

CONTRIBUTED PAPER

Greater sage-grouse dynamics are influenced by winter temperature rather than indices of grazing, drought, and breeding season weather in a northern Great Plains population

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Abstract

High climatic variability and livestock grazing are ubiquitous across greater sage-grouse (*Centrocercus urophasianus*) range and may influence the population dynamics of this imperiled rangeland species. We examined how annual variability in climate, vegetation productivity, grazing intensity, and conservation grazing program enrollment influenced a greater sage-grouse population in a 1500-km² rangeland landscape in central Montana (2002–2022). Using a Gompertz density-dependent population model, we found that winter temperatures positively influenced annual population dynamics (standardized coefficient = 0.18; 95% CRI: 0.02–0.34). We found no clear evidence that annual dynamics were influenced by variation in the previous year's breeding season weather, drought indices, or remotely sensed rangeland productivity, unlike findings documented in other parts of sage-grouse range (e.g., Great Basin). We found no compelling evidence that landscape-scale variation in grazing intensity or percent area enrolled in 3-year conservation grazing program contracts affected populations. Our results suggest that, in a relatively intact rangeland of the northern Great Plains, drought sensitivity and prevailing grazing management did not limit populations. Strategies to protect or expand intact rangelands including those that encompass winter habitat should be evaluated further.

KEYWORDS

Centrocercus urophasianus, climatic variability, conservation grazing, drought, population dynamics, vegetation productivity

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1 | INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) populations in North America have declined substantially since the mid-20th century due to range-wide habitat losses and degradation, highlighting the urgent need for effective conservation strategies (Connelly et al., 2004; Connelly & Braun, 1997; Garton et al., 2011). High climatic variability and livestock grazing across the sage-grouse range (Dettenmaier et al., 2017) may also have important implications for their population dynamics. While climatic effects on sage-grouse are well documented in parts of their range (e.g., Coates et al., 2018; Lundblad et al., 2022; O'Neil et al., 2025), their broader applicability and magnitude remain unclear. Similarly, although conservation-focused grazing management has been proposed to benefit sage-grouse and other imperiled rangeland species (DelCurto et al., 2023), its benefits for sage-grouse populations are not yet clearly established. A better understanding of these factors across sage-grouse range is essential for interpreting population trends and developing effective conservation strategies to improve habitat.

Climatic variation can affect sage-grouse adults, their nests, and their offspring directly through thermoregulatory challenges or indirectly through habitat and forage productivity. Direct effects of below average temperatures or above average precipitation during the nesting and early brood-rearing seasons may negatively influence nests (Dinkins et al., 2016; Moynahan et al., 2007; Smith et al., 2018a; Street et al., 2022) or chicks with limited thermoregulatory capacity (Aulie, 1976; Pederson & Steen, 1979). Severe winters have been documented to negatively affect sage-grouse survival at the northern extent and high-elevation portions of the sage-grouse range (Dzialak et al., 2013; Moynahan et al., 2006). However, it is unclear whether these vital rate effects translate to measurable effects on annual population growth.

Precipitation variability is strongly correlated to primary productivity in the arid sagebrush steppe (Donnelly et al., 2018; Reintsma et al., 2024), potentially creating indirect effects on sage-grouse populations through habitat changes. Drought, characterized by persistent below average precipitation or above average temperatures, may reduce vegetative nesting cover and limit the availability of forage-rich mesic areas critical for brood-rearing hens (Donnelly et al., 2018; Severson et al., 2022). Precipitation effects on vital rates and population growth have been documented in Great Basin sage-grouse populations (Blomberg et al., 2012; Coates et al., 2018; Gibson et al., 2016; Guttery et al., 2013; Lundblad et al., 2022; O'Neil et al., 2025), which supports the hypothesis that climate-driven sage-grouse dynamics are mediated by vegetation productivity (Donnelly et al., 2018; Severson

et al., 2022). Similar patterns have not yet been consistently observed in other regions such as the Great Plains (Berkeley et al., 2024).

Livestock grazing is the dominant land use in sagebrush steppe habitats (Dettenmaier et al., 2017) and can alter the vegetation community composition, structure, and productivity (Davies et al., 2010; Davies et al., 2018; Krausman et al., 2009; Manier & Hobbs, 2007; Reintsma et al., 2024). Habitat management for sagebrush-dependent wildlife can be achieved through specific grazing management regimes (Chambers et al., 2017; Connelly et al., 2004; Fuhlendorf & Engle, 2001), although outcomes may vary based on regional and site-specific conditions (Johnson et al., 2012; Kraft et al., 2021; Malm et al., 2020; Milchunas & Lauenroth, 1993; Vermeire et al., 2008). Studies of grazing effects on sage-grouse breeding success have shown mixed results. Several studies have not found clear grazing effects on nest success (Conway et al., 2025; Dettenmaier, 2018; Smith et al., 2018a, 2018b), whereas Cutting et al. (2019) found decreased nest survival with increasing grazing intensity. Neither Conway et al. (2025) nor Berkeley et al. (2024) found grazing intensity effects on chick survival. However, Monroe et al. (2017) described both positive and negative grazing effects on annual population growth rates, depending on timing of grazing and underlying vegetation productivity.

The Natural Resource Conservation Service's (NRCS) Sage Grouse Initiative (SGI) implemented a rest-rotation conservation grazing incentive program in central Montana over a period of 10 years. Its primary objectives were to help producers adopt sustainable grazing practices that enhance sage-grouse habitat, improve rangeland health, and maintain operational ranches. Early evaluations of the effects of this conservation-based grazing program (hereafter referred to as CGP) have not found benefits to nest or chick survival (Berkeley et al., 2024; Smith et al., 2018a, 2018b), and no selection preference from breeding females (Helm, 2023). However, a comprehensive assessment of effects on annual population growth rates has yet to be completed. Population growth analysis should not be overlooked as vital rate effects may be difficult to detect individually but have meaningful cumulative influence (Milligan & McNew, 2022), and also because affected vital rates can be compensated for in other parts of the annual cycle, muting their impact on population growth rate.

We assessed the relative effects of climatic variability and grazing on sage-grouse population dynamics using 21 years (2002–2022) of sage-grouse lek monitoring, climate, and remotely sensed vegetation data along with 10 years (2011–2020) of detailed grazing management data and 11 years (2010–2020) of CGP enrollment. We

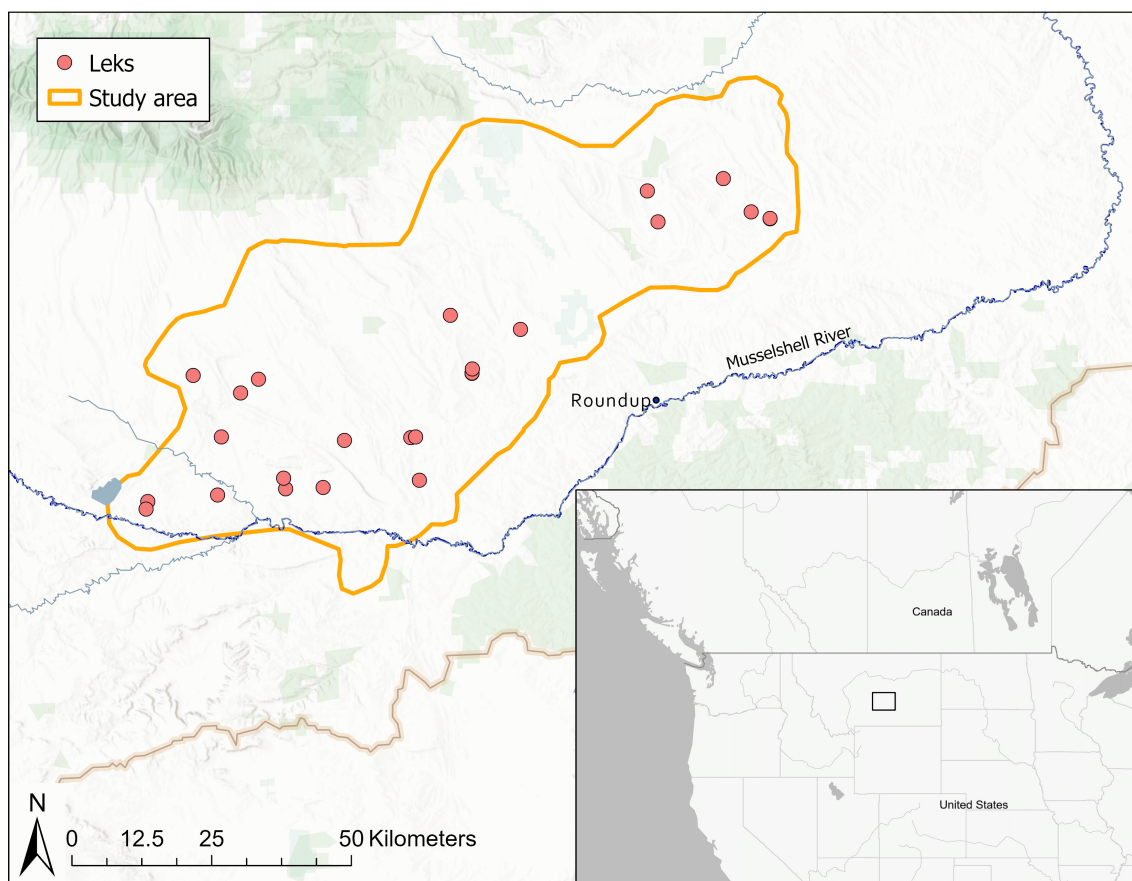


FIGURE 1 Map showing the study area boundary where climatic, vegetation, and grazing data were collected. Sage-grouse abundance was monitored at lek locations (blue dots). The study area encompasses portions of Musselshell, Golden Valley, and Petroleum counties, Montana USA, 2002–2022.

evaluated several non-mutually exclusive hypotheses for annual factors that could affect sage-grouse annual growth rates: (1) direct effects of weather during critical nesting and brood rearing periods, (2) direct effects of winter severity, (3) habitat-mediated effects of precipitation, drought, and overall vegetation productivity, (4) habitat-mediated effects of grazing intensity, and (5) habitat-mediated effects of the percent of rangelands enrolled in a CGP. Further, we conduct these analyses at the study area population scale, which is generally the scale used for large-scale, long-term monitoring. These analyses will help distinguish the relative roles of climatic variability and grazing management in a northern area of sage-grouse range.

2 | METHODS

2.1 | Study area

The study area was in central Montana in rolling topography that ranged from 975 to 1250 m in elevation and

covered approximately 150,000 ha in Musselshell, Golden Valley, and Petroleum counties (Figure 1). 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, 2018b; 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). Average monthly temperatures from the Roundup, MT weather station near the study area ranged from -3.8°C (January) to 21.8°C (July), and average annual precipitation was 37.8 cm (1991–2020 data; National Centers for Environmental Information, 2024). Potential predators of adult sage-grouse in our study area include golden eagles (*Aquila chrysaetos*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), red foxes (*Vulpes vulpes*), bald eagles (*Haliaeetus leucocephalus*), great horned owls (*Bubo virginianus*), and badgers (*Taxidea taxus*) (Berkeley et al., 2024; Smith et al., 2018a). The study area was largely private ownership but was intermixed with federal, state, and county

land used for cattle grazing, with some sheep grazing and dryland farming (Smith et al., 2018a, 2018b).

Within the study area, the CGP was implemented on private ranches designated as sage-grouse habitat, which was defined by Montana Fish, Wildlife and Parks as sagebrush canopy cover $\geq 5\%$ (NRCS, personal communication). Sagebrush cover is lower in Montana than in locations farther south and west because stands of sagebrush are often more mesic with more grass and fewer shrubs. 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). Further, in our study area, sagebrush cover can be even lower, particularly in portions dominated by silver sagebrush.

2.2 | Indexing study area population size

We obtained counts of male sage-grouse at 20 surveyed lek sites (Figure 1) from Montana Fish, Wildlife and Parks for the years 2002–2022 (Data S1). Trained observers surveyed leks 1–9 times each spring (mean visits = 3.6, SD = 1.3) from mid-March through the first week of May and completed male counts from 0.5 h before sunrise to 2 h after following standardized protocol (Montana Sage Grouse Work Group, 2005). Observers were instructed to obtain accurate male counts with binoculars or spotting scope from a distance that would not disturb lek behavior and from a vantage point that minimized visual obstruction. Data from temporary satellite leks (leks with ≤ 2 years of consecutive use; Haukos & Smith, 1999) were excluded because there was no consistent protocol to search and discover these. Comparison of annual total maximum male lek counts for the study area with and without the satellite lek counts were highly correlated ($r = 0.96$), indicating our decision to exclude them from further analysis was unlikely to obscure the underlying population dynamics signal in the data. To produce annual, study area-scale male population estimates, we used an N-mixture model developed by McCaffery et al. (2016) specifically for lek count data from a similar sampling design. Male lek attendance rate is not 100% on a daily or seasonal basis and subadult males have lower attendance rates (Fremgen et al., 2019; Walsh et al., 2004; Wann et al., 2019), and we did not attempt to estimate the female population size, so our estimates are an index of abundance. While N-mixture models are believed to be a robust method to interpret repeated lek counts where detection probability < 1 (McCaffery et al., 2016; Ross et al., 2019), we also compared this population index to a simpler index, the annual mean of the maximum counts across all leks, and found a high correlation ($r = 0.98$). We used the N-mixture model

population index and measures of uncertainty as input in our population model described below. We fit this model using JAGS (Plummer, 2003) interfaced through the R2jags package (Su & Yajima, 2024) in R version 4.4.0 patched (R Core Team, 2024), using three chains of 100,000 iterations each, a burn-in of 5000, and a thinning rate of 10. We assessed model convergence by visually inspecting trace plots for good mixing and confirming that the potential scale reduction factor (R^2) was close to 1 indicating adequate convergence (Gelman & Rubin, 1992). We evaluated model fit using a posterior predictive check based on a chi-squared discrepancy statistic where a posterior predictive p -value between 0.1 and 0.9 was considered to indicate adequate fit to the data (Gelman et al., 2014).

2.3 | Covariates

2.3.1 | Seasonal weather and drought conditions

We extracted all weather data from Daymet (daily 1-km resolution; Thornton et al., 2020). We separated breeding season weather into 3 separate windows based on our study area's breeding chronology (Simpson et al., 2024): nesting (April 15–May 31), early brood-rearing (May 22–July 6), and late brood-rearing (July 22–September 6) for which we extracted mean minimum daily temperatures and cumulative precipitation (Table 1). We also considered interactions between temperature and precipitation over the same calendar windows, given that cold wet springs common to the northern Great Plains may negatively affect nest survival more than relatively warmer wet springs. For the winter season, we averaged minimum daily winter temperatures over the period of January 1–March 15 and estimated an index of snow cover using mean snow water equivalent (SWE) estimates from Daymet (direct estimates of snow cover at matching resolutions were not available). We tested for an interaction of temperature and SWE as an indicator of overall winter severity. We matched seasonal weather data to the breeding season or winter immediately preceding the spring lek count.

We extracted Palmer drought severity index (PDSI; Palmer, 1965) from Climate Engine (2024) as an index of drought conditions. PDSI values are calculated using a modified version of the Palmer formula, which uses reference evapotranspiration and precipitation from Gridmet (Abatzoglou, 2013) and a static soil water holding capacity layer (top 1.5 m) from STATSGO (Rhee & Carbone, 2007). As such, PDSI is a more mechanistic representation of soil moisture conditions and presence of drought than a simple summary of precipitation and temperature, and it also

TABLE 1 Annual covariates representing direct and indirect effects of seasonal weather, drought, vegetation productivity, grazing intensity, and conservation grazing program (CGP) enrollment and hypothesized relationships with annual population growth rates for the central Montana study area.

Covariate	Covariate windows	Source	Hypotheses
Mean daily minimum temperature	Nesting season: April 15–May 31 Early brood-rearing: May 22–July 6 Late brood-rearing: July 22–September 6 Winter: January 1–March 15	Daymet (2002–2022)	Warmer conditions may favor higher nest and early brood survival, but higher values in late brood rearing may reduce survival via drought stress. Low winter temperatures may reduce grouse survival via thermoregulatory stress.
Cumulative precipitation	Nesting season: April 15–May 31 Early brood-rearing: May 22–July 6 Late brood-rearing: July 22–September 6	Daymet (2002–2022)	Wetter conditions may reduce nest and early brood survival via thermoregulatory stress, whereas precipitation in late-brood rearing may improve survival by reducing drought stress.
Mean daily Snow water equivalent (SWE)	Winter: January 1–March 15	Daymet (2002–2022)	Low values indicate reduced snow cover and may favor higher survival via increased access to food resources
Palmer drought severity index	Nesting season: April 15–May 31 Early brood-rearing: May 22–July 6 Late brood-rearing: July 22–September 6	gridMET (2002–2022)	Higher values represent absence of drought conditions and may favor higher nest and brood survival
Vegetative productivity	Growing season	Rangeland Assessment Platform (2002–2022)	High values may indicate enhanced habitat condition and increase survival or recruitment
Mean animal unit months (AUM)	Growing season	Sample of pasture managers (2011–2020)	High values may reduce habitat condition and reduce survival or recruitment
% Area enrolled CGP	Annual	Enrollment data (2010–2020)	Immediate benefits of enrollment to habitat condition
% Area enrolled or post-CGP	Annual	Enrollment data (2010–2020)	Immediate and lagged benefits of enrollment to habitat condition
% Area post-CGP	Annual	Enrollment data (2010–2020)	Lagged benefits of enrollment to habitat condition

encapsulates cumulative conditions from preceding seasons. It is slow to recover from drought based on short-term precipitation increases. We averaged the sub-monthly values of PDSI over the same nesting and brood rearing windows described above (Table 1) and lagged these variables to the year preceding the spring lek count to evaluate their effect on population growth rate.

2.3.2 | Remotely sensed vegetation data

To index vegetation productivity, we obtained remotely sensed above-ground perennial forb and grass annual

biomass from the Rangeland Analysis Platform at 30-m resolution (Jones et al., 2021; Robinson et al., 2018) and averaged these values across the study area for each year (2002–2022). Years with higher overall vegetation productivity could indicate increased availability of mesic resources and possible bottom-up trophic enrichment that may benefit sage-grouse in multiple life stages, possibly most acutely in the brood stage when higher above-ground vegetative productivity may enhance foraging and escape cover. As with weather covariates, we lagged productivity to the year preceding the spring lek count to evaluate the effect on population growth rate.

2.3.3 | Grazing intensity and conservation grazing program enrollment

Grazing data were collected over a subset of the study period (2011–2020). We calculated the stocking rate in used animal unit months (AUMs) at the pasture level to serve as a metric of annual grazing intensity for the study area using data collected from private landowners. We calculated AUMs by multiplying the total number of livestock by the total number of months grazed and then dividing by the pasture area in square meters. We accounted for differences in livestock type by multiplying the total number of livestock by the appropriate animal use equivalent (e.g., 454 kg cow and her calf is equal to 1.0 animal use equivalent). AUMs were averaged across the study area to index grazing intensity in each study year and lagged to the year preceding the spring lek count to represent the effect on population growth. We predicted that sage-grouse populations may respond positively to relative reductions in grazing intensity because this could result in more residual grass and forb cover, less trampling during nesting, and better escape and foraging cover during the brood rearing season.

We determined CGP annual enrollment status directly from producers or the local NRCS office for 2010–2020. Enrolled producers implemented a grazing plan developed in coordination with NRCS rangeland 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 at least three consecutive years. The CGP was implemented primarily with cow-calf operations, with only one producer grazing a mix of cattle and sheep. The grazing systems were rotational and used a combination of rest and deferment (Natural Resources Conservation Service 2017; Smith et al., 2018b) with four minimum criteria intended to support sage-grouse habitat: (1) grazing utilization rates of $\leq 50\%$ of the current year's key forage species growth, (2) ≥ 20 -day annual shift in the timing of grazing, (3) a plan to address circumstances like drought or fire, and (4) ≤ 45 -day continuous grazing durations within any one pasture (Smith et al., 2018b). The CGP occurred in individual pastures of varying sizes (mean pasture area = 2.90 km², range = 0.01–33.80 km²) intermixed across the study area. We created a spatial layer that accounted for spatial and temporal changes to the CGP enrollment status of each pasture (Berkeley et al., 2021; Reintsma, 2023) and calculated the percentage of study area enrollment into three categories: (1) percent study area currently enrolled in the 3-year program, representing an immediate effect of the program, (2) percent study area currently or previously enrolled, representing

both the immediate and the delayed effects, and (3) percent study area previously enrolled, representing only the delayed effects. We predicted that if sage-grouse populations did not immediately respond to grazing treatments during implementation, they might show delayed responses to affected habitat such as changes in vegetation composition and structure. We lagged these variables to the year preceding the spring lek count to evaluate their effect on population growth rate and included 1 year prior to initiation of the program (2010) where all CGP covariates equaled 0.

2.4 | Population model

We used a stochastic Gompertz density dependent growth model to test for covariate effects on growth rate. The model is commonly used to represent growth of vertebrate populations with synchronous annual birth pulses and growth rates subject to environmental stochasticity and density dependence (Lande et al., 2003). With the abundance index on the log scale the process model is:

$$x_t = \theta \times x_{t-1} + r + \beta \times c_{t-1} + \varepsilon_t$$

$$\varepsilon_t \sim \text{Normal}(0, \sigma_{\text{process}}^2)$$

where x_t is natural log of the latent abundance index at time t , θ represents the strength of density dependence, r represents the intrinsic rate of growth (per capita) from small population size, β is the effect of a covariate c_{t-1} , and ε_t is a normally distributed random variable with zero mean and constant variance $\sigma_{\text{process}}^2$ representing the random effect of unmeasured demographic and environmental stochasticity on growth rate. If a lag-1 covariate effect was not supported at the 95% confidence level, we tested for a lag-2 effect to account for the possibility that lower lek attendance among yearling males could delay observation of population change (Walsh et al., 2004; Wann et al., 2019). We report lag-2 estimates only if their 95% credible intervals excluded zero, recognizing that detecting such delayed dynamics reliably requires substantial sample sizes (e.g., Monroe et al., 2017 found limited support for lag-2 effects despite analyzing 743 leks over 11 years).

To incorporate uncertainty in the estimated abundance index, we included an observation model using SEs from the N-mixture model:

$$N_{\text{index}_t} = \exp(x_t)$$

$$x_t \sim \text{Normal}(N_{\text{index}_t}, \text{SE}_t).$$

where N_{index_t} is the N-mixture model population index estimate and SE_t is the associated standard error. We fit this model using JAGS (Plummer, 2003) interfaced through the R2jags package (Su & Yajima, 2024) in R, using three chains of 50,000 iterations each, a burn-in of 5000, and a thinning rate of 5. The abundance index and covariate data for this analysis are provided in Data S2. We assessed model convergence by visually inspecting trace plots for good mixing and confirming that the potential scale reduction factor (R) was close to 1 indicating adequate convergence (Gelman & Rubin, 1992). We assessed the adequacy of our lag-1 population model for capturing temporal autocorrelation by examining the autocorrelation function of the model residuals, which showed no substantial autocorrelation at higher lags, indicating that the lag-1 structure was sufficient.

We compared standardized covariate effect estimates from a set of univariable population models, each including a single environmental or grazing covariate (and an interaction term only when explicitly hypothesized), to assess the relative importance of predictors. If interaction terms were not supported (i.e., their 95% CRI included 0), we did not report them. Because groups of covariates had differing time series lengths, total years included in analyses varied: AUM models used 10 years, CGP enrollment models used 11 years, and weather and vegetation productivity models used 21 years. We evaluated correlations among covariates using Pearson correlation coefficients, considering absolute values of 0.4–0.6 as moderate and >0.8 as indicating potentially redundant variables. Because our models were univariable, we used these correlations to qualitatively flag covariates that might contain largely overlapping information.

3 | RESULTS

We applied the N-mixture model to data from 20 lek locations from 2002 to 2022 to generate the annual population indices for the study area. N-mixture model diagnostics indicated good convergence (effective sample size >340 for each year's estimate and $\hat{R}$ were between 1.001 and 1.007), and a chi-squared discrepancy posterior predictive p -value of 0.35 indicated adequate fit to the data. The estimated annual population growth rates varied substantially across years ($\text{CV} = 41\%$; Figure 2a). Climatic variables during the study period generally encompassed the 30-year climate range for the region (Table 2). Annual variation in vegetation productivity was strongly correlated with late brood-rearing PDSI ($r = 0.83$) and temporally adjacent PDSI summary

windows were also strongly correlated ($r > 0.88$) (Table S3). Colder winter temperatures were moderately correlated with reduced drought ($r = -0.53 - -0.61$) during the following breeding season (Table S3). Precipitation and temperature were generally uncorrelated ($|r| < 0.25$) within summary periods, and their late brood-rearing values were unrelated to respective values in preceding periods ($|r| < 0.18$), whereas nesting and early brood-rearing values were moderately correlated ($r = 0.45$ and 0.64 from temperature and precipitation, respectively; Table S3). Percent area actively enrolled in the CGP was 0% at both the beginning and end of the time series with a maximum of 25% (Table 2). Percent area previously enrolled increased linearly throughout the study from 0% to 38%, whereas the percent area currently and previously enrolled increased from 0% to peak of 38% in 2016 and onward. There was no trend in mean AUMs, the grazing intensity variable.

For the covariate estimates within the population models, effective sample sizes were between 5100 and 9600 and $\hat{R}$ between 1.001 and 1.002 indicating adequate model convergence. We detected a positive effect of winter temperatures (mean minimum daily temperature January 1–March 15; standardized $\beta = 0.18$, 95% CI: 0.02–0.34), where growth rates were lower when winter temperatures were colder than average (Figure 2b, Figure 3). Because the model response is on the log scale the coefficient can be interpreted as a percent change ($(\exp(\beta) - 1) \times 100\% = 18\%$) in population growth for a 1 SD change in temperature. Additive and interactive effects of winter temperature with the snow cover index, SWE, were not supported. We found no evidence of relationships between population growth rates and nesting, early brood-rearing or late brood-rearing period temperatures, precipitation, or their interactions (Figure 3). Likewise, we did not find evidence of PDSI or vegetation productivity influencing growth rates (Figure 3). No lag-2 covariate effects were supported.

Annual population growth rates were not statistically related to the AUM grazing intensity variable (Figure 3). We found weak marginal support for the hypothesis that the CGP benefited populations via a delayed mechanism as its 95% CRI slightly overlapped 0 (standardized $\beta = 0.41$, 95% CI: $-0.02 - 0.84$; Figure 3). Alternative formulations of the CGP enrollment variables were not supported. This marginal effect indicated that annual percentage of study area pastures that had previously been enrolled in the CGP was related to an increase in annual growth rates. However, the variable was correlated with year (i.e., increased toward the end of the study) and may be conflated with other unmeasured factors that changed toward the end of the study. Additionally, a single year (2020) had strong leverage on the

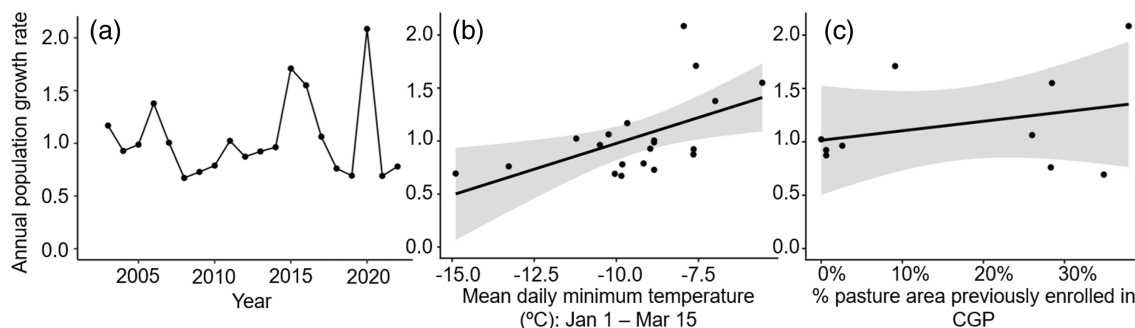


FIGURE 2 (a) N-mixture model estimates of annual population growth rate for greater sage-grouse in central Montana study area 2002–2022. (b) Representation of the winter temperature effect (minT: January 1–March 15) on annual population growth rate (2002–2022). (c) Representation of the delayed conservation grazing program (CGP) effect on annual population growth rate (2010–2020). Regression lines and shaded 95% CI ribbons are from a simplified model of annual population growth rate (N_t/N_{t-1}) as a linear function of the covariates because simple bivariate plots of effects from the Gompertz model reported in text are not possible.

Covariate	Mean	SD	Minimum	Maximum
Nesting: minT	2.3	1.0	0.3	4.6
Early brood: minT	8.3	0.9	6.6	10.4
Late brood: minT	10.9	1.0	9.7	13.4
Winter: minT	−9.4	2.1	−14.9	−5.6
Winter: SWE	11.0	11.2	1.0	45.0
Nesting: precip	109.5	46.7	56.0	238.4
Early brood: precip	124.9	55.6	32.9	228.2
Late brood: precip	51.9	42.9	4.5	190.2
Nesting: PDSI	0.33	2.37	−3.13	4.81
Early brood: PDSI	0.38	2.49	−2.62	5.49
Late brood: PDSI	0.30	2.87	−3.13	6.62
Vegetative productivity	693	98	517	848
Mean AUMs	268	77	155	354
% During CGP	5%	9%	0%	25%
% During & Post CGP	15%	18%	0%	38%
% Post CGP	10%	15%	0%	38%

TABLE 2 Descriptive statistics of environmental covariates for the central Montana study area.

Note: Mean minimum temperature (minT; °C), cumulative precipitation (precip; mm), Palmer drought severity index (PDSI), and snow-water equivalent (SWE), covariates were summarized over 2002–2022. PDSI >4 represents very wet conditions, PDSI <−4 represents an extreme drought, and values between −0.5 and 0.5 represent average moisture conditions. Mean animal unit months (AUMs) is the mean per pasture across the study area (2011–2020). Percent of study area enrolled in conservation grazing program (CGP) was summarized 2010–2020.

parameter estimate (Figure 2c) and the covariate effect was not statistically supported if this year was removed from analysis.

4 | DISCUSSION

We investigated the role of climatic variability, vegetation productivity, and grazing on the annual dynamics of a northern Great Plains sage-grouse population. Our sage-grouse

abundance index fluctuated widely during the 21-year study period (e.g., >400% change between minimum and maximum values), and annual variation in seasonal precipitation and temperature matched the ranges in the 30-year climate averages. We detected a clear positive correlation between winter temperature and annual population growth rates but found that variables representing direct and habitat-mediated effects of breeding season weather, vegetation productivity, grazing intensity, and CGP enrollment were unable to explain additional variance.

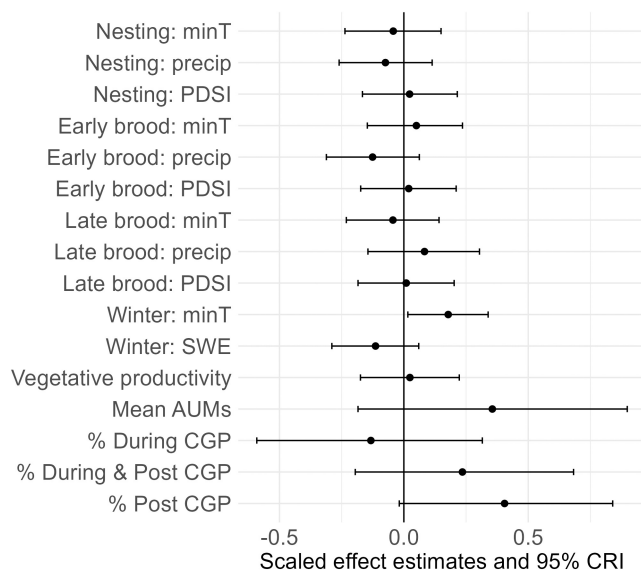


FIGURE 3 Effect estimates (mean $\pm$ 95% credible intervals) for model coefficients of candidate covariates included in the Gompertz population growth model for greater sage-grouse in central Montana study area. Points represent posterior means, and horizontal bars indicate the 95% credible intervals (CRI). Total years differ for some covariates: mean minimum temperature (minT), sum of precipitation (precip), Palmer drought severity index (PDSI), and snow-water equivalent (SWE) were evaluated over 2002–2022, mean animal use months (AUMs) from 2011 to 2020, and conservation grazing program (CGP) from 2010 to 2020.

The winter temperature effect on population dynamics is corroborated by two separate vital rate analyses from the same study area (2011–2019): Simpson et al. (2024) detected a positive effect of mean annual temperatures on female survival and Helm (2023) found that annual population growth rates were most sensitive to adult female survival (similar to a separate range-wide sensitivity analysis by Taylor et al., 2012). Other studies have detected winter severity effects on female sage-grouse survival in high latitudes or elevations of sage-grouse range (Anthony & Willis, 2009; Moynahan et al., 2006). This is consistent with our findings and those in other taxa where winter severity constrains population growth near cold edges of species range (Messmer et al., 2020; Sirén et al., 2021; Sirén & Morelli, 2020).

By contrast, adult female survival in the Great Basin and adjacent regions appears higher and possibly more stable across years (Blomberg et al., 2013; Hausleitner, 2003; Wik, 2002). Winter severity effects in our study area could be amplified by low sagebrush percent cover (<25%) and a preponderance of shorter growth forms of Wyoming big sagebrush and silver sagebrush which are characteristic of the northeastern extent of sage-grouse range in northern Montana and southern

Alberta and Saskatchewan (Miller et al., 2011; Smith et al., 2018a, 2018b; Montana Natural Heritage Program, 2021). Because sage-grouse winter diet is composed entirely of sagebrush (Schroeder et al., 1999), these characteristics likely resulted in less forage availability and thermal cover compared to sagebrush communities in other parts of sage-grouse range where sagebrush characteristics and growth forms vary substantially (Dzialak et al., 2013; Smith et al., 2020; Wanner, Pratt, & Beck, 2024; Wanner, Pratt, Reinking, et al., 2024). Although we hypothesized that these low growth forms might increase vulnerability to deep snow, support for the snow cover index was weak, with credible intervals overlapping zero despite the predicted direction. This may reflect spatial heterogeneity in snow distribution, where wind-driven snow redistribution maintains forage availability even in years of high snow accumulation.

Finally, it is unlikely that the winter effects on population growth we detected were confounded with depressed male lek attendance due to late spring phenology or winter precipitation or temperature effects described by Wann et al. (2019). Winter temperature and snow water equivalent were essentially uncorrelated with lek monitoring period measurements ($r = 0.18$ and $r = -0.15$, respectively), and leks were surveyed multiple times throughout the spring (mean visits = 3.6), reducing the risk that delayed peak attendance biased our indices. Moreover, the negative winter temperature effect on lek attendance reported by Wann et al. (2019) is opposite in sign to the positive winter temperature effect on population growth that we detected, so a similar attendance bias in our system would likely have led us to underestimate, rather than overestimate, the winter temperature effect. Wann et al. (2019) also found a positive effect of winter precipitation on lek attendance, whereas our weakly supported snow water equivalent effect on population growth was negative, again suggesting that any unmodeled attendance response to winter conditions would tend to diminish, not inflate, the winter climate signals we observed.

We did not find support for direct effects of breeding season weather on sage-grouse population dynamics, despite documented effects on breeding season vital rates in the same study area. For example, Smith et al. (2018a) documented a negative 5-day cumulative precipitation effect on daily nest survival, and Berkeley et al. (2024) detected a marginal positive effect of cooler mean brood-rearing season temperatures on chick survival. Despite the plausibility that cold, wet springs common in the northern Great Plains could negatively influence nest or early brood survival, our analysis found that spring temperature, precipitation, or their interactions did not explain variation in population growth. It is possible

these effects were compensated for in other periods of the annual cycle, or simply too small to translate into detectable population-level effects. This finding highlights the importance of recognizing that detectable vital rate effects do not necessarily translate into observable changes in population growth. Nevertheless, we acknowledge that breeding season weather could still influence populations through more complex mechanisms than those assessed here. For instance, discrete weather events or sequences of events could directly or indirectly influence grouse dynamics, but may not be well characterized by our seasonal summaries. Additionally, because population growth rates were inferred from lek count data which only index the male segment of the population (Fremgen et al., 2019; Wann et al., 2019), our analyses may have reduced our power to detect effects. However, despite this limitation, lek counts are the primary way of monitoring sage-grouse populations and ultimately, large-scale climatic effects and management intervention efficacy will be judged by their detectability in lek monitoring data.

Previous research from the Great Basin has indicated that sage-grouse vital rates and population dynamics are negatively influenced by drought during or leading up to the breeding season (Blomberg et al., 2013; Coates et al., 2018; Gibson et al., 2016; Guttery et al., 2013; Lundblad et al., 2022; O'Neil et al., 2025). Donnelly et al. (2018) hypothesized that a reduction in the area and distribution of mesic areas important to sage-grouse reproductive success drives this relationship. They showed that Great Basin and Great Plains landscapes had similar patterns of decreasing mesic resource availability with decreasing precipitation during the breeding season, though average distance to mesic resources grew more quickly in the Great Basin during drought. Brood-rearing females in our study area and in southeast Alberta selected mesic habitats (Aldridge & Boyce, 2007; Helm, 2023). However, selection for mesic areas in Alberta increased chick mortality risk, whereas no such effect was detected in our study area (Berkeley et al., 2024). Collectively, these findings suggested that we could expect similar drought-sensitivity in our study population.

However, despite measuring temperature, precipitation, and PDSI across multiple breeding season temporal windows, and directly measuring annual vegetation productivity with remote sensing, we did not detect effects on population dynamics. While our study area is geographically small within the broader northern Great Plains sage-grouse population, our results do not support the hypothesis that climate-driven annual vegetative productivity is a key driver of sage-grouse demographics (Donnelly et al., 2018; Lundblad et al., 2022). To our

knowledge, there are no other direct tests of this hypothesis in the northern Great Plains. Research in southeast Alberta showed daily chick survival declined with increasing intraseasonal drought (Aldridge & Boyce, 2008), but those within-season effects were not evaluated in terms of their consequences for interannual population growth.

In comparison to Great Basin sage-grouse study areas, our study area averaged slightly higher annual precipitation (2002–2022 range = 25.3–58.1 cm, compared to a range of 17.5–30.0 cm in low elevations reported by Guttery et al., 2013) and falls in a region of cool and moist soil regimes (Pyke et al., 2015). These inherent differences may partly explain why drought did not seem to be a factor for the sage-grouse population in our study. An alternative explanation is that drought effects are muted or delayed if adult female survival increases when reproductive investment or success is lower (Behnke et al., 2023; Blomberg et al., 2013), and females reduce reproductive investment in dry years (Blomberg et al., 2017; Behnke et al., 2023). However, vital rate analyses in our study area did not indicate drought effects on nest, brood, or hen survival (Berkeley et al., 2024; Simpson et al., 2024; Smith et al., 2018a), and we did not detect delayed (lag-2) precipitation or drought effects on population growth. Moreover, in the Great Basin, lag-1 growing season precipitation effects on population growth were expressed in the immediately following lek counts (O'Neil et al., 2025), suggesting that if similar dynamics were strongly influential in our system, they should have been detectable at this lag.

Our evaluation of an annual grazing intensity index (AUMs) and CGP enrollment is consistent with previous research on sage-grouse vital rates from the same study area and in Idaho which found no evidence of grazing effects on nesting success (Conway et al., 2025; Smith et al., 2018a, 2018b) or brood survival (Berkeley et al., 2024; Conway et al., 2025). Likewise, concurrent research on another ground-nesting bird species in the study area, thick-billed longspur (*Rhynchophanes mccownii*), did not detect CGP effects on nest density or success (Reintsma et al., 2022). The CGP focused on rotational grazing management practices including utilization limits ($\leq 50\%$ of key forage growth), timing shifts (≥ 20 -day annual shifts), and continuous grazing duration restrictions (≤ 45 days per pasture) rather than explicit stocking-rate reductions. Stocking decisions remained under producer control based on environmental and economic conditions, though some enrolled producers reduced stocking rates to achieve these management criteria. At the study area scale, total AUMs did not decrease with the percent of the study area enrolled. While we observed a weak marginally positive effect of

the total percent of the study area that had been previously enrolled in the grazing program, this relationship was driven by a single data point (study year 2020) from the end of the time series when percent area previously enrolled was at its maximum and the population index also reached its maximum, climbing 295% from the previous year.

Considering that previous study area research indicated no effects on vital rates, mixed effects on seasonal habitat selection, limited evidence of vegetation changes between enrolled and non-enrolled rangelands during the brood rearing season (Berkeley et al., 2024; Helm, 2023; Simpson et al., 2024; Smith et al., 2018a, 2018b), and the current result, we conclude that the CGP likely did not confer an appreciable benefit to the sage-grouse population during our study. Indeed, NRCS reduced their investment in rotational grazing management plans across the West because previous studies (Berkeley et al., 2021) did not conclude that sage-grouse or their habitat benefited from these plans on the timeline originally predicted. The SGI has shifted focus to other practices that have more clearly demonstrated benefits including providing landowner assistance to reduce exotic annual invasives, restoring mesic areas of pastures, and controlling woodland expansion (Olsen et al., 2021; Severson et al., 2017; Silverman et al., 2019).

Despite our lack of detected grazing effects, we suggest caution in generalizing this finding across the rest of sage-grouse range. For instance, Monroe et al. (2017) documented that grazing intensity and timing influenced sage-grouse population growth on Bureau of Land Management lands in Wyoming. These contrasting results may reflect differences in long-term grazing histories, prevailing management systems, and the interaction of grazing with climate and underlying vegetation productivity. Our study occurred in an area of relatively intact multi-generational family ranches that may have independently adopted grazing management practices that are generally neutral to sage-grouse populations. This supposition is supported by a lack of clear vegetation differences between enrolled and non-enrolled pastures in late summer (Simpson et al., 2024; Smith et al., 2018a, 2018b). Our study area also had a cooler and wetter climate than the Wyoming Basin (Monroe et al., 2017; Pyke et al., 2015). Monroe et al. (2017) found that sites with greater moisture and primary productivity responded differently to grazing intensity and timing than drier, less productive sites, with the direction of grazing effects depending on when grazing occurred. Because our study area falls toward the cooler, wetter end of the gradient described by Monroe et al. (2017), such interactions could have obscured grazing intensity effects in our analyses. However, inconsistent documentation of livestock

turnout and removal dates on private ranches prevented formal evaluation of a timing-by-intensity interaction in our system.

Other research evaluating the benefits of a rest-rotation grazing system for sharp-tailed grouse (*Tympanuchus phasianellus*) in a relatively intact rangeland landscape in eastern Montana and western North Dakota also found a lack of apparent benefits to breeding vital rates (Milligan et al., 2020a, 2020b), but in that study area, rotational grazing management was correlated to cumulative positive effects on population growth despite undetectable effects on individual vital rates (Milligan & McNew, 2022). Grazing management systems in other geographies may differ in their influence on habitats and sage-grouse dynamics, although our findings suggest a more targeted approach which could include identifying rangelands that are clearly impaired by overgrazing. We also caution not to overlook conservation grazing benefits that may take place over longer time periods than the duration of the CGP in our study (Kitti et al., 2008; Oesterheld & Semmartin, 2011; Schieltz & Rubenstein, 2016).

Overall, our results suggest that sage-grouse conservation plans seeking near-term population improvements in areas of relatively intact rangelands may not directly benefit from grazing programs designed to improve habitat through rest-rotation regimes. However, the loss of intact grasslands remains a major challenge to conservation on the Great Plains (Lipsey et al., 2015; Niemuth et al., 2022; Olimb & Robinson, 2019), and programs targeted at retaining or expanding intact rangelands are clearly important. Our northern Great Plains study population did not appear to be drought-sensitive, and this may indicate that annual weather-driven fluctuations in mesic habitat availability are not as limiting as in the Great Basin. Further evaluation is needed to determine if this is a local or widespread characteristic of northern Great Plains sage-grouse populations. Given the apparent effects of winter weather on population dynamics, future research could evaluate whether these effects could be mitigated through conservation or restoration of winter habitats. However, even if winter habitat is limiting, its prioritization should be weighed against the need to maintain existing habitats that currently support successful reproduction and other stages of the annual cycle.

AUTHOR CONTRIBUTIONS

Conceived and designed study: David Messmer, Lorelle Berkeley, Justin Gude, Victoria Dreitz. Analyzed data: David Messmer, Kaitlyn Reintsma, Jennifer Helm. Collected field data: Lorelle Berkeley, Mark Szczypinski. Wrote paper: David Messmer, Kaitlyn Reintsma, Lorelle Berkeley, Jennifer Helm, Mark Szczypinski, Victoria Dreitz, Justin Gude.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are provided in the Supporting Information.

ETHICS STATEMENT

All animal handling associated with this project 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).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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