{i,t-1} = 1 \end{cases}$$

We modeled daily survival probability ($\phi_{i,t}$) as a function of nest- and time-varying covariates using a logit link. We estimated a global intercept and included group-level effects

α_j and δ_k for each year (j) and ranch (k). We used a Bayesian variable selection technique to quantify support for the effects of date, age, SGI-RGS, and rest on daily nest survival (Converse et al. 2013). We multiplied regression coefficients β_p for each variable p by binary indicator variables (w_p ; Kuo and Mallick 1997, O'Hara and Sillanpää 2009):

$$\text{logit}(\phi_{i,t}) = \beta_0 + w_1\beta_1 \times \text{date}_{i,t} + w_2\beta_2 \times \text{age}_{i,t} + w_3\beta_3 \times \text{SGI-RGS} + w_4\beta_4 \times \text{rest}_i + \alpha_j + \delta_k$$

$$\alpha_j \sim N(0, \sigma^\alpha)$$

$$\delta_k \sim N(0, \sigma^\delta)$$

We placed a Normal(0,1.7) prior on β_0 , yielding a prior on ϕ that is approximately Uniform[0,1]. We gave standard deviations for group-level year and ranch effects, σ^α and σ^δ , vague half-Normal priors with mean 0 and standard deviation 100 (Gelman 2006). We scaled coefficient priors according to the number of parameters in the model at each Markov chain Monte Carlo (MCMC) iteration such that total model uncertainty was constant across candidate models. Thus, priors for all β_p were distributed Normal(0, $(V/M)^{-1}$) where M was the number of non-zero indicator variables and we placed a Gamma (3.29,7.8) prior on V so the marginal prior distribution on daily nest survival probability was approximately Uniform[0,1] (Link and Barker 2006, Smith et al. 2011). We placed Bernoulli(0.5) prior distributions on all indicator variables, representing no prior information about individual variable importance and equal prior probability of all 16 possible models (O'Hara and Sillanpää, 2009).

We calculated Bayes factors (BF) to quantify support for variables of interest using the prior inclusion probability (w_p^{prior}) and posterior mean inclusion probability ($\hat{w}_p^{\text{posterior}}$) as $\text{BF}_p = \frac{\hat{w}_p^{\text{posterior}} / (1 - \hat{w}_p^{\text{posterior}})}{w_p^{\text{prior}} / (1 - w_p^{\text{prior}})}$ (Smith et al. 2011). A $\text{BF} \geq 3.2$ is indicative of a coefficient with substantial support and a $\text{BF} > 10$ indicates strong support (Kass and Raftery 1995). We therefore report Bayes factors and base our inference on variables with $\text{BF} \geq 3.2$, using the posterior distributions of β_p under the most supported model based on model frequencies in the MCMC samples to derive parameter estimates and 95% credible intervals (CRI).

We ran 100,000 iterations following 100,000 samples for burn-in. We visually assessed convergence and mixing and calculated Gelman-Rubin convergence statistics (Gelman and Rubin 1992, Brooks and Gelman 1997) for all coefficients using 2 independent chains with different initial values. We fit models using JAGS (version 4.2.0, mcmc-jags.sourceforge.net, accessed 19 Feb 2016) via the `runjags` package (Denwood 2016) in program R (version 3.3.0, www.r-project.org, accessed 3 May 2016). We derived an estimate of annual nest success by exponentiating estimated daily survival rate from the full model with all covariates set to zero by the 27-day incubation period typical in our study area.

We performed a posterior predictive check (Gelman et al. 1996, 2014) of our nest survival model to determine whether our model could faithfully reproduce our observed data. Often termed Bayesian p -values, posterior predictive checks offer a convenient goodness-of-fit test for Bayesian models by comparing an attribute of the observed data to that of data produced by the model. For our test statistic, we used the number of hatched nests (229 out of 495), which we compared to the predicted number of nests surviving through the incubation period by the model. Drawing from the joint posterior distribution, we calculated daily survival probabilities, $\phi_{i,t}$ for each nest i on day t from the first date of observation to 27 days after the estimated nest initiation date. We predicted the outcome, hatch_i , of each nest by taking successive Bernoulli draws of nest state $y_{i,t}$ from $\phi_{i,t}$ until $y_{i,t} = 0$ (failed nest) or until $t =$ estimated hatch date (hatched nest). We then calculated the proportion of MCMC samples for which the observed number of nests hatched was greater than the predicted number. A value near 0.5 indicates the model generated data similar to our observations, whereas values < 0.05 or > 0.95 suggest a poor fit.

Response of Vegetation Structure to Grazing Management

Because expected benefits of SGI-RGS are predicated on effects on vegetation structure, we sought to directly test for differences in vegetation structure between SGI-RGS ranches and non-SGI ranches. We hypothesized SGI-RGS would increase hiding cover provided by herbaceous vegetation, particularly live and senesced grass height and areal cover, relative to other grazing systems used in the region. Metrics considered indicators of rangeland health, such as litter cover and bare ground, were also of interest. In addition to differences among grazing systems we wanted to quantify effects of rest from grazing. Pastures rested from grazing were rotated on an annual basis, and we were unable to get reliable grazing schedules for most ranches ahead of the grazing season. Additionally, some ranches began ($n = 3$) or ended ($n = 5$) their enrollment during the study. We were therefore unable to use permanent vegetation plots, and instead generated random locations for field plots (vegetation response plots) each year. We did not sample SGI-RGS treatments during the first year of implementation because a given pasture in a rotational grazing system may not be grazed for several months following a change in grazing management. We conducted a pilot study in 2012, sampling 100 plots (50 SGI-RGS, 50 non-SGI) to determine necessary sample sizes in following years. Based on earlier studies (Gregg et al. 1994, Doherty et al. 2014) reporting positive effects of grass height on nest survival, we chose target sample sizes to achieve 80% power to detect a 10% difference in grass height (i.e., ~ 2 cm) between treatments at $\alpha = 0.05$. From our pilot data we found variation in topographic position (i.e., hilltops, flats, valley bottoms, or drainages), slope, and soil series, which are associated with ecological site potential, accounted for much of the observed variation in grass height. Thus, to standardize for site potential among our samples, we stratified the study area by

topographic position, soil series, and distance from water and restricted future samples on all treatments to a range of conditions that were representative of sage-grouse nesting habitat and were sufficiently accessible to livestock to respond to grazing management (Appendix Table A1). We conducted statistical tests only on plots sampled from 2013 to 2016.

Though not among our primary objectives, we were interested in exploring whether vegetation structure experienced by nesting grouse in our study was substantially different than what might exist in the absence of livestock grazing in this region. Beginning in 2014, we extended our vegetation sampling to 2 properties managed by USFWS where livestock grazing had been absent for 4–12 years (i.e., idled). These plots, which were added to address separate management questions, serve as a useful reference point to which our 2 primary grazing management treatments can be compared. We present these data here to allow a visual comparison of the distribution of herbaceous vegetation structure on idled lands with the distributions observed within our grazing treatments.

At vegetation response plots, we examined several metrics of herbaceous plant structure that we hypothesized were likely to be affected by grazing management. We established plots by stretching 2 18-m tapes perpendicular to one another and intersecting at the plot center, with one tape oriented north-south and the other oriented east-west. We estimated areal cover of herbaceous plants, litter, and bare ground using 12 20 × 60-cm quadrats (Daubenmire 1959) per plot, placed at 3, 6, and 9 m from plot center in each cardinal direction. At the same points, we measured the tallest vertical height of undisturbed live and senesced material on the nearest herbaceous plant, excluding inflorescences. We also estimated visual obstruction at the plot with a Robel pole (Robel et al. 1970), taking readings from 1 m above the ground 4 m from the pole with the pole placed 1, 3, 5, and 7 m from the plot center in each cardinal direction. We designed methods to generate vegetation structure data comparable to measurements made at sage-grouse nests in a concurrent study, which used a modified BBIRD grassland protocol (<http://www.umt.edu/bbird/>). We did not measure shrub density or cover because we were primarily interested in effects on herbaceous vegetation and did not anticipate differences in the shrub component due to differences in grazing management over 1–6 years, especially given the predominance of cattle grazing in the study area (Angell 1997, Bates and Davies 2014). We restricted plots to sites dominated by native rather than invasive or planted vegetation so they would be representative of vegetation used by sage-grouse. We measured all vegetation response plots during July to minimize variation due to plant phenology.

We used linear mixed-effects models to test for grazing system and pasture rest effects (fixed effects) on vegetation metrics while accounting for variation among years and ranches (random effects). We fit models using the lme4 package (Bates et al. 2015) in R. We assessed significance of fixed effects with likelihood ratio tests comparing models with and without fixed effects for SGI-RGS and pasture rest.

RESULTS

We captured 340 female sage-grouse between 2011 and 2016 and located and determined the fate of 501 nests from 256 females. We removed 4 nests from the survival analysis because of early observer-induced abandonment, and removed 2 nests because they were found already predated. Among the remaining 495 nests, 229 (46.3%) hatched ≥ 1 egg, predators destroyed 254 nests (51.3%), 10 nests (2.0%) were abandoned for unknown reasons, and 2 nests (0.4%) were abandoned because of predation of the female while off the nest. Nests in the SGI-RGS treatment ($n = 148$) were represented by 6 enrolled ranches, nests on non-SGI lands ($n = 347$) were represented by 28 ranches, and 26 nests were in rested pastures across 4 ranches.

Visual inspection and Gelman-Rubin statistics indicated convergence among MCMC chains for our nest survival analysis. Estimated annual nest success was 40.0% (95% CRI from 23.8% to 52.5%) on non-SGI ranches and 48.8% (95% CRI from 31.0% to 62.2%) on SGI-RGS ranches (Fig. 2). The model appearing most frequently across MCMC samples included SGI-RGS (positive) and rest (negative) effects, though the distribution of posterior model weights indicated substantial model uncertainty (Table 1). Bayes factors, likewise, indicated nest survival was independent of nest age, ordinal date, SGI-RGS, and pasture rest, and 95% credible intervals of all coefficients overlapped zero (Table 2). The posterior predictive check indicated adequate model fit ($P = 0.31$).

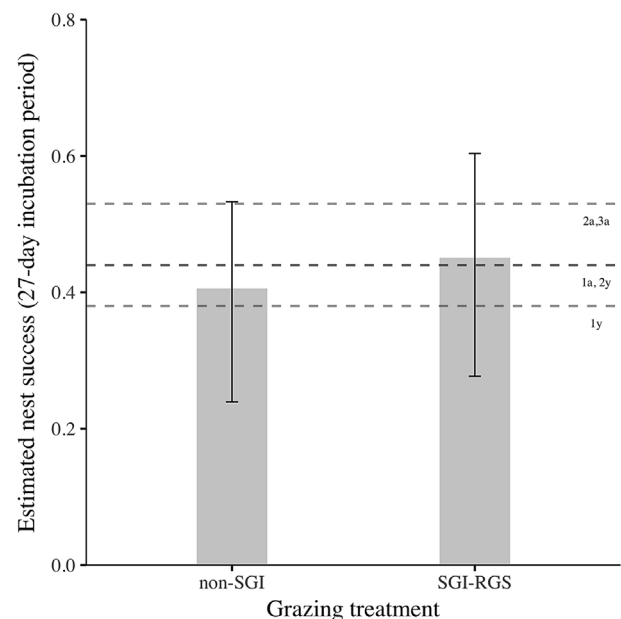


Figure 2. Nest success of greater sage-grouse on land enrolled in Sage Grouse Initiative rotational grazing systems (SGI-RGS) and on neighboring, non-participating ranches (non-SGI) in central Montana, USA, 2011–2016. Error bars depict upper and lower 95% credible intervals. Though a trend toward greater nest survival was apparent on SGI-RGS lands, the evidence for an effect was weak. Our estimates are consistent with range-wide average nest success, depicted by dashed horizontal lines, where 1a = first nesting attempts by adult females, 2y = second nesting attempts by yearling females, and so on (from Taylor et al. 2012).

Table 1. Model weights of all 16 possible models explaining daily nest survival of greater sage-grouse in central Montana, USA, 2011–2016.

Model structure (1 = included, 0 = not included)				
Date	Age	SGI-RGS ^a	Rest	Model weight ^b
0	0	1	1	0.26
0	0	0	0	0.23
0	0	1	0	0.22
0	0	0	1	0.14
0	1	1	1	0.05
0	1	1	0	0.04
0	1	0	1	0.02
0	1	0	0	0.02
1	0	1	1	<0.01
1	0	1	0	<0.01
1	1	1	1	<0.01
1	0	0	0	<0.01
1	0	0	1	<0.01
1	1	1	0	<0.01
1	1	0	1	<0.01
1	1	0	0	<0.01

^a Sage Grouse Initiative rotational grazing system.

^b Proportion of 200,000 Markov chain Monte Carlo samples in which the particular vector of indicator variables appears.

We sampled 451 vegetation response plots on non-SGI ranches and 556 vegetation response plots on SGI-RGS ranches, including 226 plots in rested pastures, from 2013 to 2016 (Fig. 3). Likelihood ratio tests indicated that live grass height ($\chi^2 = 6.96$, $P = 0.008$), senesced grass height ($\chi^2 = 5.87$, $P = 0.015$), and litter ($\chi^2 = 12.28$, $P < 0.001$) were greater on SGI-RGS ranches than non-SGI ranches. Bare ground ($\chi^2 = 2.55$, $P = 0.109$), herbaceous vegetation cover ($\chi^2 = 0.68$, $P = 0.411$), and visual obstruction ($\chi^2 = 0.32$, $P = 0.569$) did not differ between grazing systems. After accounting for grazing system differences, only visual obstruction ($\chi^2 = 9.92$, $P = 0.002$) differed between rested and grazed pastures, with greater visual obstruction associated with rested pastures (Fig. 3).

Grazing system and rest effect sizes were modest relative to annual variation (Fig. 3). Live grass height was 1.1 ± 0.40 (SE) cm greater on SGI-RGS ranches, and the estimated standard deviation among years was 1.5 cm. Senesced grass height was 0.9 ± 0.35 cm greater on SGI-RGS ranches, and the estimated standard deviation among years was 2.9 cm. Litter cover was $4.7 \pm 1.3\%$ greater on SGI-RGS ranches,

and the estimated standard deviation among years was 7.3%. Rest was associated with a 1.4 ± 0.43 -cm increase in visual obstruction, and the estimated standard deviation among years was 1.4 cm.

DISCUSSION

Our findings lend little support to the hypothesis that rotational grazing increases nesting habitat quality by increasing hiding cover (Doherty et al. 2014). The equivocal support for beneficial effects of rotational grazing and rest may stem from relatively minor differences in vegetation structure between our treatments, selection for concealed nest sites counteracting treatment effects, lack of a causal relationship between herbaceous concealing cover and nest survival, or some combination of these factors. Although the top survival model included SGI-RGS and rest effects, a model with only an intercept and group-level effects for ranch and year had nearly equal model weight (Table 1), and posterior inclusion probabilities for SGI-RGS and rest effects were 0.58 and 0.48, respectively. Furthermore, we found SGI rotational grazing systems and rest from grazing had negligible effects on herbaceous hiding cover relative to other grazing management strategies used in our study area. Although SGI-RGS was associated with detectable increases in live and senesced grass height and litter cover, estimated effect sizes were small and other metrics such as herbaceous cover, bare ground cover, and visual obstruction did not differ between treatments.

Grazing management likely played a minor role in determining nest survival in our study area relative to other factors (e.g., weather, predators). This was evident in the relative magnitudes of the standard deviations for ranch and year effects (Table 1), which indicated variation among years was >2.5 times greater than among ranches. This is suggestive that factors such as weather or annually fluctuating predator abundance overwhelm the effects of grazing management, and is consistent with the emerging understanding that effects of local vegetation manipulation on prairie grouse are relatively minor in comparison to processes and patterns operating at broader scales, such as weather and landscape fragmentation (Jorgensen et al. 2014, Hovick et al. 2015, Fuhlendorf et al. 2017). With only 6 years of observation, however, our estimate of σ^α is imprecise (Table 2).

Table 2. Parameter estimates and credible intervals for daily nest survival of greater sage-grouse in central Montana, USA, 2011–2016.

Parameter	Posterior inclusion probability	Bayes factor ^a	Estimate ^b	Lower 95% CRI	Upper 95% CRI
β_0			3.36	2.91	3.72
$\sigma^{\alpha c}$			0.33	0.10	1.02
$\sigma^{\gamma d}$			0.13	0.01	0.34
β_1 (date)	0.02	0.02			
β_2 (age)	0.15	0.17			
β_3 (SGI-RGS ^e)	0.58	1.38	0.25	-0.04	0.55
β_4 (rest)	0.48	0.92	-0.22	-0.72	0.27

^a Bayes factors >3.2 are indicative of variables with support (Kass and Raftery 1995).

^b Estimates and credible intervals (CRI) are conditional on the top model.

^c Standard deviation among years.

^d Standard deviation among ranches.

^e Sage Grouse Initiative rotational grazing system.

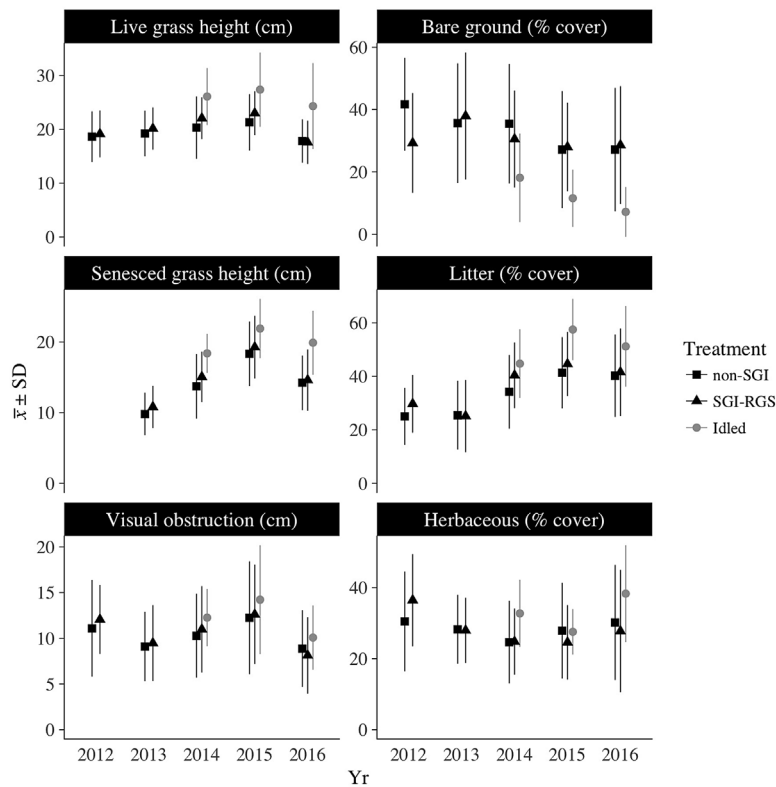


Figure 3. Vegetation structure ($\bar{x} \pm SD$) measured at vegetation response plots on central Montana, USA ranches enrolled in Sage Grouse Initiative rotational grazing systems (SGI-RGS, $n = 556$), on non-enrolled (non-SGI, $n = 451$) ranches, and in pastures not grazed by livestock from 4 to 12 years (idled, $n = 57$) from 2013 to 2016. Pilot data collected in 2012 are also depicted, though not used in statistical tests. Linear mixed effects models revealed that live grass height, senesced grass height, and litter differed between non-SGI and SGI-RGS ranches. Visual obstruction measured with a Robel pole was higher and litter cover was lower in rested pastures. Estimated effect sizes were small, however, relative to annual variation.

Vegetation structure on long-term idled lands differed from that observed in either grazing treatment in some key regards. Live and senesced grasses were taller, and sites were characterized by more litter and less bare ground, on idled lands than in either grazed treatment (Fig. 3). These observations are largely consistent with previous findings of greater herbaceous standing biomass associated with livestock exclusion in sagebrush plant communities (West et al. 1984; Davies et al. 2010, 2016). With few exceptions, however, means of structural metrics on idled land were within 1 standard deviation of the means of those metrics in both grazing treatments. This suggests vegetation resembling that found on lands idled for several years was likely abundant even on lands managed for livestock production. If selective pressure favored nests with greater herbaceous concealing cover, we would expect similar vegetation structure among nests in grazed and long-term idled lands because of selection of highly concealed nest sites (Hagen et al. 2007). We did not observe any nesting females using idled lands during the study, however, precluding a comparison of nest survival between long-term idled and grazed areas.

Recently, the importance of tall concealing cover to sage-grouse and other ground nesting birds was brought into question by Gibson et al. (2016), who demonstrated that common field methods employed in nest survival studies contain a built-in bias which inflates type I errors when

testing for a positive effect of grass height. Specifically, measurement of vegetation following nest fate (failure or hatch) induces a bias in the timing of vegetation measurement such that failed nests are measured earlier in the season, on average, than successful nests. Because the nesting season coincides with rapid vegetation growth, differences in vegetation height or cover may be the result of plant growth rather than an effect of concealment on survival. In a separate analysis, we found no association between cover or height of herbaceous vegetation and nest survival in our study area after correcting for this methodologically induced bias (Smith 2016). Thus, grazing strategies designed to increase herbaceous hiding cover may have little ability to influence this vital rate regardless of their effect on vegetation.

It is unlikely nest success was limiting population growth in our study area, as suggested by our estimated mean annual nest survival from onset of incubation of 41%, a rate typical of studied sage-grouse populations (Fig. 2; Connelly et al. 2000, Taylor et al. 2012). Nest survival, however, is only 1 among several influential vital rates influencing population growth; fitness benefits may still accrue if SGI-RGS positively affects resources needed during other life stages. Although we detected negligible differences in upland vegetation associated with SGI-RGS, the scope of this analysis precluded an evaluation of resources thought to be important for chick survival such as forb diversity and

abundance, arthropod abundance, and vegetation structure in mesic areas used by brood-rearing females in late summer. Data collection will continue in this study system for an additional 4 years (2017–2020) to assess factors associated with adult female and individually marked chick survival.

Because our study area was characterized by a different precipitation regime than much of the range of sage-grouse, our findings should be extrapolated with caution. Although we observed negligible or null effects of SGI-RGS on bare ground, litter, and herbaceous cover, these and other indicators of rangeland health may respond differently to grazing management treatments in regions differing in climate, vegetation community composition, and evolutionary history of grazing such as the Great Basin (Mack and Thompson 1982). Recently, Monroe et al. (2017) reported population-level responses of sage-grouse to timing of grazing interacted with primary productivity in Wyoming, such that negative responses to early season grazing were not evident in highly productive regions. Our finding of a lack of response to variation in grazing management or rest is consistent with this pattern because our study area was productive relative to sage-grouse habitat in Wyoming. Negative effects of grazing—and their corollary, positive responses to altered grazing management—may manifest in less productive regions.

Readers should not infer from our study that grazing management is irrelevant to sage-grouse conservation. Rather, grazing management that promotes robust, diverse native plant communities resistant to invasion by exotic annuals and resilient to disturbances such as drought and fire (Davies et al. 2011, Bansal and Sheley 2016, Chambers et al. 2016) and prevents transitions to less desirable vegetation community states (Cagney et al. 2010) is critical to maintain the basic habitat components needed by sage-grouse over the long term. However, it is likely no single grazing strategy will be equally effective in achieving these goals, nor will any single formula serve as an adequate gauge of sage-grouse habitat quality, across the geographic range of the species. The need for replication of research regarding effects of grazing management on the sagebrush ecosystem, and sage-grouse in particular, across a range of ecological contexts is difficult to overstate.

MANAGEMENT IMPLICATIONS

Our findings suggest a variety of grazing management strategies can provide adequate habitat quality for nesting sage-grouse. Relationships between grazing management and other influential vital rates such as chick and adult female survival are, however, still largely unknown. Managers should continue to pursue locally appropriate grazing management strategies focused on fundamental rangeland health principles. Ultimately, the foremost conservation priority should be the prevention of further loss and fragmentation of sagebrush landscapes from land uses and activities that negatively affect sage-grouse populations such as infrastructure (Knick et al. 2013), energy development

(Naugle et al. 2011, Green et al. 2017), and conversion of native rangelands to cropland (Smith et al. 2016).

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APPENDIX

Table A1 Criteria for selecting plots to measure vegetation response to Sage Grouse Initiative rotational grazing systems (SGI-RGS) and pasture rest in central Montana, 2013–2016.

Variable	Acceptable range	Data source
Slope	0–5 degrees	10-m DEM ^a
Soil map unit symbol ^b	60C, 60D, 64A, 64B, 68C	NRCS SSURGO database ^c
Distance to water	200–1,500 m	Local NRCS records, National hydrography dataset ^d

^aDigital Elevation Model; <http://nationalmap.gov/3DEP>

^bSoil map unit symbols chosen for inclusion are composed largely of silty clay loams that typically support sagebrush in the study area.

^c<http://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx>

^d

<http://nhd.usgs.gov>; verified in the field.