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RESEARCH ARTICLE



Greater sage-grouse chick mortality risk relative to livestock grazing management, environmental factors, and morphometric measurements

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Abstract

Greater sage-grouse (Centrocercus urophasianus; sage-grouse) populations in the western United States have declined, necessitating conservation efforts. The United States Department of Agriculture Natural Resources Conservation Service and livestock producers implemented the Sage Grouse Initiative (SGI) to improve sage-grouse habitat using regional-specific management actions such as rotational grazing. We assessed the effect of SGI grazing management, the influence of brood female and chick morphometric traits, and multiple environmental and anthropogenic disturbance factors on chick mortality risk in a sage-grouse population in central Montana, USA, from 2011-2019. We used a Kaplan-Meier survival function to evaluate chick survival, Cox proportional hazards models to evaluate chick mortality risk as a function of brood female and chick morphometric traits, and the Andersen-Gill formulation of the Cox proportional hazards model to assess the effects of time-dependent habitat characteristics on chick mortality risk. Survival to 45 days post-hatch for 510 chicks varied annually from 0.26 ± 0.07 (SE) to 0.69 ± 0.07. The 45-day survival rate for all years combined was 0.51 ± 0.03. Chick mortality risk was not affected by changes in livestock grazing management

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implemented through the SGI grazing program. Brood female age and body condition, sex of chicks, vegetation, and anthropogenic variables were also unassociated with chick mortality risk. There were small protective effects of chick mass adjusted for age and mean minimum monthly temperature; greater chick mass and lower monthly temperatures correlated with reduced mortality risk. Overall, our study suggests the SGI grazing program does not confer additional benefits to sagegrouse chicks beyond existing grazing practices. Incentivizing grazing practices that adhere to fundamental principles of rangeland ecology and maintain intact rangelands may be more effective than specific prescribed grazing systems for sagegrouse conservation in this region.

KEYWORDS

Centrocercus urophasianus, chick survival, grazing, greater sage-grouse, Montana, rangeland management, SGI, telemetry

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) populations in the western United States have experienced declines since the mid-twentieth century, largely due to widespread habitat loss and degradation (Connelly and Braun 1997, Connelly et al. 2004, Garton et al. 2011). These declines have made sage-grouse a focal species for conservation efforts and prompted several petitions for Endangered Species Act (ESA) protection (U.S. Fish and Wildlife Service 2010). Conservation initiatives have successfully prevented ESA protection, leading to the subsequent removal of sage-grouse from the candidate species list in 2015 (U.S. Fish and Wildlife Service 2015). Ongoing threats to sagebrush (*Artemisia* spp.) ecosystems necessitate continued research and management (Allred et al. 2015, Lark et al. 2015, Severson et al. 2017, Kirol et al. 2020, Dudley et al. 2021). Specifically, understanding the relationships between land use practices and sage-grouse ecology is a key step in developing conservation strategies that incorporate science-based management of land use practices in sagebrush ecosystems (Dettenmaier et al. 2017).

Livestock grazing is the most widespread land use practice globally (Krausman et al. 2009), and the dominant land use practice in sagebrush steppe (Dettenmaier et al. 2017). Grazing can alter the vegetation structure, composition, and productivity of sagebrush ecosystems (Manier and Hobbs 2007, Krausman et al. 2009, Davies et al. 2010, Bates and Davies 2014, Davies et al. 2018), though these changes depend on the timing and intensity of grazing (Holechek et al. 1999, Fuhlendorf and Engle 2001, Holechek et al. 2011). Consequently, desired habitat conditions for sagebrush-dependent wildlife may be achieved by manipulating vegetation structure through specific grazing management regimes (Fuhlendorf and Engle 2001, Connelly et al. 2004, Chambers et al. 2017). Results from several studies indicate promising outcomes for using grazing to manage exotic annual grasses (Davies et al. 2021, Rhodes et al. 2021) and enhance habitat quality for some vulnerable grassland bird species (Augustine and Derner 2015, Kraft et al. 2021). The utility of any particular grazing strategy is context-dependent, requiring region-and species-specific assessments to determine the suitability of grazing for achieving conservation goals.

Using grazing to manage habitat has been one of several conservation strategies employed by the Sage Grouse Initiative (SGI), a conservation program implemented by the United States Department of Agriculture Natural Resources Conservation Service (NRCS), to help alleviate threats to sage-grouse and their habitat on private working rangelands (Beck et al. 2023). Since 2010, SGI has invested \$536.2 million and partnered with 2,366 livestock producers to manage 3.47 million ha of land across 11 western states (NRCS, 2021). In Montana, USA, the primary goals of SGI have been to work with producers to implement sustainable grazing strategies that improve sage-grouse habitat, promote rangeland health, and keep working ranches intact. Previous studies have evaluated outcomes from SGI-led habitat management strategies including conifer removal (Severson et al. 2017, Olsen et al. 2021) and riparian area and wet meadow restoration (Silverman et al. 2019). Early evaluations of the SGI grazing program, specifically, found that program adoption did not confer additional benefits to sage-grouse nest success (Smith et al. 2018*a*, *b*). Further assessment of additional sage-grouse demographic rates is still necessary to fully gauge effects of the SGI grazing program on sage-grouse populations.

Several studies across the sage-grouse range have been initiated to evaluate grazing effects on sage-grouse vital rates (Cutting et al. 2019, Conway et al. 2021, Behnke et al. 2022). No studies to date have investigated the relationships between grazing and chick survival or mortality risk. Chick survival is among the 3 most influential vital rates affecting greater sage-grouse population growth, yet it is the least-studied with the most variable methods and definitions (Taylor et al. 2012). We define the chick life stage as the period from hatch to 35 days post-hatch, and the juvenile stage from 35 days until 1 year post-hatch (Taylor et al. 2012). These life stages exhibit the lowest and most variable survival for grouse, particularly during the first few weeks after hatching (Aldridge and Brigham 2001, Hannon and Martin 2006, Manzer and Hannon 2008, Davis et al. 2016, Barker et al. 2022). While several studies have assessed sage-grouse chick survival within the first few weeks post-hatch (Gregg and Crawford 2009, Dahlgren et al. 2010, Thompson 2012, Guttery et al. 2013*a*, Gibson et al. 2017), there is a need for research specifically addressing relationships between sage-grouse chick survival and grazing.

Our objective was to determine how the SGI grazing program affected sage-grouse chick mortality risk in central Montana to help guide conservation and management for this life phase. We also evaluated the influence of additional biotic and abiotic variables on sage-grouse chick mortality risk. We hypothesized that chick mortality risk would not be affected by the SGI grazing system, based on results regarding nest success by Smith et al. (2018*b*). Beyond the effects of grazing, we hypothesized that chick mortality risk would be greater for chicks with yearling versus adult brood females, higher for males than females, and primarily influenced by weather variables based on previous research (Guttery et al. 2013*a*, Apa et al. 2017, Pratt and Beck 2021).

STUDY AREA

The study area was in central Montana in rolling topography that ranged from 975-1,250 m in elevation and covered approximately 150,000 ha in Musselshell and Golden Valley counties (Figure 1) centered around the town of Roundup, Montana (46.4423°N, -108.5390°W). The vegetation was consistent with sagebrush steppe, the most widely distributed sagebrush system in Montana. Wyoming big sagebrush (A. tridentata ssp. wyomingensis) and silver sagebrush (A. cana) were both common and co-dominant, with a mix of perennial bunchgrasses, perennial rhizomatous grasses, and forbs composing up to 25% of cover (Smith et al. 2018a, b; Montana Natural Heritage Program 2021). This region has cooler soil temperature and higher soil moisture than other parts of the sage-grouse range (Pyke et al. 2015). The climate is cold semiarid (Pyke et al. 2015), with distinct seasons that include cool and wet springs (April to early June), hot and dry summers (mid-June through mid-September), cool and wet autumns (mid-September through November), and cold, snowy winters (December through March). Average monthly temperatures in Roundup (2009-2020) ranged from -3.8°C (January) to 21.8°C (July; National Centers for Environmental Information 2021). Average annual precipitation in Roundup (2009-2020) ranged from 9.40 mm (January) to 73.41 mm (June; National Centers for Environmental Information 2021). Common predators of adult sage-grouse in our study area include golden eagles (Aquila chrysaetos), coyotes (Canis latrans), bobcats (Lynx rufus), and red foxes (Vulpes vulpes), with less common predation by bald eagles (Haliaeetus leucocephalus), great horned owls (Bufo virginianus), and badgers (Taxidae taxus). Sage-grouse chicks are susceptible to predation by golden eagles and other raptors (e.g., ferruginous hawks [Buteo regalis]), common ravens (Corvus corvax), coyotes, red foxes,

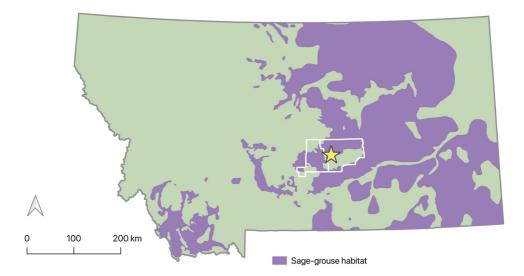


FIGURE 1 State-designated greater sage-grouse habitat (purple) in Montana, USA, 2011–2019 (Montana Sage Grouse Working Group 2005, State of Montana, 2015). The yellow star represents the location of the study area for this project in Golden Valley and Musselshell counties (outlined in white).

bobcats, badgers, prairie rattlesnakes (*Crotalus viridis*), and gophersnakes (*Pituophis catenifer*), as indicated by Conover and Roberts (2017) and by evidence from monitoring or kill sites in this study. Musselshell and Golden Valley counties are largely in private ownership but intermixed with federal, state, and county land used for cattle grazing with some sheep grazing and dryland farming (Smith et al. 2018*a*, *b*). Within the study area, the SGI program was implemented on private ranches containing sage-grouse habitat, defined by flat to rolling topography and sagebrush canopy cover ≥5% (NRCS, personal communication), and in areas designated as sage-grouse habitat by Montana Fish, Wildlife and Parks (Figure 1). Sagebrush cover is less in Montana than in locations farther west because stands of sagebrush in Montana are more mesic with more grass and less shrub diversity. In Montana, average shrub cover, dominated by Wyoming big sagebrush, ranges from 10% to 25%, with perennial grasses and forbs providing >25% cover (Montana Natural Heritage Program 2021).

METHODS

Chick monitoring

We found and monitored nests using females marked with radio transmitters (Burkepile et al. 2002, Dahlgren et al. 2010, Apa et al. 2017). We captured broods by hand just after sunset 1–10 days after hatching (mean = 2.8 days, SE = 0.11 days) using methods described by Dahlgren et al. 2010. Because we approached broods on foot and captured chicks by hand, we sprayed our clothes and shoes with a scent killer spray and wore latex gloves when handling chicks to minimize scent trails and transferring scent to chicks. We did not capture chicks during or immediately after rain and avoided wet conditions. We also did not capture chicks unless the temperature was 10° C or above because we thought doing so would minimize effects on chicks. We sutured a 1.3-g backpack very high frequency radio transmitter with a pulse rate of 30 pulses per minute (model A1065; Advanced Telemetry Systems, Isanti, MN, USA) on up to 4 randomly selected chicks per brood (mean number of chicks hatched per nest = 6.8, SD = 1.94, range = 2–10; Burkepile et al. 2002). This method has been the most successful (<1% accidental death rate) and common method used to attach radio transmitters to sage-grouse chicks (Burkepile et al. 2002, Dahlgren et al. 2010). Transmitters were on average <5%

of the youngest chick's body mass at the time of marking (mean chick mass up to 3 days post-hatch = 38.1 g, SE = 0.44 g), as recommended by Fair et al. (2010). We spent no longer than 30 minutes handling chicks. If marking was going to take longer, we stopped and released the brood, even if we were not done marking chicks.

We monitored chicks every other day for the first 2 weeks and ≥ 2 times per week after that until 45 days posthatch or the chicks died, their tags expired, or we lost their signals. We obtained chick locations at ≥ 30 m but did not approach <30 m to avoid flushing the brood female or chicks. If the signal was lost, we attempted to locate the transmitter by aerial telemetry for a general location, followed by a ground survey.

Female and chick covariates

We assessed chick mortality risk in relation to individual brood female characteristics and individual chick characteristics. We used brood female age and body condition index as variables in Cox proportional hazards models (analysis described in Analyses section below). We predicted that chicks would have a higher probability of mortality with yearling versus adult females because sage-grouse broods have exhibited higher survival with adults versus yearlings (Gregg 2006, Gibson et al. 2017, Pratt and Beck 2021). Further, adult sage-grouse females have higher nest success than yearlings (Connelly et al. 2011*a*), suggesting that older individuals have more experience that might translate into increased chick survival (Dinkins et al. 2014*a*). We aged brood females as either yearlings (second year) or adults (after second year) according to characteristics of primary wing feathers and weights (Braun and Schroeder 2015). Female weights may vary during their annual life cycle; thus, we used body condition only for females captured in April–May (*n* = 196 females). We recorded morphometric measures, including female mass, tarsus lengths, and natural wing chord lengths to calculate the body condition indices of females. We used a principal components analysis to combine wing chord lengths and tarsi lengths from both right and left sides (R packages FactorMineR version 2.4 [Husson et al. 2020] and stats version 4.0.0 [R Core Team 2020]). We regressed female mass on the first principal component and used the residuals as the body condition indices (Warren et al. 2014).

We also used chick body mass and sex as predictors. We recorded chick mass at the time of capture and adjusted for age by calculating the difference between the observed mass and the predicted mass (derived from a regression of all recorded chick masses versus age at capture). This yielded a residual mass adjusted for age at capture. During 2014–2017, we collected a blood quill from each chick during capture for genetic sex determination by Utah State University's Molecular Ecology Laboratory.

Spatial habitat covariates

We also explored differences in mortality risk based on habitat features, including SGI grazing program enrollment status, weather, remotely sensed vegetation, terrain, and anthropogenic disturbance covariates for each individual chick location. We determined SGI enrollment status directly from producers or the local NRCS office to assess the effects of SGI grazing management on sage-grouse chick mortality risk. Producers enrolled in the SGI program implemented a grazing system developed in coordination with NRCS range management specialists. After appropriate infrastructure needed to facilitate the grazing system was installed (e.g., fencing or water sources), the landowner implemented the prescribed grazing system for 3 consecutive years. The SGI grazing systems were implemented with primarily cow-calf operations, with one producer that grazed a mix of cattle and sheep. The systems were rotational and used a combination of rest and deferment (Hormay 1970). The SGI grazing systems varied with the unique configuration of each ranch, but all adhered to the NRCS Conservation Practice Standard for Prescribed Grazing (NRCS, 2017, Smith et al. 2018*b*). Additionally, plans aligned with 4 minimum criteria intended to support sage-grouse habitat including grazing utilization rates of ≤50% of the current year's key forage species

growth, \geq 20-day annual shift in the timing of grazing, a plan to address unexpected circumstances like drought or fire, and \leq 45-day continuous grazing durations within any one pasture (Smith et al. 2018b).

The SGI and non-SGI grazing systems occurred in individual pastures of varying sizes (mean pasture area = 2.90 km², range = 0.01-33.80 km²) intermixed across 1,516 km². Although we collected quantitative data describing grazing system metrics (e.g., number of livestock, timing of grazing), these data were provided voluntarily and were incomplete for many pastures, particularly non-SGI pastures. As a result, we elected to only use SGI enrollment status, the variable for which complete data were available. We created a spatial layer that accounted for spatial and temporal changes to the SGI enrollment status of each pasture, as the enrollment status of pastures could change annually (Berkeley et al. 2021, Reintsma 2023). We binned the SGI program in 2 distinct categories that enabled us to explore short- and long-term effects in addition to direct and indirect effects. We predicted that if sage-grouse did not respond to grazing during implementation (i.e., direct effects of grazing such as trampled nests), they might show delayed responses after grazing occurred because of changes in vegetation composition and structure (indirect effects). Our 2 categorizations (Table 1; Figure S1, available in Supporting Information) included an immediate response and a cumulative response. The immediate response included the direct effects of the grazing systems that we assessed with binary subcategories: yes for pastures actively undergoing SGI grazing and no for pastures that were never enrolled or were not actively implementing SGI grazing practices. The cumulative response included the indirect effects of the grazing systems that we assessed with 2 subcategories: nopre and post. The no-pre subcategory included pastures that were never enrolled and those that were enrolled but were being prepared to implement SGI rotation by, for example, installing fences or water (e.g., where grazing management was not yet being implemented). The post subcategory was assigned to pastures that were actively undergoing SGI grazing, or that previously underwent SGI grazing and were no longer enrolled.

We assigned individual chick locations to grazing subcategories based on the subcategory assigned to a particular pasture at the time the chick was there (Table 1). Thus, an individual could have locations in multiple subcategories, and we used time-varying analysis techniques to account for the changes in grazing subcategories.

We tested the effects of daily and monthly weather variables on chick mortality risk. Chicks cannot thermoregulate during the early post-hatch period (Aulie 1976, Pederson and Steen 1979) and rely on the female to maintain their body heat. Weather can also indirectly affect chick survival through its influence on vegetation and food availability (Wenninger and Inouye 2008, Gregg and Crawford 2009). Because precipitation and temperature have been linked to sage-grouse chick survival (Guttery et al. 2013*a*, Blomberg et al. 2014), we examined daily precipitation, minimum daily temperature, total monthly precipitation, and mean minimum monthly temperature. We extracted all weather data from DAYMET (1-km resolution; Thornton et al. 2014).

We explored vegetation metrics suggested to influence sage-grouse vital rates (Connelly et al. 2011*a*, Smith et al. 2018*a*), all at a 30-m resolution. We obtained remotely sensed vegetation metrics, including annual percent cover of annual forbs and grasses, perennial forbs and grasses, litter, and shrubs from the Rangeland Analysis Platform (Jones et al. 2021). We used Google Earth Engine (Gorelick et al. 2017) to extract annual gross primary

Grazing category	Grazing subcategory	Number unique chicks	Number of locations (all chicks combined)	Number of mortality events
Immediate response	No	453	3,393	152
	Yes	91	431	18
Cumulative response	No or pre	362	2,554	103
	Post	230	1,270	67

TABLE 1 Sample sizes of chick locations per grazing management category and subcategory for a marked population of greater sage-grouse chicks in Golden Valley and Musselshell counties, Montana, USA, 2011–2019, all years combined. Chicks could have locations in multiple subcategories.

production data, a measure of vegetative productivity (Robinson et al. 2018). Gross primary production may serve as an indicator of early brood-rearing habitat, where elevated vegetation productivity signals increased availability of forbs—a crucial resource for chick development (Smith et al. 2019). Vegetative productivity has been associated with sage-grouse habitat selection and population growth and recruitment (Blomberg et al. 2012, Dinkins et al. 2014b). We used the United States Geological Survey National Elevation data set (U.S. Geological Survey 2021) to extract slope, compound topographic index, vector ruggedness measure (VRM), and heat load index covariates. Compound topographic index is a wetness index that may indicate productive mesic areas that sage-grouse broods rely on later in the summer (Gessler et al. 1995, Aldridge and Boyce 2007). Vector ruggedness measure quantifies terrain ruggedness within a 5-pixel neighborhood (tool adapted from Hobson 1972, and Sappington et al. 2007). Sage-grouse tend to avoid rugged terrain (Fedy et al. 2014), possibly because of the prevalence of features that can provide vantage points for avian predators (e.g., hilltops, knolls, and cliff edges; Dinkins et al. 2014b). Heat load index is a measure of radiation that accounts for slope and aspect (Evans et al. 2014). Areas with higher heat loads may be important during early brood-rearing when chicks cannot thermoregulate, while areas with lower heat loads could serve as refugia during periods of hot and arid weather.

We included the distance to the nearest cropland and distance to nearest road as covariates. Sage-grouse exhibit avoidance of paved roads and areas with greater anthropogenic disturbance (Aldridge and Boyce 2007, Fedy et al. 2014); therefore, we expected proximity to cropland and roads would increase mortality risk of chicks. We calculated these covariates by measuring the distance between each chick location and the nearest major road (e.g., paved or county roads) or cropland using ArcGIS version 10.8.1 (Esri, Redlands, CA, USA). We also obtained a human disturbance index (Montana Natural Heritage Program 2022) that includes development, transportation, agriculture, resource extraction and energy development, introduced vegetation, and forestry practices.

Analyses

We performed analyses in program R version 4.0.0 (R Core Team 2020). We estimated chick survival to 45 days post-hatch using separate analyses for missing chicks (i.e., individuals whose signals were lost or had unknown fates) treated as 1) right-censored at the last date a signal was obtained and 2) treated as mortalities in a sensitivity analysis. Causes of unknown fates could include radio expiration, undetected mortality (e.g., avian predator or scavenger moves chick), or a brood-mixing event with a female without a radio-collar (Dahlgren et al. 2010). If censoring of chicks with unknown fates was non-informative, the first analysis approach minimizes bias in the estimate of chick survival. Alternatively, the second analysis approach treating chicks with unknown fates as mortalities provides a conservative estimate of chick survival by accounting for potential confounding of censorship with undetected mortalities (Lebreton et al. 1992, Millsap et al. 2004, Murray 2006, Dahlgren et al. 2010). In both analyses, we right-censored individuals that were alive at the end of the study period. For individuals found dead, we estimated the fate date as the mid-point between the last date they were found alive and the date they were found dead. We censored from analyses any individuals that we found dead within 50 m of the capture site and <48 hours after tagging to control for capture-related mortalities. We entered chicks into the analysis at age at capture and defined the nest hatch date as time zero. In calculating survival, we assumed that mortality was unaffected by transmitter attachment (Korschgen et al. 1996, Davis et al. 1999, Hagen et al. 2010, Lees et al. 2019).

We estimated an overall chick survival rate and survival as a function of female age and sex of chicks using a staggered entry Kaplan-Meier model in package survival (Therneau 2021). We used univariate Cox proportional hazards models to test for differences in mortality risk between female age, chick sex, female body condition index, and chick mass adjusted for age (coxph function in package survival in Program R; Therneau 2021). The Cox proportional hazards model computes a hazard ratio (HR), which quantifies the proportional change in the hazard rate associated with a 1-unit increase in the predictor, holding all other predictors constant, relative to baseline. We considered an HR of 1.00 as the baseline, with >1.00 indicating an increased risk of mortality, and <1.00 indicating a

decreased risk of mortality. We tested the proportional hazards assumption by examining plots of scaled Schoenfeld residuals for each covariate and assessed for significant deviations from a slope of zero (cox.zph function in package survival in Program R; Therneau and Grambsch 2000, Therneau 2021). By marking up to 4 chicks per brood, there could be intrabrood dependence, which can cause underestimation of the variance but does not bias survival or mortality risk estimates (Ringelman and Longcore 1982, Pollock et al. 1989, Flint et al. 1995). Thus, we incorporated a cluster term in all models to account for correlation among siblings and the effects of brood female condition and experience. We also calculated robust variance for the model and allowed variances to differ by brood female. Because previous research has shown the importance of chick age in survival, we included the age of chicks at capture as a continuous covariate in all Cox proportional hazards models (Dahlgren et al. 2010, Thompson 2012, Schreiber et al. 2016).

We used the Andersen-Gill formation of the Cox proportional hazards model to explore the effects of spatially dependent covariates including SGI program enrollment status, weather, vegetation, terrain, and anthropogenic disturbance (coxph function in package survival in Program R; Andersen and Gill 1982, Therneau 2021). Encounter histories for each individual chick recorded the interval between successive relocations including the beginning and end of the interval, the individual's fate at the end of the interval (e.g., right-censored or mortality), and the spatial covariate value associated with the individual's location at the end of the interval. Prior to fitting models, we assessed correlations between every pair of covariates ($r \ge 0.6$; Table S1, available in Supporting Information). We also examined the scaled Schoenfeld residuals for each spatial covariate to test the proportional hazards assumption.

We used an information-theoretic approach to assess support for Andersen-Gill models (Burnham and Anderson 2002). Specifically, we used Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Akaike 1973) to rank competing models describing variation in chick mortality risk. Prior to model development, we screened covariates by running univariate models and retaining variables when they showed improvement over the null model (i.e., intercept only model). We explored covariates retained following the initial screening in all combinations of 6 or fewer covariates, with all models including age at capture and a cluster term for brood female. Limiting models to a maximum of 6 covariates reduced the potential for model overfitting (Burnham and Anderson 2002). We used minimization of AIC_c (Δ AIC_c < 2 from best-fit model) to inform model selection. We considered models with Δ AIC_c < 2.0 differing by a single parameter from the top model or parameter estimates with 85% confidence intervals overlapping 1 for the hazard ratio to be uninformative (Arnold 2010).

RESULTS

During 2011–2019, we captured and placed transmitters on 539 sage-grouse chicks from 274 broods and 200 individual brood females (56 females had multiple broods over multiple years). The average age of chicks at capture was 2.76 ± 0.07 (SE) days and ranged from 0–10 days post-hatch. At the end of the 45-day monitoring period for all years combined, 146 chicks were alive, 161 were censored because of unknown fate (e.g., transmitter failure or disappeared), and 232 had died. We excluded 29 chicks from analyses that we considered capture-related mortalities (Table 2). Remaining mortalities were attributed to predation (n = 172), exposure (n = 29; carcass found intact within 2 weeks of tagging), and unknown causes (n = 2; Table 2). We estimated survival to 45 days using 510 radio-tagged chicks (Table 3). With all years combined, the Kaplan-Meier median survival rate was 0.511 ± 0.03 (95% CI = 0.46-0.56). The survival rate varied each year, ranging from 0.26-0.69 (Figure 2; Table 3). In the sensitivity analysis treating chicks with unknown fates as mortalities, the Kaplan-Meier survival rate estimate was 0.29 ± 0.02 (95% CI = 0.25-0.33; Table S2, available in Supporting Information).

Brood female age was uncorrelated with chick mortality risk (baseline = adult, HR = 0.87, 95% CI = 0.55–1.36), with the Kaplan-Meier survival rate for chicks with adult females at 0.50 ± 0.03 (95% CI = 0.45–0.56) compared to 0.52 ± 0.07 (95% CI = 0.38–0.66) for chicks with yearling females. Similarly, brood female body condition also was

TABLE 2	Annual sample sizes, number of mortalities, and number of censors for marked greater sage-grouse chicks in Golden Valley and Musselshell counties, Montana,
USA, 2011–2019. M	2019. Mortality and censors are subdivided into specific causes.

		Mortalities					Censors				
Year	Chicks marked Capture-related	Capture-related	Predation	Exposure	Unknown	Total	Signal lost	Dropped tag	Tag expired	Unknown	Total
2011	23	1	5	т	0	6	2	1	e	5	11
2012	81	2	37	2J	1	45	18	0	0	2	20
2013	59	6	16	4	0	26	6	2	0	12	23
2014	77	4	17	1	0	22	2	с	1	32	38
2015	58	4	11	2	1	18	12	0	0	1	13
2016	45	2	16	5	0	23	1	0	2	7	10
2017	84	1	29	1	0	31	4	1	0	24	29
2018	52	1	27	7	0	35	З	1	0	6	10
2019	60	8	14	1	0	23	1	0	0	6	7
All years	539	29	172	29	2	232	52	8	6	95	161

2011-2017.					
Year	Chicks in analysis	Mortality events	Survival rate	SE	95% CI
2011	22	8	0.45	0.16	0.09-0.76
2012	79	43	0.34	0.06	0.21-0.46
2013	53	20	0.48	0.09	0.30-0.66
2014	73	18	0.63	0.07	0.48-0.78
2015	54	14	0.69	0.07	0.55-0.83
2016	43	21	0.43	0.09	0.25-0.60
2017	83	30	0.55	0.06	0.41-0.67
2018	51	34	0.26	0.07	0.09-0.39
2019	52	15	0.69	0.07	0.56-0.82
All years	510	203	0.51	0.03	0.46-0.56

TABLE 3 Kaplan-Meier 45-day survival rate estimates, standard errors (SE), and 95% confidence intervals (CI) by year for marked greater sage-grouse chicks in Golden Valley and Musselshell counties, Montana, USA, 2011–2019.

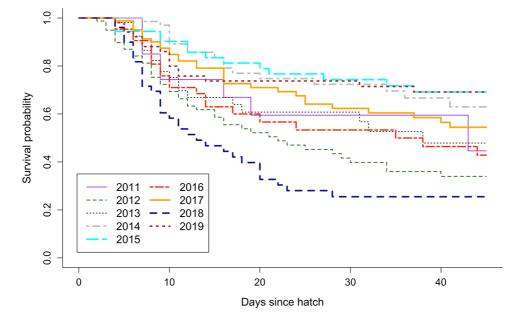


FIGURE 2 Kaplan-Meier survival curves by year (2011–2019) for marked greater sage-grouse chicks in Golden Valley and Musselshell counties, Montana, USA. The 95% confidence intervals were removed to facilitate interpreting the figure.

unassociated with chick mortality (HR = 1.00, 95% CI = 1.00–1.00, P = 0.21). During 2014–2017, we identified the sex of 246 chicks: 118 females and 128 males. The sex of chicks did not significantly affect mortality risk (baseline = female, HR = 1.24, 95% CI = 0.79–1.95). The Kaplan-Meier survival rate for male chicks was 0.54 ± 0.05 (95% CI = 0.44–0.65 days) and for female chicks was 0.62 ± 0.05 (95% CI = 0.52–0.73). There was a small protective effect of chick body mass on mortality risk, suggesting the hazard decreased by approximately 2.3% for every 1-g increase in chick mass at initial capture when adjusted for age (HR = 0.98, 95% CI = 0.96–1.00). All female and chick

morphometric covariates met the proportional hazards assumption. The sensitivity analysis yielded lower survival rate estimates in the Kaplan-Meier models and comparable results for Cox proportional hazards models (Tables S3–S4, available in Supporting Information).

Preliminary covariate screening procedures indicated that the distance to the nearest road, distance to cropland, mean minimum monthly temperature, slope, and SGI cumulative response had more model support than the null model (Table S5, available in Supporting Information). We used these variables to build our final candidate model set, which included 32 models (Table 4). Based on inspection of plotted Schoenfeld residuals, spatial covariates met the proportional hazards assumption. Of the 32 models evaluated, our data supported 4 models, though there was considerable model uncertainty (Table 4). The remaining models had >2 ΔAIC_c relative to the best model. The SGI cumulative response appeared in 2 of the top models and accounted for 47% of the cumulative weight across all models. We considered one of these models uninformative because it was within 2 ΔAIC_c of the top model with only 1 parameter difference (Table 4). In the other model, the SGI cumulative response parameter estimate was uninformative (HR = 1.27, 85% CI = 0.96-1.69). There was no evidence for an effect of remotely sensed vegetation covariates on mortality risk. The best model contained the distance to nearest road, distance to nearest cropland, and mean minimum monthly temperature. Distance to nearest road (HR = 1.00, 85% CI = 1.00-1.00) and distance to nearest cropland (HR = 1.00, 85% CI = 1.00-1.00) had negligible effects on mortality risk (Table 5). There was a slight effect of mean minimum monthly temperature on mortality risk, where every 1°C increase in mean minimum monthly temperature increased mortality risk by 1.09 times (HR = 1.09, 85% CI = 1.01–1.17). Slope was present in 2 of the top models and accounted for 53% of the cumulative weight across all models (Table 4). One of the models including slope was uninformative and parameter estimates were uninformative in the other model (HR = 1.01, 85% CI = 1.00-1.01).

In the sensitivity analysis, distance to the nearest road, distance to cropland, mean minimum monthly temperature, slope, and VRM performed better than the null model. There were 8 models supported by data, but there was greater model uncertainty than in the first analysis where chicks with uncertain fates were right-censored (Table S6, available in Supporting Information). The best model contained the distance to nearest cropland, mean minimum monthly temperature, slope, and VRM (Tables S6–S7, available in Supporting Information). Mean minimum monthly temperature again showed a weak effect with a 1.07 times higher risk per 1°C increase (HR = 1.07, 85% CI = 1.01-1.13). Slope (HR = 1.01, 85% CI = 1.00-1.01) and VRM (HR = 2.01, 85% CI = 0.93-2.33) were both uninformative, and the effects of distance to cropland were negligible (HR = 1.00, 85% CI = 1.00-1.00). There was no evidence for remotely sensed vegetation or SGI enrollment effects on mortality risk.

DISCUSSION

Our study provides evidence that the SGI grazing program in central Montana does not confer additional benefits to sage-grouse chicks beyond existing grazing practices. We also demonstrate, contrary to our predictions, that several morphometric and environmental variables did not influence chick mortality risk.

Chick survival is a key vital rate influencing population growth and persistence for gallinaceous species, including sage-grouse (Wisdom and Mills 1997, Sandercock et al. 2008, Hagen et al. 2009, Schole et al. 2011, Taylor et al. 2012). We are unaware of any previous research that evaluates this vital rate in relation to livestock grazing management. Our estimates of chick survival to 45 days were relatively high compared to survival rates reported across the species' range. For example, Aldridge and Boyce (2007) estimated 56-day chick survival at 0.12 in Alberta, Canada. Estimates from 42–49 days post-hatch ranged from 0.25–0.60 in Great Basin populations (Dahlgren et al. 2010, Baxter et al. 2013, Guttery et al. 2013*a*). Additionally, 112-day chick survival estimates in Colorado, USA, varied between 0.088–0.446 (Thompson 2012). Our sensitivity analysis treating chicks with unknown fates as mortalities yielded a more conservative overall survival estimate (0.29). We observed substantial

TABLE 4 Model selection results for Andersen-Gill models assessing mortality risk in relation to habitat characteristics for marked greater sage-grouse chicks in Golden Valley and Musselshell counties, Montana, USA, 2011–2019. Model covariates included the Sage Grouse Initiative (SGI) grazing program cumulative response (cumSGI), mean minimum monthly temperature (tminMO), distance to the nearest road (road), distance to the nearest cropland (cropland), and slope. All models included a covariate for chick age at capture and a cluster term for brood female. The number of parameters (*K*), Akaike's Information Criterion adjusted for small sample sizes (AIC_c) values, ΔAIC_c values, model weights (*w_i*), and log-likelihoods (LL) are reported.

Model	к	AIC _c	ΔAIC_c	Wi	LL
Road + cropland + tminMO	4	1,636.77	0.00	0.20	-814.38
Road + cropland + tminMO + slope	5	1,636.96	0.19	0.19	-813.47
Road + cropland + tminMO + slope + cumSGI	6	1,637.29	0.52	0.16	-812.63
Road + cropland + tminMO + cumSGI	5	1,637.73	0.96	0.13	-813.86
Cropland + tminMO + slope + cumSGI	5	1,639.80	3.03	0.04	-814.89
Road + cropland	3	1,639.86	3.09	0.04	-816.93
Road + cropland + slope	4	1,639.97	3.20	0.04	-815.98
Road + cumSGI + slope + tminMO	5	1,640.88	4.11	0.03	-815.43
Road + cropland + cumSGI + slope	5	1,641.15	4.38	0.02	-815.57
Road + cropland + cumSGI	4	1,641.47	4.70	0.02	-816.73
Cropland + cumSGI + tminMO	4	1,641.67	4.89	0.02	-816.83
Road + slope + tminMO	4	1,641.75	4.98	0.02	-816.87
Cropland + slope + tminMO	4	1,641.82	5.05	0.02	-816.90
Road + tminMO	3	1,641.99	5.22	0.02	-817.99
Road + cumSGI + tminMO	4	1,642.04	5.27	0.01	-817.01
Cropland + tminMO	3	1,642.62	5.85	0.01	-818.31
CumSGI + slope + tminMO	4	1,643.70	6.93	0.01	-817.85
Road + slope	3	1,643.76	6.99	0.01	-818.88
Road	2	1,643.98	7.21	0.01	-819.99
Road + cumSGI + slope	4	1,644.01	7.24	0.01	-818.00
Road + cumSGI	3	1,644.92	8.14	0.00	-819.45
Cropland + cumSGI + slope	4	1,645.29	8.52	0.00	-818.64
Cropland + slope	3	1,645.99	9.22	0.00	-819.99
CumSGI + tminMO	3	1,646.63	9.86	0.00	-820.31
Cropland	2	1,647.01	10.24	0.00	-821.50
Cropland + cumSGI	3	1,647.25	10.48	0.00	-820.62
Slope + tminMO	3	1,647.74	10.97	0.00	-820.86
CumSGI + slope	3	1,648.45	11.68	0.00	-821.22
TminMO	2	1,649.26	12.49	0.00	-822.63
Slope	2	1,650.92	14.15	0.00	-823.46
CumSGI	2	1,651.31	14.54	0.00	-823.65
Null	0	1,672.29	35.52	0.00	-836.15

Covariate	β	HR	Robust SE	85% CI
Distance to nearest road (m)	0.00	1.00	0.00	1.00-1.00
Distance to nearest cropland (m)	0.00	1.00	0.00	1.00-1.00
Mean minimum monthly temperature (°C)	0.08	1.09	0.05	1.01-1.17
Age at capture (days)	-0.29	0.75	0.07	0.67-0.83

TABLE 5 Parameter (β) estimates, hazard ratios (HR), robust standard errors (SE), and 85% confidence intervals (CI) for covariates in the top Andersen-Gill model used to assess mortality risk relative to habitat characteristics for marked greater sage-grouse chicks in Golden Valley and Musselshell counties, Montana, USA, 2011–2019.

interannual variation in chick survival from a low of 0.26 in 2018 to a high of 0.69 in 2015 and 2019, a pattern consistent with previous sage-grouse research (Gibson et al. 2017).

The SGI management strategy we evaluated seems similar in practice to other management strategies that manipulate sage-grouse habitat because they are assumed to benefit the species, but their efficacy has not been evaluated. One example is reducing sagebrush canopy cover for the assumed benefit of sage-grouse, particularly for sage-grouse broods (Smith et al. 2023). Smith et al. (2023) conducted an experimental study in Wyoming to determine if treatments to reduce sagebrush canopy cover benefited sage-grouse demography or resource selection. Similar to this study, Smith et al. (2023) showed that sage-grouse had a neutral response to this management strategy. What Smith et al. (2023) and similar studies illustrate, including this study and Smith et al. (2018a, b), is the response of target species to management strategies should be evaluated before broad-scale implementation, as was the case with the rotational grazing management program of SGI. The initial rollout of SGI involved implementation of a series of different management approaches in different focal areas along with accompanying research (and funding) to evaluate the effectiveness of each management approach. Our study area represented the focal area for rotational grazing management, and was the only place that kind of large-scale, targeted approach was implemented. Previous publications and agency reports suggested similar results to what we report here (Smith et al. 2018a, b; Berkeley et al. 2021). Based on close communication and collaboration among our research team and SGI program managers, NRCS reduced their investment in rotational grazing management plans to benefit sage-grouse across the West because studies did not conclude that sage-grouse or their habitat benefitted from these plans as originally predicted. The biological benefits for sage-grouse were not as clear as other habitat management practices in the SGI portfolio (Severson et al. 2017, Silverman et al. 2019, Olsen et al. 2021), so SGI program investments now focus on those practices.

While there are some parallels between our study and Smith et al. (2023), one main difference is knowledge at the outset of each study: the known, negative effects of treatments employed to reduce sagebrush canopy cover on sage-grouse demographics (Connelly et al. 2000*a*, Beck et al. 2012, Hess and Beck 2012) versus the effects of properly managed grazing that have been reported in the literature. Davies et al. (2011) and Chambers et al. (2016) report benefits of grazing characterized by practices that incorporate rest or growing season deferment on sage-grouse habitat and that maintain or increase diverse native perennial vegetation communities. We found no evidence that the SGI grazing system influenced mortality risk of sage-grouse chicks. The SGI grazing system was designed to improve sage-grouse habitat by administering more temporally and spatially variable and conservative grazing practices that were hypothesized to produce greater vegetative cover and variability in grass and forb height. Accordingly, we expected SGI enrollment status would elicit varying chick mortality risk responses based on vegetative differences between SGI and non-SGI grazing systems. Smith et al. (2018*b*) reported negligible vegetation differences between SGI and unenrolled grazing systems in our study area during 2011–2016 (Smith et al. 2018*b*). Furthermore, the absence of SGI program effects on chick mortality risk may be a product of a more productive, grazing-resilient system in our study area relative to more arid regions within the sage-grouse range (e.g., Great Basin; Robinson et al. 2018). Temperature and moisture conditions strongly shape rangeland productivity (Reintsma 2023).

Thus, interannual fluctuations in weather likely generate greater habitat variation that is more relevant to chick mortality risk than grazing management. Grazing management that used more available forage or occurred during a drought year might show more pronounced short-term grazing effects (Patel-Weynand et al. 2019). Collectively, these findings indicate that the SGI grazing program did not induce habitat changes that affected chick mortality risk.

The producer-specific, adaptable nature of grazing plans under the SGI program may have limited our ability to detect SGI program effects. All SGI plans adhered to the same criteria regulating the timing, intensity and duration of grazing, but individual ranches could differ in specific grazing actions they used to satisfy these criteria. For example, an SGI-enrolled pasture may have deferred grazing until late summer the first year, grazed in early spring the second year, and rested the pasture during the third year. A separately enrolled pasture could have followed a different multi-year rotation. Additionally, flexible enrollment resulted in a shifting mosaic of SGI and non-SGI pastures, as ranches entered and exited the SGI program throughout the 9-year study period (Smith et al. 2018*b*). As a result, we were unable to collect adequate samples for identical grazing rotations. Finally, the relatively short period (3 years) during which SGI grazing plans were implemented may have been too brief for measurable shifts in vegetative conditions to occur (Copeland et al. 2021).

The SGI was developed to benefit nesting habitat, and pastures with $\geq 5\%$ sagebrush cover were considered potential nesting habitat. This definition is not supported by the literature (Connelly et al. 2000*b*, 2011). In central Montana, nests were located in areas with $\geq 15\%$ canopy cover (Wallestad and Pyrah 1974) and Wallestad (1975) showed that 90% of used brood habitat during June and July had 10–25% sagebrush cover. Other studies across the range of sage-grouse have demonstrated that sage-grouse use, even with variation among life-history stages, typically occurs in areas of $\geq 10\%$ cover (Connelly et al. 2011*b*). Habitat use during brood-rearing occurs in areas of less sagebrush cover; early brood-rearing habitat is closely associated with nesting habitat (Connelly et al. 2000*b*). Defining areas with $\geq 5\%$ sagebrush cover as nesting habitat suggests an incomplete understanding of sage-grouse habitat needs and may be at least partially responsible for the failure of SGI grazing systems to reduce chick mortality risk (this study) or improve nest success (Smith et al. 2018*b*). Consequently, it is not surprising that SGI grazing systems did not reduce chick mortality risk.

Because the response of chick mortality risk to vegetation is sensitive to spatial scale (Aldridge and Boyce 2008, du Toit 2010), our grazing (annual, pasture-level) and remotely sensed vegetation covariates (annual, 30-m resolution) may have been too coarse to adequately measure the influence of grazing on chick mortality risk. The specific mechanisms linking grazing to both vegetation and chick mortality risk, like forb availability and concealment from predators, may only emerge at a finer spatial scale more closely aligned with chick movements. Indeed, some studies have documented an association between sage-grouse chick survival and fine-scale food availability and vegetation characteristics (Gregg and Crawford 2009, Gibson et al. 2017). Examining chick mortality risk relative to finer temporal and spatial measures of both grazing occurrence and vegetation patterns (e.g., shrub cover), regional climate, and availability of mesic areas, may regulate chick survival beyond the spatial extent we considered. Resource and grazing management typically occur at larger scales (Roche et al. 2015), making the attainment of precise fine-scale metrics challenging. Ultimately, incorporating multiple spatial scales will likely be the most informative approach to understanding chick survival responses to grazing (Londe et al. 2019, Stevens et al. 2023).

Contrary to our prediction that chicks would experience lower mortality risk with adult females, brood female age was not associated with chick mortality risk. The relationship between female age and chick survival has been examined in previous studies with varying outcomes. Pratt and Beck (2021) reported higher survival rates for broods with adult females compared to those with yearling females, whereas Guttery et al. (2013*a*) and Dahlgren et al. (2010) found the inverse to be true. Consistent with our results, other studies have found limited support for an association between female age and chick survival (Baxter et al. 2013, Davis et al. 2016). Mixed results have also been reported in other gallinaceous species (Riley et al. 1998, Fields et al. 2006, Ludwig et al. 2010, Barker et al. 2022). The varying outcomes of these prior studies, along with our findings, suggest that the effect of brood female age on chick survival may depend on the specific population and location.

Our results did not support differential survival between male and female chicks. Some researchers have reported no significant differences in sage-grouse chick and juvenile survival between sexes (Thompson 2012, Guttery et al. 2013b, Hagen et al. 2018). Conversely, several studies have demonstrated higher survival in juvenile sage-grouse females compared to males (Swenson 1986, Zablan et al. 2003, Caudill et al. 2014, Apa et al. 2017). The greater sexual dimorphism exhibited in sage-grouse, capercaillie (*Tetrao urogallus*), and black grouse (*Tetrao tetrix*) requires a higher energy expenditure from males, who grow much faster and larger than females (Lindén 1981, Swenson 1986). The larger sex, typically males in grouse species, may also be more vulnerable to decreased survival when habitat quality is poor or during years when resources are limited or weather is unfavorable (Maynard Smith 1980, Slagsvold et al. 1986, Teather and Weatherhead 1989). This negative relationship between male survival and poor habitat quality has been observed in capercaillie and black grouse (Wegge 1980, Caizergues and Ellison 1997). Studies demonstrating greater female survival in sage-grouse have primarily focused on juvenile survival, rather than chick survival (Swenson 1986, Zablan et al. 2003, Caudill et al. 2014, Apa et al. 2017). The greater demands and subsequent effects of sexual dimorphism may not manifest until the fall when chicks transition to brood independence. Thus, sex-related differences in survival may vary across developmental stages.

We detected a small protective effect of greater chick mass at capture, adjusted for age, on mortality risk. Chick mass has been identified as an important factor influencing early survival for several gallinaceous species including sage-grouse (Thomspon et al. 2015), Columbian sharp-tailed grouse (*Tympanuchus phasianellus* ssp. *columbianus*; Barker et al. 2022), northern bobwhites (*Colinus virginianus*; Lusk et al. 2005), and lesser prairie chickens (*Tympanuchus pallidicinctus*; Pitman et al. 2006). Greater mass may confer survival advantages via enhanced ability to thermoregulate and evade predation in the crucial early weeks after hatching (Rhymer 1983, Anderson and Alisauskas 2001). Chick mass may be determined by pre-hatch incubation conditions and food availability, where suboptimal incubation temperatures and inadequate nutrition can limit chick growth (DuRant et al. 2013, Belnap et al. 2019). Consequently, land uses that reduce disturbance for nesting females and optimize food resource availability for chicks may support higher chick survival through production of heavier, faster-growing chicks (Jørgensen and Blix 1985, Park et al. 2001, Gregg and Crawford 2009, Blomberg et al. 2013).

Given the substantial interannual variability we observed in chick survival and the established connection between weather and chick survival, we anticipated more pronounced effects of precipitation and temperature. We found marginal support for an association between reduced chick mortality risk and lower mean minimum monthly temperature. Chick survival has also been shown to benefit from lower monthly temperatures in other regions (Guttery et al. 2013*a*, Blomberg et al. 2014). These results suggest that lower minimum temperatures increase soil moisture, which contributes to heightened forb production and higher quality brood-rearing habitat (Bates et al. 2006, Engda et al. 2016). We did not find evidence for precipitation effects on chick mortality risk. Precipitation has been shown to negatively affect chick survival in other gallinaceous species. For instance, inclement weather or extreme precipitation events reduced survival rates of greater prairie chicken (*Tympanuchus cupido*) and sharp-tailed grouse chicks (*Tympanuchus phasianellus*) during the first few weeks post-hatch (Goddard and Dawson 2009, Schole et al. 2011). Conversely, higher moisture or decreased drought has been shown to increase sage-grouse chick survival and brood success in more arid regions (Guttery et al. 2013*a*, Blomberg et al. 2014, Caudill et al. 2014, Gibson et al. 2017).

No anthropogenic variables explored were associated with chick mortality risk. We expected to find heightened mortality risk closer to croplands (Coates et al. 2016). While distance to cropland was present in all the top models, we estimated negligible effects on chick mortality risk. Cropland has been established as a limiting factor for sage-grouse at broad scales, where lek occurrence and persistence are negatively correlated with increasing cultivation (Walker et al. 2007, Smith et al. 2016). Aldridge and Boyce (2007) found females and broods tended to avoid areas near cultivated land but found no effect of proximity to cropland on chick survival. Manzer and Hannon (2008) also did not find an effect of cropland on Columbian sharp-tailed grouse chick survival. The effects of cropland may be less important at fine scales given the dynamic movements of precocial sage-grouse chicks. Similarly, we expected chick mortality risk to increase with proximity to roads. Extensive research has established the negative effects of roads on sage-grouse, including nest success (Smith et al. 2018*a*), brood survival (LeBeau et al. 2017), population

occurrence (Shirk et al. 2017), and lek persistence (Blickley et al. 2012). Our results indicate proximity to roads does not translate to higher chick mortality risk. Other forms of anthropogenic disturbance, such as tall structures (e.g., powerline poles or fence posts) that provide perches or travel corridors for predators (Cutting et al. 2019, Geaumont and Graham 2020), may have greater effects on chick mortality and merit further investigation.

MANAGEMENT IMPLICATIONS

Because there was a neutral response of sage-grouse to SGI grazing management practices, we recommend protecting large expanses of intact sagebrush over employing particular grazing management practices. Moreover, our results underscore the importance of evaluating conservation and management programs to better predict their success or failure before broad-scale implementation. Specifically for metrics such as chick survival, we recommend collecting vegetation metrics on the ground when evaluating land management programs rather than using remotely sensed data. Regarding sage-grouse chick survival and grazing, we also recommend that managers continue to promote and incentivize grazing management strategies that adhere to fundamental rangeland health principles, while incorporating the unique ecological contexts of each region. This will provide the social benefit that accrues from involving private landowners in sage-grouse conservation actions and help conserve the remaining large, intact tracts of sagebrush grasslands while acknowledging the limited effect of SGI rest-rotation grazing programs on chick survival and other sage-grouse vital rates.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All animal handling was approved under University of Montana's Institutional Animal Care and Use Committee Animal Use Protocols 011-14DNWB-031914 (2011-2016), 006-17DNWB-021017 (2017) and 009-18VDWB-031418 (2018-2019).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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