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Short communication

Survival of juvenile greater sage-grouse in Wyoming

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An understanding of vital rate contributions to population growth is necessary for species of conservation concern, such as greater sage-grouse *Centrocercus urophasianus*. Sage-grouse demographic rates are generally well described; however, a notable exception is juvenile survival during the post-fledging period. We evaluated juvenile survival at two study areas in central and south–central Wyoming. We captured and monitored 124 juvenile sage-grouse (77 females and 47 males) in 2017–2019 in the central Wyoming study area and 68 (29 females and 39 males) in 2020–2021 in the south–central Wyoming study area. Monthly survival generally increased from September to March in each year and study area. In both study areas, we found no evidence that monthly mortality risk differed between male and female juvenile sage-grouse. In central Wyoming, seven-month survival estimates from September to March were 0.28 (85% CI: 0.18–0.44) from 2017–2018, 0.28 (85% CI: 0.20–0.39) from 2018–2019, and 0.43 (85% CI: 0.34–0.55) from 2019–2020. In south-central Wyoming, survival estimates were 0.34 (85% CI: 0.25–0.47) from 2020–2021 and 0.78 (85% CI: 0.68–0.90) from 2021–2022. Overall, we found evidence that body condition at time of capture and weather (temperature and precipitation) during the pre-fledging period influenced juvenile mortality risk, but the most supported intrinsic and extrinsic factors varied between study areas. Our results provide additional estimates of juvenile survival that will be useful for understanding sage-grouse demography. However, the spatial and temporal variation in juvenile survival that we documented should be accounted for when evaluating how management actions may influence sage-grouse populations.

Keywords: *Centrocercus urophasianus*, demographic rates, juvenile, mortality risk, survival

Introduction

The advent of novel analytical tools provides robust methods for wildlife managers to better understand vital rate contributions to population dynamics. For example, incorporating multiple vital rates to identify how management actions or other extrinsic

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factors influence species of conservation concern, such as greater sage-grouse (*Centrocercus urophasianus*; 'sage-grouse'), can identify important sources of variation that contribute to population growth (Coates et al. 2018, Olson et al. 2021). Given numerous logistical constraints with field data collection, many studies often rely on demographic rates from published literature when local information is unavailable. Sage-grouse demographic rates are well described; however, a notable exception is juvenile survival during the post-fledging period (Taylor et al. 2012).

Survival during the post-fledging period is considered an important vital rate contributing to sage-grouse population growth (Taylor et al. 2012, Dahlgren et al. 2016). As such, an understanding of spatial and temporal factors that may contribute to changes in post-fledgling survival is necessary to adequately address how this vital rate may influence sage-grouse population dynamics. The literature evaluating juvenile survival has developed more recently (Beck et al. 2006, Blomberg et al. 2014, Caudill et al. 2014, Apa et al. 2017), yet only Blomberg et al. (2014) evaluated whether extrinsic factors contributed to variation in juvenile survival rates. Furthermore, understanding regional differences in demographic rates is necessary to better understand sage-grouse demography range-wide (sensu Dahlgren et al. 2016). We evaluated juvenile sage-grouse survival at two study areas in central and south–central Wyoming. Our objectives were to evaluate the effects of intrinsic factors including sex and body condition, and extrinsic factors including temperature and precipitation on juvenile survival to better understand factors contributing to variation in mortality risk.

Across taxa, juveniles in better condition often have higher survival (Ronget et al. 2018), and this relationship is supported by juvenile sage-grouse research (Blomberg et al. 2014). We hypothesized that survival of juvenile sage-grouse is a function of intrinsic (e.g. body condition) and extrinsic (e.g. weather) factors. We predicted that body condition at time of capture would be positively correlated with juvenile survival. We also predicted that growing season precipitation would be positively, and growing season temperature negatively correlated with juvenile survival. Weather conditions influence herbaceous and invertebrate production and abundance in sagebrush (*Artemisia* spp.) communities (Noy-Meir 1973, Wenninger and Inouye 2008). In particular, forb production is positively associated with early growing season precipitation (Copeland et al. 2022), but higher temperature is generally associated with lower forb biomass (Pennington et al. 2016). The availability of forbs and invertebrates corresponds with chick growth rates (Blomberg et al. 2013, Smith et al. 2019), which could lead to individuals in better condition during the post-fledging period. Therefore, conditions that increase the availability of important foraging resources for chick sage-grouse may result in positive effects on post-fledging survival. Based on previous research (Beck et al. 2006, Blomberg et al. 2014), we did not expect to find differences in juvenile survival between males and females. However, we included sex in our analysis to provide additional empirical estimates that may be useful for future research.

Study area

We studied juvenile sage-grouse survival in two study areas (Fig. 1). Our central Wyoming study area was in portions of Fremont and Natrona counties, Wyoming. Elevation ranged from 1593 to 2534 m. The 30-year (1991–2020) normal precipitation from 1 May to 31 August was 11.7 cm (PRISM Climate Group 2023). The central Wyoming study area received 9.1 cm of precipitation from 1 May to 31 August in 2017, 15.9 cm in 2018, and 15.9 cm in 2019. Mean monthly maximum temperature was 24.7°C in 2017, 25.1°C in 2018, and 22.8°C in 2019. The predominant land use across the study area was livestock grazing. Our south–central Wyoming study area was in Carbon County, Wyoming. Elevation ranged from 1982 to 2529 m. Average 30-year normal precipitation from 1 May to August 31 was 12.5 cm (PRISM Climate Group 2023). The south–central Wyoming study area received 7.5 cm of precipitation from 1 May to 31 August in 2020, and 8.4 cm in 2021. Mean monthly maximum temperature was 24.5°C in 2020 and 25.4°C in 2021. Extraction of natural gas, coalbed methane, and oil, and livestock grazing were all common within the study area. In both study areas, Wyoming big sagebrush *A. tridentata* was the dominant shrub species at lower elevations and mountain big sagebrush *A. t. vaseyana* was common at higher elevations. Understories included a diversity of native perennial forbs including arrowleaf balsamroot *Balsamorhiza sagittata*, buckwheat (*Eriogonum* spp.), desert parsley (*Cymopterus* spp.), phlox (*Phlox* spp.), tailcup lupine *Lupinus caudatus*, and common yarrow *Achillea millefolium*.

Material and methods

We captured and radio-marked juvenile sage-grouse during August and September 2017, 2018 and 2019 (central Wyoming), and 2020 and 2021 (south–central Wyoming) using spotlighting and hoop-netting techniques (Giesen et al. 1982, Wakkinen et al. 1992). Our capture, handling, and monitoring protocols were approved by the Wyoming Game and Fish Department (Chapter 33 permit numbers 801, 1303 and 1160) and the University of Wyoming Institutional Animal Care and Use Committee (protocols 20170322JL00266 and 20200317JB00413-01). We recorded sex (Crunden 1963), mass (± 1 g), and tarsus and wing chord length (± 1 mm) for each grouse. Wings were placed against a measuring board and the length between the carpal joint and the end of the longest feather was recorded. To verify the sex of captured individuals in the south–central Wyoming study area, we collected blood samples by clipping a hallux toenail. We used Omega E.Z.N.A. DNA extraction kits (Omega Bio-Tek, Norcross, Georgia, USA) to extract DNA and used PCR to amplify a region of the chromodomain helicase DNA binding (CHD) gene using CHD1F/CHD1R primers (Çakmak et al. 2017). We ran PCR products on 2% agarose gel for 30 min at 85 V and 400 mAmp in standard Tris Acetate–EDTA buffer.

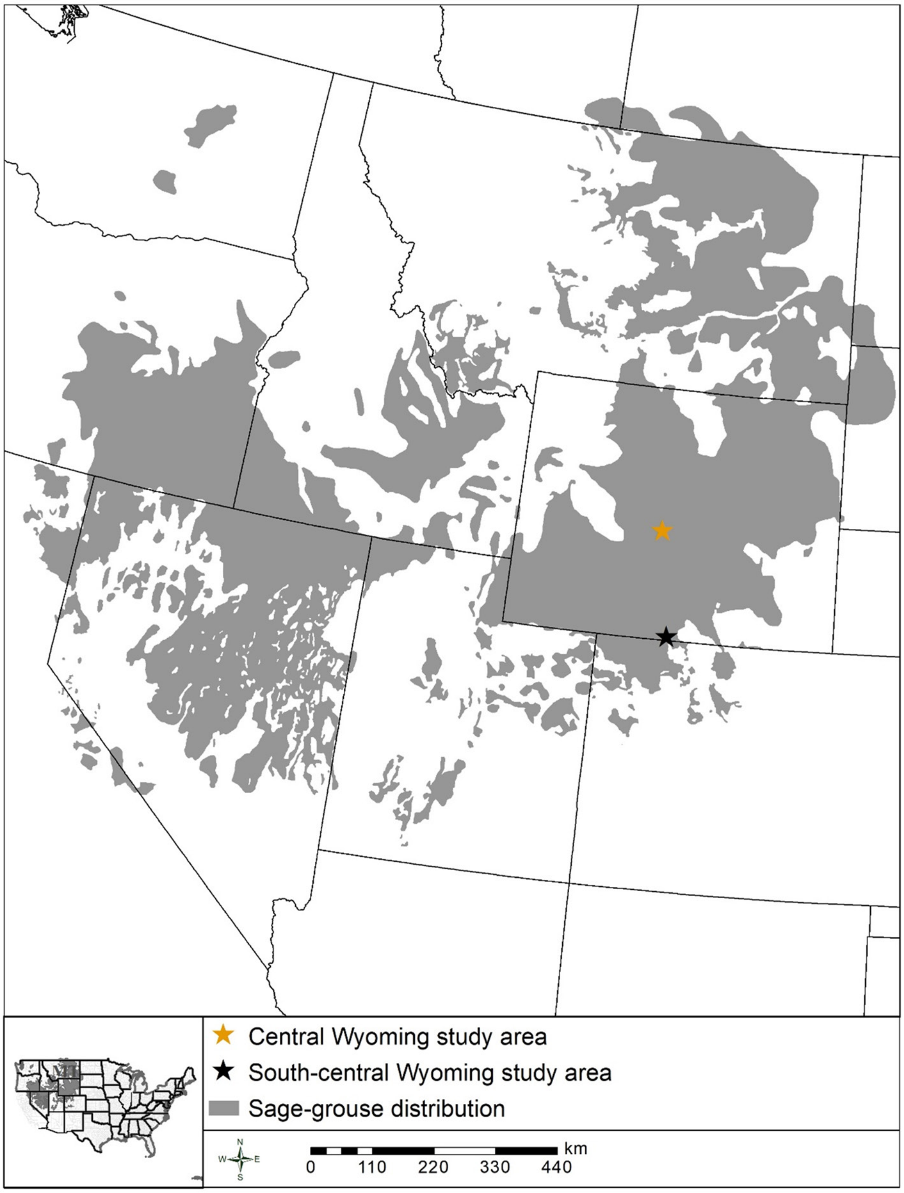

Figure 1. Location of the central and south–central Wyoming, USA study areas, relative to the estimated current distribution of greater sage-grouse (Schroeder et al. 2004), where we evaluated juvenile greater sage-grouse from September to March 2017–2022.

In the central Wyoming study area, we attached 15 g radio transmitters (Model A3960 Advanced Telemetry Systems Incorporated, Isanti, MN, USA) to individuals. In summer 2020 at the south–central Wyoming study area, we fit juveniles with either 10 or 15 g (RI-2B, Holohil Systems Ltd., Carp, Ontario, Canada), or 22 g VHF transmitters (A4060, Advanced Telemetry Systems, Isanti, MN, USA), while in 2021 we attached either modified 12 g (A3950, ATS, Isanti, MN, USA), or 15 g (A3960, ATS, Isanti, MN, USA) VHF necklace transmitters to juveniles. Transmitters were modified (wider and more circular instead of taller oval shape) following communication with another grouse researcher who observed higher mortality rates using standard Advanced Telemetry Systems model A3960 transmitters (Gillette pers. comm.). Transmitters manufactured by Advanced Telemetry Systems and Holohil were affixed to individuals with PVC-covered or PVC shrink covered elastic necklaces. For all individuals, we ensured that transmitters did not exceed 3% of body mass (Phillips et al. 2003). We monitored juveniles monthly (September–March) using fixed-wing aircraft. Although it is possible that some transmitters fell off (Riley and Fistler 1992), we assumed that retention was 100% and that transmitters emitting a mortality signal were a true mortality.

We used mixed Cox proportional hazards regression models (Cox 1972) with the counting process (Anderson and Gill

1982) to assess monthly mortality risk of juvenile sage-grouse from September to March in each study area. We used individual as a random intercept term in our models. Intrinsic covariates included sex and an index of body condition. We followed Blomberg et al. (2014) to develop a body condition index, for each study area and sex separately, where we used the first principal component from a principal component analysis (PCA) of tarsus and wing chord lengths. We used general linear models to regress individual mass on the size index generated from the PCA. Models included Julian date of capture to standardize body condition among individuals captured on different dates (Blomberg et al. 2014). We used model residuals to assign body condition values to each individual, with values greater than zero signifying individuals in above average condition, and values less than zero reflecting individuals in below average condition. An assumption of the body condition index was that the relationship between individual mass and size does not change throughout periods of growth and is therefore independent of individual age. Although we do not know hatch dates of each juvenile, we performed simple correlation between mass and wing chord ($r = 0.88$), and mass and tarsus length ($r = 0.81$) across all individuals and believe this assumption was reasonably met. We obtained weather covariates from PRISM (PRISM Climate Group 2023) and included temperature (average monthly maximum) and precipitation (total) from 1 May to 31 August. This period generally aligned with the timing of spring green up in the region (Brown et al. 2019) and extended into the late summer preceding most grouse captures. We considered a model containing sex as the base model and compared it to models including sex and all combinations of body condition index, precipitation, and temperature covariates. In both study areas, the correlation coefficient ($|r|$) assessing correlation among covariates did not exceed 0.23. In the south–central study area, we also tested for an effect of transmitter type, but it was not informative, so transmitter type was not included in the final model. We used Akaike's information criterion adjusted for small sample size (AIC_c) to identify the most parsimonious model but interpreted all models within 4 AIC_c of the top model (Burnham and Anderson 2002). We considered regression coefficients from each competitive model to be informative if 85% confidence intervals surrounding estimates did not overlap zero (Arnold 2010). We performed analyses in R ver. 4.1.3 (www.r-project.org).

Results

We captured and monitored 192 juvenile sage-grouse, including 124 (77 females and 47 males) in the central Wyoming study area and 68 (29 females and 39 males) in the south–central Wyoming study area. In central Wyoming, juvenile survival from September to March was 0.28 (85% CI: 0.18–0.44, $n = 25$) from 2017–2018, 0.28 (85% CI: 0.20–0.39, $n = 49$) from 2018–2019 and 0.43 (85% CI: 0.34–0.55, $n = 50$) from 2019–2020. In south–central Wyoming, survival estimates were 0.34 (85% CI: 0.25–0.47, $n = 38$) from 2020–2021 and 0.78 (85% CI: 0.68–0.90, $n = 30$) from 2021–2022. Monthly survival rates generally increased from September to December, then remained relatively constant through March in each year and study area (Fig. 2).

The most supported Cox proportional hazards model in central Wyoming included body condition (Table 1). This model did not provide evidence for differences in mortality risk between male and female juvenile sage-grouse ($\beta_{male} = -0.03$, 85% CI $= -0.40$ to 0.34; Fig. 3); however, this model indicated that juveniles in better body condition had lower mortality risk ($\beta = -0.01$, 85% CI $= -0.007$ to -0.003). On average, relative mortality risk was predicted to decrease by 9.2% for each 20 g increase in body mass (Figure 4). Other models within 4 AIC_c of the top model suggested that mortality risk was positively associated with monthly maximum temperature ($\beta = 0.08$, 85% CI $= -0.07$ to 0.22; Table 1, model 2) and total precipitation ($\beta = 6.1 \times 10^{-4}$, 85% CI $= -5.6 \times 10^{-3}$ to 6.8×10^{-3}; Table 1, model 2) from May through August; however, we considered these

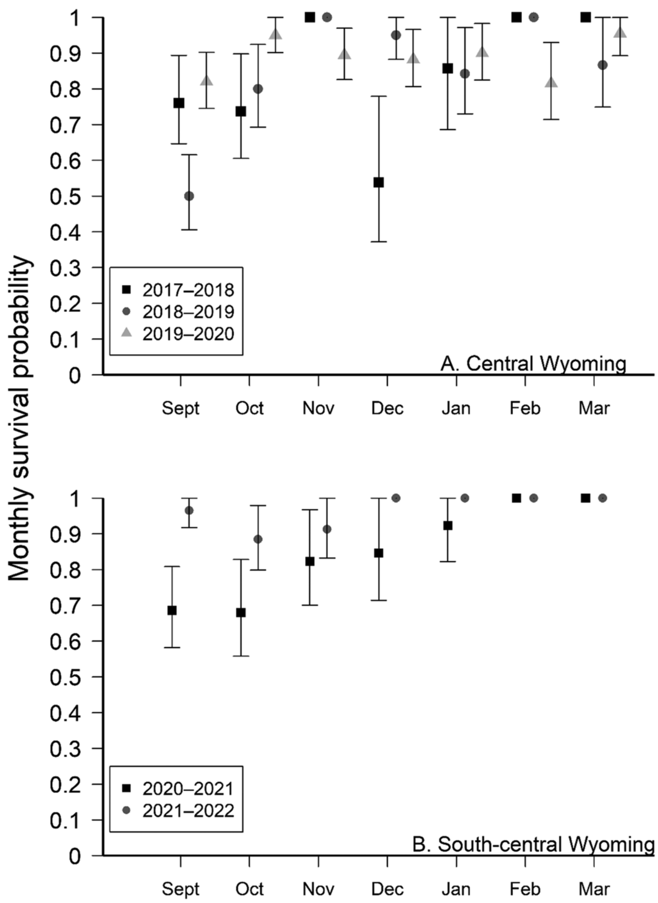

Figure 2. Monthly survival probabilities with 85% confidence intervals (vertical lines) of juvenile greater sage-grouse from September to March in central Wyoming (A; 2017–2018, 2018–2019 and 2019–2020) and south–central Wyoming (B; 2020–2021 and 2021–2022). Point estimates without confidence intervals represent monthly survival estimates of 100%.

Table 1. Relative support for competing Cox proportional hazards regression models evaluating monthly survival for juvenile greater sage-grouse (September–March) in central Wyoming (77 females and 47 males) and south–central Wyoming (29 females and 39 males), USA, 2017–2022.

Model	ΔAIC_c	w_i	K
Central Wyoming study area			
(1) Sex + body condition	0.00	0.50	3
(2) Sex + body condition + $temperature_{May–August}$	1.68	0.22	4
(3) Sex + body condition + $precipitation_{May–August}$	1.83	0.20	4
(4) Sex + body condition + $precipitation_{May–August}$ + $temperature_{May–August}$	3.69	0.08	5
(5) Sex	24.57	0.00	2
(6) Sex + $precipitation_{May–August}$	26.21	0.00	3
(7) Sex + $temperature_{May–August}$	26.30	0.00	3
(8) Sex + $precipitation_{May–August}$ + $temperature_{May–August}$	28.02	0.00	4
South–central Wyoming study area			
(1) Sex + $precipitation_{May–August}$ + $temperature_{May–August}$	0.00	0.54	4
(2) Sex + body condition + $precipitation_{May–August}$ + $temperature_{May–August}$	1.84	0.22	5
(3) Sex + $precipitation_{May–August}$	2.40	0.16	3
(4) Sex + body condition + $precipitation_{May–August}$	4.28	0.06	4
(5) Sex + $temperature_{May–August}$	8.40	0.01	3
(6) Sex + body condition + $temperature_{May–August}$	10.24	0.00	4
(7) Sex	11.68	0.00	2
(8) Sex + body condition	13.55	0.00	3

covariates uninformative because 85% confidence intervals overlapped zero.

The most supported model in south–central Wyoming included temperature and precipitation (Table 1). Juvenile mortality risk did not vary by sex ($\beta = 0.27$, 85% CI $= -0.26$ to 0.81), but models suggested individuals exposed to greater total precipitation ($\beta = -0.04$, 85% CI $= -0.06$ to -0.02) and higher monthly maximum temperatures from May to August ($\beta = -0.48$, 85% CI $= -0.83$ to -0.13) had lower mortality risk. Relative mortality risk was predicted to decrease by 34.9% for every 1.0 cm increase in total precipitation and by 21.7% for each 0.5°C increase in monthly maximum temperature (Fig. 4). Other models within 4 AIC_c suggested that individuals in better body condition had lower mortality risk ($\beta = -9.1 \times 10^{-4}$, 85% CI $= -4.2 \times 10^{-3}$ to 2.3×10^{-3}; Table 1, model 2); however, we considered this effect to be uninformative because 85% confidence intervals overlapped zero.

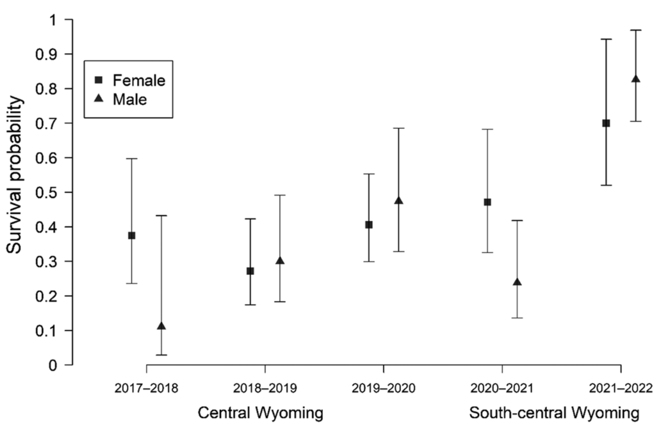

Figure 3. Survival probabilities for juvenile female and male greater sage-grouse from September to March in central (2017–2018, 2018–2019 and 2019–2020) and south–central (2020–2021 and 2021–2022) Wyoming, USA. Vertical lines represent 85% confidence intervals surrounding each estimate.

Discussion

Estimated survival rates of juvenile sage-grouse in central Wyoming were generally lower than estimates in south–central Wyoming and those reported elsewhere. In Idaho, Beck et al. (2006) found that survival from 1 September through 29 March was 0.86 (± 0.06 SE) and 0.64 (± 0.13 SE) in a lowland and mountain valley population, respectively. In Colorado, juvenile survival from 1 September to 31 March ranged from 0.41 (± 0.08 SE) to 0.75 (± 0.05 SE) during a three-year study (Apa et al. 2017). These estimates were also comparable with reported juvenile survival rates in Nevada, ranging from 0.13 (± 0.03 SE) to 0.77 (± 0.05 SE; Blomberg et al. 2014). Most mortalities in both of our study areas occurred during fall (September–December), which aligns with seasonal trends reported elsewhere (Beck et al. 2006, Caudill et al. 2014, Apa et al. 2017). In addition, we did not detect differences in survival between juvenile males and females in either study area, which is consistent with some previous studies (Beck et al. 2006, Blomberg et al. 2014, Apa et al. 2017). However, our results differ from Swenson (1986) who found lower juvenile male survival in poorer reproduction years based on data obtained from hunter-harvested wings.

Overall, we found evidence that both carry-over effects (body condition at time of capture) and weather conditions (temperature and precipitation) during the growing season influenced juvenile survival. Consistent with our prediction, individuals in better body condition had lower risk of mortality, at least in the central Wyoming study area, a finding consistent with another study (Blomberg et al. 2014). In the

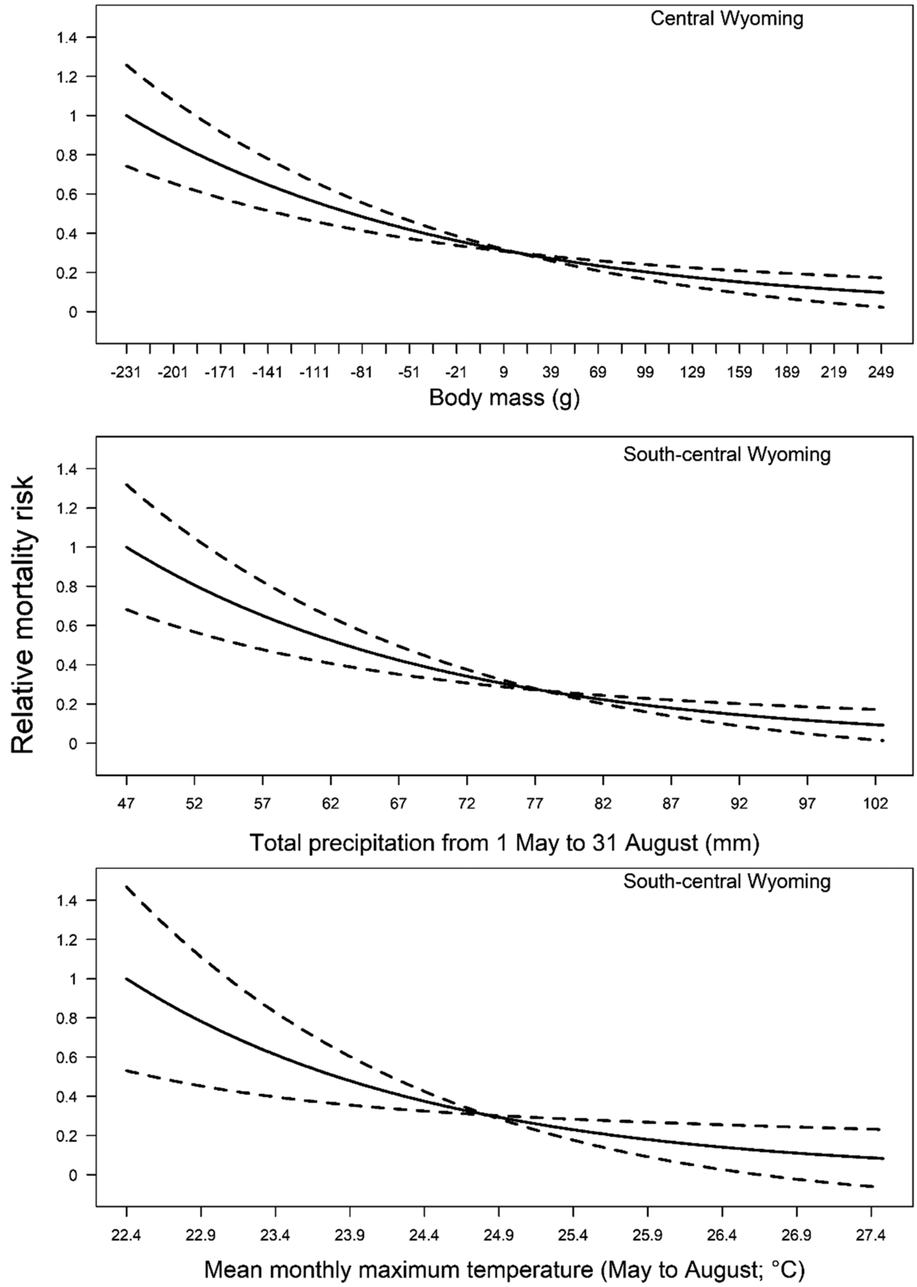

Figure 4. Relative mortality risk and 85% confidence intervals (dashed lines) of juvenile sage-grouse in relation to covariates in the most-supported model in central Wyoming (body condition index; top panel) and south–central Wyoming (total precipitation from May to August [middle panel] and mean maximum May–August temperature [bottom panel]).

south–central Wyoming study area, we a found a positive correlation with juvenile survival and precipitation, which supports our prediction that greater precipitation during the growing season could lead to greater foraging opportunities during early life stages. This also aligns with the greater precipitation and higher juvenile survival estimates during 2021. In contrast to our prediction, we found that maximum monthly temperature was positively associated with juvenile survival, which partially contradicts Blomberg et al. (2014) who found that cooler and wetter growing season conditions were positively associated with juvenile survival in Nevada. Differences in regional temperature extremes between Nevada and Wyoming could potentially explain these contradictory results. Our finding could also indicate that relatively small differences in maximum monthly temperature between years did not result in lower forb phytomass as we predicted. Further work is needed to better understand how precipitation and temperature influence the production of sage-grouse foods during the growing season (sensu Pennington et al. 2016).

In both of our study areas, body condition was not correlated with either temperature or precipitation (|r| < 0.20), suggesting that intrinsic and extrinsic factors may have independently influenced survival. Weather likely influences the availability of important foraging resources for pre-fledging juvenile sage-grouse (Guttery et al. 2013). However, because our body condition index only included individuals that survived the pre-fledging period and we did not assess chick survival, we could not adequately disentangle the relationship between body condition and weather during the growing season. In addition, inconsistencies in the most supported factors contributing to survival between study areas suggest that other unmeasured factors contribute to the regional variation in post-fledging juvenile sage-grouse survival. Although the number of individuals and temporal replication was comparable to other studies, we cannot rule out that sample sizes potentially influenced our findings. It is plausible that high juvenile survival in 2021–2022 compared to 2020–2021 in south–central Wyoming may have driven our findings, but we lacked data to compare to the central Wyoming study area over the same period. Nonetheless, our results provide additional estimates of juvenile survival that will be useful for understanding sage-grouse demography. The spatial and temporal variation in juvenile survival that we documented in this study should be considered when evaluating how management actions may influence sage-grouse populations.

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Permits – Our capture, handling, and monitoring protocols were approved by the Wyoming Game and Fish Department (Chapter 33 permit no. 801, 1303 and 1160) and the University of Wyoming Institutional Animal Care and Use Committee (protocols 20170322JL00266 and 20200317JB00413-01).

Author contributions

Kurt T. Smith: Conceptualization (equal), Data Curation (lead), Formal Analysis (lead), Funding Acquisition (supporting), Investigation (equal), Methodology (lead), Project Administration (supporting), Resources (equal), Software (lead), Supervision (equal), Validation (lead), Visualization (lead), Writing – original draft preparation (lead), Writing – review and editing, (lead). **Aaron C. Pratt:** Conceptualization (equal); Methodology (equal); Writing – review and editing (equal). **Jonathan D. Lautenbach:** Conceptualization (equal); Methodology (equal); Writing – review and editing (equal). **Holly M. North:** Conceptualization (supporting); Data curation (supporting); Methodology (supporting). **Jeffrey L. Beck:** Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Supervision (lead); Writing – original draft preparation (equal), Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the Zenodo Repository: https://zenodo.org/records/10606578 (Smith et al. 2024).

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