




# Regional variability in pregnancy and survival rates of Rocky Mountain bighorn sheep

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**Abstract.** In the Rocky Mountains, bighorn sheep restoration has been only marginally effective; this iconic wilderness species currently exists at a fraction of their historic abundance and often in fragmented and small populations. To inform bighorn sheep conservation and restoration efforts, it is critical to understand sources of variation in key vital rates. Our objectives were to characterize the spatiotemporal variations and factors affecting survival and pregnancy rates of bighorn sheep (*Ovis canadensis*) using data from 19 bighorn sheep populations in Montana and Wyoming that occupied diverse landscapes ranging from the Northern Great Plains to the Rocky Mountains. We used a hierarchical modeling approach to estimate survival and pregnancy rates of adult females and identify the important intrinsic and environmental factors affecting these vital rates. Survival of prime-aged animals was relatively high and stable, and pregnancy rates for prime-aged animals showed more overall variation in response to intrinsic and extrinsic factors. Summer growing season, as indexed by integrated NDVI, positively influenced the probability of pregnancy and winter survival. This highlights the important relationship between summer growing season conditions and bighorn sheep physiological status. An index of mountain lion population abundance was related weakly to winter survival of bighorn sheep, with mountain lion abundance on winter ranges negatively affecting winter survival. Our results regarding the distribution of the estimated probabilities of pregnancy and survival, and the identification of factors associated with regional variability in these vital rates provide a foundation for understanding the dynamics of bighorn sheep populations in the Rocky Mountains. The importance of summer growing season conditions suggests management efforts should focus on maintaining and improving nutritional resources on bighorn sheep summer ranges, in efforts to enhance the condition of animals entering the breeding season and nutrient-limited winter season. Although we document nontrivial changes in both pregnancy and winter survival rates associated with environmental variation, our results broadly support the dominant paradigm of ungulate demography insofar as survival rates of adult females were relatively higher and had less variation than pregnancy rates.

**Key words:** growing season conditions; hierarchical modeling; Montana; mountain ungulates; NDVI; *Ovis canadensis*; vital rates; Wyoming.

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## INTRODUCTION

Given the important social and ecological role of ungulates (Hobbs 1996, Augustine and McNaughton 1998, Côté et al. 2004), identification of vital rates having the greatest influence on population growth is necessary for developing effective management actions to influence population growth rate. The degree to which vital rates influence population growth rate is determined by the effect of proportional changes in the vital rate on population growth rate (i.e., elasticity; de Kroon et al. 1986) and variability of the vital rate (Gaillard et al. 2000). The canonical paradigm for population dynamics of ungulates is that adult survival has the highest elasticity, but because of low variability, this vital rate has a comparatively small impact on population growth rate. In contrast, juvenile survival has a lower elasticity compared with adult survival but high variability and a larger impact on population growth rate. A wealth of empirical work strongly supports this canonical paradigm by demonstrating that the majority of variation in population growth rates is explained by variation in juvenile survival (Gaillard et al. 1998, 2000, Raithel et al. 2007, Eacker et al. 2017). However, our understanding of ungulate population dynamics has evolved as studies demonstrate that the influence of adult and juvenile survival on population growth rates can vary across landscapes and environmental conditions, which influence the relative importance of both vital rates (Coulson et al. 2005, Nilsen et al. 2009, Eacker et al. 2017). For example, adult survival has been demonstrated to explain a majority of variation in population growth rates in ecosystems with large predators (Owen-Smith and Mason 2005, Eacker et al. 2017). Moreover, the classic paradigm may not be applicable to small or declining populations (Nilsen et al. 2009, Johnson et al. 2010). For example, in three small and isolated populations of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*), different vital rates have different levels of influence on population growth among populations (Johnson et al. 2010). Thus, to better understand the dynamics of individual populations of

management interest, it is important to understand the mechanisms responsible for variability of vital rates and their resulting influence on population dynamics (Garrott et al. 2003).

Although the relative influence of fecundity on population growth rates of ungulates is generally less than that of adult or juvenile survival (Gaillard et al. 1998, Raithel et al. 2007, Eacker et al. 2017), in some populations where fecundity is low and variable it may have an important effect on population growth (Milner-Gulland et al. 2003, Johnson et al. 2010). In addition, because fecundity may be sensitive to annual variations in weather and growing season conditions, low fecundity may be an indicator of nutritional deficiencies (Julander et al. 1961, Boertje et al. 2007, Cook et al. 2013). Nutritional condition is an important determinant of animal performance, influencing neonatal birth mass and survival, juvenile growth, adult fat accretion, probability of pregnancy, and overwinter survival (Cook et al. 2004, 2013, Parker et al. 2009, Monteith et al. 2014). An animal's nutritional condition (e.g., percent body fat), as influenced by habitat, density dependence, and weather, has direct consequences for reproduction and population dynamics (Hobbs 1989, Monteith et al. 2014). Understanding these relationships between habitat, nutritional condition of animals, and corresponding vital rates is increasingly important given the potential for changes in the environment or climate to modify these relationships (Parker et al. 2009). In particular, mountain ungulates may be sensitive to changing climatic conditions (Jacobson et al. 2004, Aublet et al. 2009, White et al. 2011, 2018), as these species occupy extreme and highly seasonal environments that are predicted to experience changes in vegetation phenology and community composition in response to climatic changes (Inouye 2008, Wipf et al. 2009, Gottfried et al. 2012).

Understanding factors influencing vital rates and the influences of vital rates on population dynamics is essential for developing strategies that effectively target influential vital rates and achieve management and conservation objectives. In the Rocky Mountains, strategies to

restore bighorn sheep (*Ovis canadensis canadensis*) populations have been only marginally effective. This iconic species historically had occupied a widespread distribution across western North America wherever rugged terrain gave protection in open range, but declined following western settlement and the introduction of nonnative respiratory pathogens from domestic livestock (Buechner 1960, Brewer et al. 2014, Cassirer et al. 2018). In spite of remarkable restoration efforts to reintroduce bighorn sheep back into every western state from which they were extirpated, including the translocation of >20,000 bighorn sheep in >1400 projects, bighorn sheep currently occupy only a small fraction of their former range and occur predominantly in small and isolated populations (Singer et al. 2000a, Brewer et al. 2014). These small bighorn sheep populations present concerns for population persistence, as they are vulnerable to loss of genetic variability and extrinsic factors such as inclement weather, predation, and pathogen introduction with associated epizootics (Berger 1990, Ross et al. 1997, Portier et al. 1998, Singer et al. 2001, Mooring et al. 2004, Festa-Bianchet et al. 2006, Poirier et al., 2019).

The important ecological and social value of bighorn sheep (Brewer et al. 2014), combined with continuing efforts to restore populations, highlights the need for additional and careful evaluation of their population dynamics, and identification of the factors affecting key vital rates to inform restoration and management efforts. Our objectives were to characterize the spatiotemporal variations and factors affecting survival and pregnancy rates of bighorn sheep using data from 19 bighorn sheep populations in Montana and Wyoming that occupied diverse landscapes ranging from the northern Great Plains to the Rocky Mountains. We used a hierarchical modeling approach to estimate survival and pregnancy rates of adult females and identify the important intrinsic and environmental factors affecting these rates.

## METHODS

### Study area

The study area was located in Montana and western Wyoming and included the annual ranges of 19 bighorn sheep populations (Fig. 1).

For 13 of 19 populations where recent survey data were available, the mean minimum count of animals per population was 180 (range: 50–419, SD = 115). We used winter capture locations to group female bighorn sheep into populations following regional management units. Seventeen of the populations were located in mountainous landscapes within western Montana and Wyoming, and two populations (Fergus and Middle Missouri) were located in prairie breaks landscapes of eastern Montana. High elevations in the mountainous landscapes contained alpine and subalpine flora, mid-elevations were predominantly characterized by mixed coniferous forests, and low elevations consisted of a mosaic of grass and shrubland communities with varying levels of irrigated and nonirrigated agricultural production. The areas occupied by the Fergus and Middle Missouri populations were characterized as prairie grasslands and badland topography with extensively eroded sedimentary rock layers producing numerous gullies and ravines.

The study area included a suite of native carnivore species, including black bears (*Ursus americanus*), coyotes (*Canis latrans*), mountain lions (*Puma concolor*), and golden eagles (*Aquila chrysaetos*). Wolves (*C. lupus*) were present in all portions of the study area except Fergus and Middle Missouri. Grizzly bears (*U. arctos*) were present in all portions of the study area except Petty Creek, Lost Creek, Fergus, and Middle Missouri. All populations were sympatric with other ungulates, including mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus canadensis*), and many were sympatric with mountain goats (*Oreamnos americanus*). The populations include a variety of management histories, including native, augmented, and restored populations. Restored populations were largely resident on low elevation winter ranges, while augmented and native populations had varying degrees of migratory behavior (Lowrey et al. 2019, 2020). A variety of Pasteurellaceae bacterial pathogens associated with respiratory disease in bighorn sheep have been detected in all populations, and *Mycoplasma ovipneumonia* was known to be resident in all populations except Galton, Grand Teton National Park, Middle Missouri, Paradise, and Petty Creek (Butler et al. 2018).

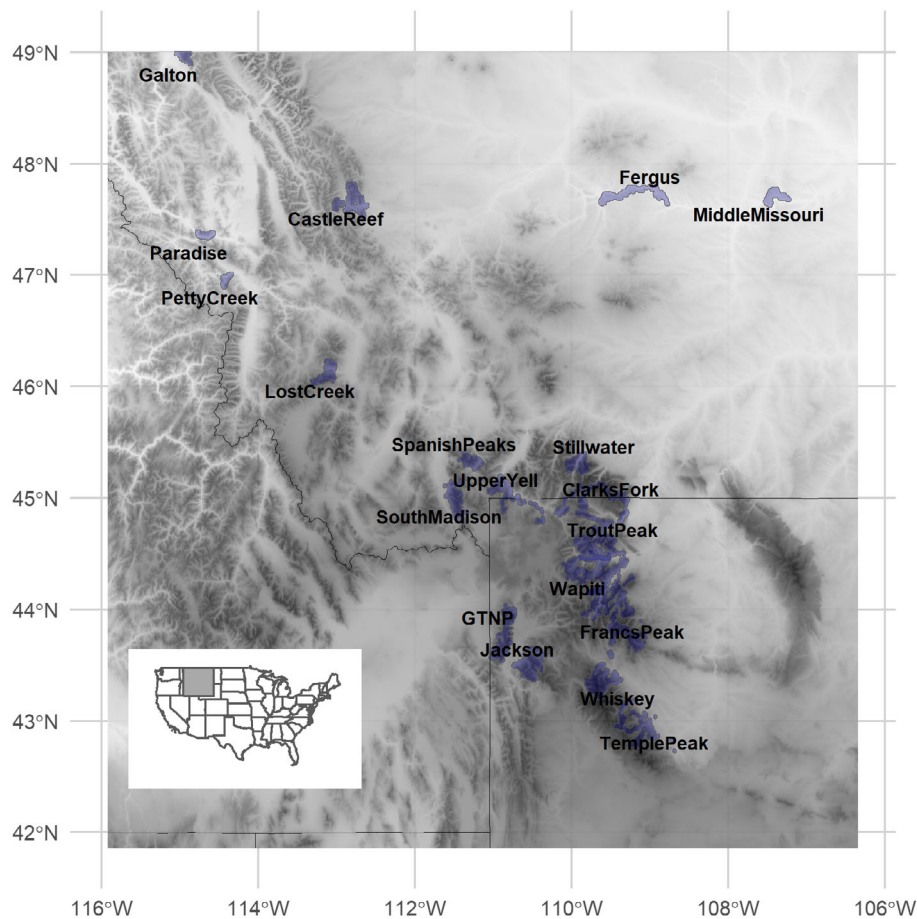


Fig. 1. The study area was located in Montana and Wyoming and included the annual ranges of 19 bighorn sheep populations, which are depicted with purple polygons. Shading corresponds to the range of elevations, with darker colors representing higher elevations.

#### Data collection

We captured adult (>1-yr-old) female bighorn sheep during January 2012–March 2019 using a combination of ground darting, drop nets, and helicopter net gunning. Animal capture and handling were approved by the Institutional Animal Care and Use Committees at Montana State University (Permit # 2011–17, 2014–32, 2016–6) and University of Wyoming (Permit # 20180305K M00296), Montana Department of Fish, Wildlife, and Parks (Permit # 2011-056, 2012-026, 2013-120, 2014-116, 2015-006, 2016-005, 2017-005, 2018-031), National Park Service (Permit # YELL-2011-2018-SCI-5886, IMR\_GRTE\_Dewey\_BighornSheep\_2017.A3, IMR\_GRTE\_Courtemanch\_2017.A3), or Wyoming Game and Fish Department (Permit #

33-798, 821, 854). We aggregated data from a number of regional research projects in this study, and as such, the number of animals and duration of sampling varied in each population.

We collected a series of measurements and samples from each animal captured. We estimated age based on tooth eruption and wear for Montana populations and a combination of tooth eruption and wear and horn annuli for Wyoming populations. We drew 20–35 mL of blood from the jugular vein. For most animals captured in December, we estimated nutritional condition using ultrasonography to measure thickness of subcutaneous rump fat and combined it with a body condition score via standardized methodology (Stephenson et al. 2020). We instrumented



most animals with store-on-board or satellite-linked GPS radio collars that recorded a median of 5 locations per day (range = 1–48, SD = 3.5) and had life expectancies of 16–48 months. Some of the animals outfitted with store-on-board GPS collars were also equipped with VHF collars programmed to start transmitting when the GPS collar was released from the animal and provide an additional 3–5 yr of survival monitoring. We equipped all collars with motion-sensitive mortality monitors.

To estimate pregnancy, we assayed blood serum based on pregnancy-specific protein B (PSPB) concentrations using an enzyme-linked immunosorbent assay (ELISA) kit (BioPRYN; Biotracking, Moscow, Idaho, USA) that is 98% accurate at predicting pregnancy in bighorn sheep at  $\geq 30$  d after conception (Drew et al. 2001). Because we collected some samples in December and early January, within 30 d of the breeding season, we also assayed serum from these animals for progesterone (P4) concentrations using an ELISA Kit (Enzo Life Sciences, Farmingdale, New York, USA) validated on domestic sheep. The combination of PSPB and P4 concentrations in samples collected within 30 d of breeding allowed detection of estrous cycling or early stages of pregnancy. For the purposes of assessing pregnancy, we assumed any animals captured in December or early January with PSPB and P4 values indicating estrous cycling or early-stage pregnancy to be pregnant or would become pregnant that year (Appendix S1). For a small ( $n = 19$ ) number of animals, we estimated pregnancy status in March using transabdominal ultrasonography (Harper and Cohen 1985, Duquette et al. 2012).

For survival analyses, we created a record for each instrumented animal that included date the animal was initially released carrying a radio collar, last date the animal was known to be alive, the first date the animal was known to be dead, and fate of the animal. We monitored instrumented animals for mortality via ground, aircraft, and satellite tracking. Monitoring intervals for non-satellite-linked collars varied widely between study areas with survival status checked at least once in the fall and again in late spring or early summer. Most animals that died were wearing functioning GPS collars, and we defined date of death as the first day the collar recorded a

mortality signal and the last date known alive as the previous day. For animals that died wearing functioning VHF collars, we defined the date of death as the date the radio signal was first heard on mortality mode and the date last known alive as the date when the collar was last heard on alive mode. We censored any animals that died within 14 d of capture. We attempted to visit most mortality sites promptly to retrieve collars. If an animal had died relatively recently when its carcass was found, we evaluated evidence to estimate the most likely cause of mortality; however, given longer monitoring intervals for VHF collars and difficulty accessing some locations seasonally, cause-specific mortality could not be definitively determined for most animals that died. We terminated monitoring of all instrumented animals for this study on 31 May 2019.

We defined population-level home ranges for summer (1 June–30 August) and winter (1 December–31 March) by buffering the locations used by instrumented animals in each population within the respective seasonal periods and merging polygons in areas where they overlapped. We filtered locations from each collar to obtain a 4- or 5-hour fix interval and used a 890-m buffer, which represented the 95th percent distribution quantile of all animal's step lengths between consecutive GPS locations. We utilized this approach for defining seasonal ranges because bighorn sheep tended to be constrained within small areas following terrain contours. Conventional approaches such as minimum polygons and kernel density estimates overestimated the seasonal ranges by including large unused areas between used patches. For 1 population without GPS collar data (Galton), we defined the summer and winter ranges based on the generalized seasonal bighorn sheep distribution generated from expert opinion ([http://gis-mtftp.opendata.arcgis.com/datasets/8571dbd4fb944052b0632fdbcb848c01d\\_0](http://gis-mtftp.opendata.arcgis.com/datasets/8571dbd4fb944052b0632fdbcb848c01d_0)).

We developed 10 covariates potentially explaining variation in rates of pregnancy, winter survival, and summer survival including weather and growing season conditions, predation risk, age class, and body fat (Appendix S2: Table S1). The seven covariates representing weather and growing season conditions were accumulated snow water equivalent ( $SWE_{acc}$ ), accumulated early-season precipitation ( $PREC_{early}$ ),

accumulated late-season precipitation ( $PREC_{late}$ ), accumulated summer precipitation ( $PREC_{cum}$ ), integrated early-season NDVI ( $NDVI_{early}$ ), integrated late-season NDVI ( $NDVI_{late}$ ), and integrated summer NDVI ( $NDVI_{cum}$ ).  $SWE_{acc}$  represented the effects of winter severity and was estimated as the mean value of cumulative daily winter snow water equivalent across each population's winter range (<https://www.nohrsc.noaa.gov/>). Precipitation and NDVI covariates represented the effects of growing season conditions on forage resources and were estimated during the early (May–June) and late summer (July–September) as the mean value across each population's summer range (Paterson et al. 2019). We evaluated one covariate that indexed population-level predation risk from mountain lions (LION) using two steps. First, we predicted winter resource selection of mountain lions for each study population's winter range following methods Robinson et al. (2015) developed for Montana (we validated predictions for Wyoming using an independent sample of harvest data; Appendix S2). Second, we averaged the relative probability of use values for mountain lions within each winter range to obtain population-level covariate values for LION. We assumed that risk varied across space but was static through time. We estimated body fat (IFBF), which was measured at the individual animal level when animals were captured and used in pregnancy analyses during the biological year of sampling. We were unable to use body fat as an individual covariate for survival due to data limitations. Specifically, of the 210 animals that were sampled for body fat and included in the survival analysis, 0 died in their first winter when we had a reliable measure of fat. In addition to indices of growing season conditions and predation, we developed a categorical age covariate (AGECLASS) that we defined as yearling (age = 1), prime age (age  $\geq 2$  and  $\leq 7$  yr), and old ( $>7$  yr; Jorgenson et al. 1997).

Additionally, we estimated the extent to which pregnancy and survival rates of bighorn sheep consistently differed among populations and years after accounting for covariates. We did so by including a random intercept term for each population and for each year and assumed that while population and year may influence the baseline pregnancy and survival rate (i.e., the intercept), the relationship between other covariates and population or year did not influence pregnancy and

survival (i.e., slopes did not vary among populations or years). These random effects were additive and therefore constrained to apply to a population across years (population-level random effect) or to all populations within a year (year-level random effect). We did not consider any disease-related covariates as highly uncertain detection probabilities for several pathogens make pathogen presence assessments for individual animals unreliable (Butler et al. 2017, 2018).

### Pregnancy and survival modeling

We used two different generalized linear models to estimate rates of pregnancy and seasonal survival, and these separate analyses evaluated relationships between covariates and each vital rate. We also evaluated levels of variation in rates among populations and years (i.e., the random intercept terms). We conducted all analyses using a Bayesian approach, which allowed us to impute missing morphometric measurements (body fat in the pregnancy analyses) and missing age data (survival analyses) as the individual level, given the variation in those covariates among other observations in our sample, and to accommodate the hierarchical structure in which individuals were nested within populations and years. We defined the biological year as 1 June–31 May and referenced the year of birth (i.e., the 1 June year). We defined summer as 1 June–30 November and winter as 1 December–31 May.

For pregnancy data, we modeled the binary results of pregnancy tests using a logistic regression framework for the probability of pregnancy as follows. For individual  $i$  within population and year, the result of the individual's pregnancy tests (0 = not pregnant, 1 = pregnant) was a Bernoulli random variable:

$$\text{Pregnancy}_{i,\text{pop},\text{year}} \sim \text{Bernoulli}(\text{Pr}(\text{preg})_{i,\text{pop},\text{year}}). \quad (1)$$

We modeled the individual's probability of pregnancy,  $\text{Pr}(\text{preg})_{i,\text{pop},\text{year}}$  as a function of covariates using the logit link, that is,

$$\begin{aligned} \text{logit}(\text{Pr}(\text{preg})_{i,\text{pop},\text{year}}) &= \mu_{\text{preg}} + \xi_{\text{pop}} + \zeta_{\text{year}} \\ &+ \beta_{\text{age class}} \times \text{age class}_i + \beta_{\text{IFBF}} \times \text{IFBF}_i + \beta \times x_{\text{pop},\text{year}} \end{aligned} \quad (2)$$

where  $\mu_{\text{preg}}$  is an overall mean on the logit scale;  $\xi_{\text{pop}}$ , population-level random effects;  $\zeta_{\text{year}}$ , yearly random effects; IFBF, the body fat

measurement of individual  $i$ ; age class $_i$ , the age class of the animal at the time of sampling (yearling, prime, or old);  $\boldsymbol{\beta}$ , the vector of regression coefficients; and  $\mathbf{x}_{\text{pop,year}}$ , the vector of weather and forage-related spatial covariates for each population (pop) and year (year) (Tables 1, 2). For the effect of age class, we estimated two adjustments to the overall mean ( $\beta_{\text{yearling}}$  and  $\beta_{\text{old}}$ ) such that the overall mean pregnancy rate represents that for the prime age class (i.e., the reference level). To complete the model specification, we used vague priors for the overall mean,

$$\mu_{\text{preg}} \sim \text{Logistic}(0, 1) \quad (3)$$

with  $\beta_{\text{IFBF}}$  and every component of the  $\boldsymbol{\beta}$  vector assigned an independent logistic prior, for example,

$$\beta_{\text{IFBF}} \sim \text{Logistic}(0, 1). \quad (4)$$

and a hierarchical structure for the random effects for populations and years,

$$\xi_{\text{pop}} \sim \text{Normal}(0, \sigma_{\text{pop}}^2) \quad (5)$$

$$\sigma_{\text{pop}}^2 \sim \text{Uniform}(0, 10), \quad (6)$$

$$\zeta_{\text{year}} \sim \text{Normal}(0, \sigma_{\text{year}}^2), \quad (7)$$

$$\sigma_{\text{year}}^2 \sim \text{Uniform}(0, 10) \quad (8)$$

We imputed missing body fat values using an informative prior based on the empirical distribution of body fat measurements in our data, and we assigned a Student  $t$ -distribution truncated at zero to allow for heavier tails (more low or high body fat measurements) than could be represented by a normal distribution. We imputed missing age-class values using a noninformative prior from a categorical distribution with three levels (representing yearling, prime, and old) such that each age class was equally likely under the prior.

Our survival models needed to account for the staggered entry and exit of individuals as well as the mortality dates of individuals that died somewhere in the interval between the end of GPS collar monitoring and the day the VHF monitoring determined a mortality, in addition to the same

hierarchical structure as the pregnancy models. We based our approach on hierarchical models developed for survival of nests and young waterfowl that accommodate a similar data structure (Schmidt et al. 2010). As in previous work, we modeled the fates of individuals  $i$  on each day  $t$  (Fate $_{i,t}$ ; 0 = dead, 1 = alive) from the time they entered the study until the time of death or right censoring (due to the end of the monitoring period) as a Bernoulli random variable:

$$\text{Fate}_{i,t} \sim \text{Bernoulli}(S_{\text{age class}_{i,t}, \text{season}_{i,t}, \text{pop}_{i,t}, \text{year}_{i,t}}^{1/182.5}) \quad (9)$$

where  $S_{\text{age class}_{i,t}, \text{season}_{i,t}, \text{pop}_{i,t}, \text{year}_{i,t}}$  was the seasonal survival rate for the age class (age class) in the season (season), population (pop), and year (year) corresponding to individual  $i$  on daily record  $t$ . We focused our analyses on seasonal survival rate rather than daily survival rate. We obtained the daily probability of survival by factoring the seasonal rate (the power of 1/182.5, approximating the interval of half of the biological year). Doing so (rather than working at the level of a daily rate and deriving a seasonal rate by raising a daily rate to the power of 182.5) resulted in improved estimation of rates at the boundary of parameter space (i.e., survival rates close to 1.0) and allowed biological inference to be made at the temporal scale of interest in our work: seasonal survival rather than daily survival. We modeled seasonal survival rates as a function of covariates using the logit link, for example,

$$\begin{aligned} \text{logit}(S_{\text{age class}_{i,t}, \text{season}_{i,t}, \text{pop}_{i,t}, \text{year}_{i,t}}) = & \mu_{\text{season}} + \xi_{\text{pop}} \\ & + \zeta_{\text{year}} + \beta_{\text{age class}} \times \text{age class}_{i,t} + \boldsymbol{\beta} \times \mathbf{x}_{\text{season}_{i,t}, \text{pop}_{i,t}, \text{year}_{i,t}} \end{aligned} \quad (10)$$

where  $\mu_{\text{season}}$  was an overall seasonal survival rate on logit scale;  $\xi_{\text{pop}}$ , population-level random effects;  $\zeta_{\text{year}}$ , yearly random effects; age class $_{i,t}$ , the age class of individual  $i$  on day  $t$ ;  $\boldsymbol{\beta}$ , the vector of regression coefficients; and  $\mathbf{x}_{\text{season}_{i,t}, \text{pop}_{i,t}, \text{year}_{i,t}}$ , the vector of covariates corresponding to season, population, and year for individual  $i$  on daily record  $t$  (Table 1). Similar to pregnancy, we estimated two adjustments to the overall mean ( $\beta_{\text{yearling}}$  and  $\beta_{\text{old}}$ ) such that the overall mean survival rate represents that for the prime age class (i.e., the reference level). To complete the model specification, we used vague priors for the overall mean,

Table 1. List of covariates explaining variations in bighorn sheep pregnancy and survival rates in 19 populations in Montana and Wyoming during 2011–2018.

Covariate	Description	Pregnancy	Winter survival	Summer survival
SWE <sub>acc</sub>	Cumulative December through April snow water equivalent derived from SNODAS	No	Yes	No
PREC <sub>early</sub>	Cumulative May through June precipitation derived from PRISM	Yes	Yes	No
PREC <sub>late</sub>	Cumulative July through September precipitation derived from PRISM	Yes	Yes	No
PREC <sub>cum</sub>	Cumulative May through September precipitation derived from PRISM	Yes	Yes	No
NDVI <sub>early</sub>	Integrated NDVI May through June	Yes	Yes	No
NDVI <sub>late</sub>	Integrated NDVI July through September	Yes	Yes	No
NDVI <sub>cum</sub>	Integrated NDVI May through September	Yes	Yes	No
FAT	Estimated ingesta-free body fat of individual animals during December	Yes	No†	No
AGECLASS	Defined as yearling (age = 1), prime age (age ≥ 2 and ≤ 7 years), and old (>7 years)	Yes	Yes	Yes
LION	Mean predicted mountain lion resource selection value within winter ranges	No	Yes	No
SEASON	Categorical covariate contrasting summer (0) and winter (1)	No	Yes	Yes
Year	An additive random effect of year	Yes	Yes	Yes
Pop	An additive random effect of population	Yes	Yes	Yes

*Notes:* The effects of season, year, and population were included in all competing survival models and the effects of year and population were included in all competing pregnancy models. The inclusion of other covariates considered as predictors of seasonal survival and pregnancy is indicated with yes/no. Additional details on covariates are found in Appendix S2.

† This covariate could not be evaluated because sample sizes were too low to allow estimation.

$$\mu_{\text{season}} \sim \text{Logistic}(0,1) \quad (11)$$

with every component of the  $\beta$  vector assigned an independent logistic prior, for example,

$$\beta_{\text{SWE}_{\text{acc}}} \sim \text{Logistic}(0,1) \quad (12)$$

and hierarchical random effects for populations and years,

$$\xi_{\text{pop}} \sim \text{Normal}(0, \sigma_{\text{pop}}^2) \quad (13)$$

$$\sigma_{\text{pop}}^2 \sim \text{Uniform}(0,10), \quad (14)$$

$$\zeta_{\text{year}} \sim \text{Normal}(0, \sigma_{\text{year}}^2), \quad (15)$$

$$\sigma_{\text{year}}^2 \sim \text{Uniform}(0,10), \quad (16)$$

We handled missing age-class values differently for survival. For individuals that had a numeric age assigned at the time of capture (or were classified as yearlings), our model allowed them to age between years such that the correct adjustment to the prime-aged reference level was made. For individuals assigned to the prime age class at capture but not given a

numeric age, we had no way of estimating the year they would enter the old age class. Therefore, we used the prime age class for the first year, but then treated the age classes in the remaining years as missing data. We assigned these missing age classes a noninformative prior from a categorical distribution such that the prime and old age classes were equally likely under the prior. We treated transitions as unidirectional: Once an individual was estimated to be in the old age class, it was not allowed to return to the prime age class. Although aging techniques are imperfect, our model assumed no uncertainty in the assignment of an age (or age class) at capture.

To assess the magnitude of pooling induced by the additive structure of our models, we estimated the parameters of a completely unpooled model wherein the probabilities of pregnancy and both summer and winter survival for each population-year were independent. For pregnancy:

$$\begin{aligned} &\text{Positive tests}_{\text{pop,year}} \\ &\sim \text{Binomial}(\text{Pr}(\text{preg})_{\text{pop,year}}, N_{\text{pop,year}}) \end{aligned} \quad (17)$$

$$\text{Pr}(\text{preg})_{\text{pop,year}} \sim \text{Beta}(1,1) \quad (18)$$



Table 2. The set of competing models explaining variations in bighorn sheep pregnancy and survival rates in 19 populations in Montana and Wyoming during 2011–2018.

Prediction	Model structure
<b>Pregnancy</b>	
Early summer conditions and body fat influence pregnancy	$\text{logit}(\text{Pr}(\text{pregnancy})) = \mu_{\text{preg}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{IFBF}} + \beta_{\text{age class}} + \beta_{\text{NDVIearly}}$
Late summer conditions and body fat influence pregnancy	$\text{logit}(\text{Pr}(\text{pregnancy})) = \mu_{\text{preg}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{IFBF}} + \beta_{\text{age class}} + \beta_{\text{NDVIlate}}$
Cumulative summer conditions and body fat influence pregnancy	$\text{logit}(\text{Pr}(\text{pregnancy})) = \mu_{\text{preg}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{IFBF}} + \beta_{\text{age class}} + \beta_{\text{NDVIcum}}$
Early summer precipitation and body fat influence pregnancy	$\text{logit}(\text{Pr}(\text{pregnancy})) = \mu_{\text{preg}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{IFBF}} + \beta_{\text{age class}} + \beta_{\text{PRECEarly}}$
Late summer precipitation and body fat influence pregnancy	$\text{logit}(\text{Pr}(\text{pregnancy})) = \mu_{\text{preg}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{IFBF}} + \beta_{\text{age class}} + \beta_{\text{PRECLate}}$
Cumulative summer precipitation and body fat influence pregnancy	$\text{logit}(\text{Pr}(\text{pregnancy})) = \mu_{\text{preg}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{IFBF}} + \beta_{\text{age class}} + \beta_{\text{PRECCum}}$
<b>Survival</b>	
Early summer conditions and winter severity influence winter survival	$\text{logit}(\text{summer survival}) = \mu_{\text{summer}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}}$ $\text{logit}(\text{winter survival}) = \mu_{\text{winter}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}} + \beta_{\text{LION}} + \beta_{\text{SWEacc}} + \beta_{\text{NDVIearly}} + \beta_{\text{PRECEarly}}$
Early summer NDVI, winter severity, and the interaction of early summer NDVI and winter severity affect winter survival	$\text{logit}(\text{summer survival}) = \mu_{\text{summer}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}}$ $\text{logit}(\text{winter survival}) = \mu_{\text{winter}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}} + \beta_{\text{LION}} + \beta_{\text{SWEacc}} + \beta_{\text{NDVIearly}} + \beta_{\text{SWEacc} \times \text{NDVIearly}}$
Early summer precipitation, winter severity, and the interaction of early summer precipitation and winter severity affect winter survival	$\text{logit}(\text{summer survival}) = \mu_{\text{summer}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}}$ $\text{logit}(\text{winter survival}) = \mu_{\text{winter}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}} + \beta_{\text{LION}} + \beta_{\text{SWEacc}} + \beta_{\text{PRECEarly}} + \beta_{\text{SWEacc} \times \text{PRECEarly}}$
Early summer conditions, winter severity, and the interaction of early summer conditions and winter severity affect winter survival	$\text{logit}(\text{summer survival}) = \mu_{\text{summer}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}}$ $\text{logit}(\text{winter survival}) = \mu_{\text{winter}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}} + \beta_{\text{LION}} + \beta_{\text{SWEacc}} + \beta_{\text{NDVIearly}} + \beta_{\text{PRECEarly}} + \beta_{\text{SWEearly} \times \text{NDVIearly}} + \beta_{\text{SWEacc} \times \text{PRECEarly}}$
Late summer conditions and winter severity influence winter survival	$\text{logit}(\text{summer survival}) = \mu_{\text{summer}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}}$ $\text{logit}(\text{winter survival}) = \mu_{\text{winter}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}} + \beta_{\text{LION}} + \beta_{\text{SWEacc}} + \beta_{\text{NDVIlate}} + \beta_{\text{PRECLate}}$
Late summer NDVI, winter severity, and the interaction of late summer NDVI and winter severity affect winter survival	$\text{logit}(\text{summer survival}) = \mu_{\text{summer}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}}$ $\text{logit}(\text{winter survival}) = \mu_{\text{winter}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}} + \beta_{\text{LION}} + \beta_{\text{SWEacc}} + \beta_{\text{NDVIlate}} + \beta_{\text{SWEacc} \times \text{NDVIlate}}$
Late summer precipitation, winter severity, and the interaction of late summer precipitation and winter severity affect winter survival	$\text{logit}(\text{summer survival}) = \mu_{\text{summer}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}}$ $\text{logit}(\text{winter survival}) = \mu_{\text{winter}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}} + \beta_{\text{LION}} + \beta_{\text{SWEacc}} + \beta_{\text{PRECLate}} + \beta_{\text{SWEacc} \times \text{PRECLate}}$
Late summer conditions, winter severity, and the interaction of late summer conditions and winter severity affect winter survival	$\text{logit}(\text{summer survival}) = \mu_{\text{summer}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}}$ $\text{logit}(\text{winter survival}) = \mu_{\text{winter}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}} + \beta_{\text{LION}} + \beta_{\text{SWEacc}} + \beta_{\text{NDVIlate}} + \beta_{\text{PRECLate}} + \beta_{\text{SWEacc} \times \text{NDVIlate}} + \beta_{\text{SWEacc} \times \text{PRECLate}}$
Cumulative summer conditions and winter severity influence winter survival	$\text{logit}(\text{summer survival}) = \mu_{\text{summer}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}}$ $\text{logit}(\text{winter survival}) = \mu_{\text{winter}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}} + \beta_{\text{LION}} + \beta_{\text{SWEacc}} + \beta_{\text{NDVIcum}} + \beta_{\text{PRECCum}}$
Cumulative summer NDVI, winter severity, and the interaction of cumulative summer NDVI and winter severity affect winter survival	$\text{logit}(\text{summer survival}) = \mu_{\text{summer}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}}$ $\text{logit}(\text{winter survival}) = \mu_{\text{winter}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}} + \beta_{\text{LION}} + \beta_{\text{SWEacc}} + \beta_{\text{NDVIcum}} + \beta_{\text{SWEacc} \times \text{NDVIcum}}$
Cumulative summer precipitation, winter severity, and the interaction of cumulative summer precipitation and winter severity affect winter survival	$\text{logit}(\text{summer survival}) = \mu_{\text{summer}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}}$ $\text{logit}(\text{winter survival}) = \mu_{\text{winter}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}} + \beta_{\text{LION}} + \beta_{\text{SWEacc}} + \beta_{\text{PRECCum}} + \beta_{\text{SWEacc} \times \text{PRECCum}}$

(Table 2. *Continued.*)

Prediction	Model structure
Cumulative summer conditions, winter severity, and the interaction of cumulative summer conditions and winter severity affect winter survival	$\text{logit}(\text{summer survival}) = \mu_{\text{summer}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}}$ $\text{logit}(\text{winter survival}) = \mu_{\text{winter}} + \xi_{\text{pop}} + \zeta_{\text{year}} + \beta_{\text{age class}} + \beta_{\text{LION}} + \beta_{\text{SWEacc}}$ $+ \beta_{\text{NDVICum}} + \beta_{\text{PRECCum}} + \beta_{\text{SWEacc} \times \text{NDVICum}} + \beta_{\text{SWEacc} \times \text{PRECCum}}$

*Notes:* In our survival model suite, we included in all competing models (1) additive random effects of population ( $\xi_{\text{pop}}$ ) and year ( $\zeta_{\text{year}}$ ) on summer and winter survival, (2) the effect of mean predicted mountain lion risk values within a population's winter range ( $\beta_{\text{LION}}$ ) on winter survival, (3) the effect of age class ( $\beta_{\text{age class}}$ ), and (4) the effects of cumulative winter severity ( $\beta_{\text{SWEacc}}$ ) on winter survival. The 12 competing survival models investigated the effects of early ( $\beta_{\text{NDVIearly}}, \beta_{\text{PRECEarly}}$ ), late ( $\beta_{\text{NDVIlate}}, \beta_{\text{PRECLate}}$ ), and cumulative ( $\beta_{\text{NDVICum}}, \beta_{\text{PRECCum}}$ ) summer weather conditions and interactive effects of summer weather conditions and winter severity on winter survival.

where Positive tests<sub>pop,year</sub> was the number of positives tests in population and year. For survival,

$$\text{Fate}_{i,t} \sim \text{Bernoulli}(S_{\text{season},i,\text{pop},i,t,\text{year},i,t}^{1/182.5}) \quad (19)$$

$$S_{\text{season},i,\text{pop},i,t,\text{year},i,t} \sim \text{Beta}(1,1) \quad (20)$$

where the daily probability of survival ( $S_{\text{season},i,\text{pop},i,t,\text{year},i,t}^{1/182.5}$ ) was based on independent probabilities of survival for each season (summer, winter), population, and year.

We approximated the posterior distribution of model parameters using the Markov chain Monte Carlo methods, implemented using the runjags interface (Denwood 2016) to the JAGS program (Plummer 2017) in the R programming environment (R Core Team 2013). We ran pregnancy models using three chains with a total of 50,000 iterations per chain and the first 5000 discarded. We ran survival models using three chains with a total of 10,000 iterations per chain and the first 5000 discarded. We graphically assessed model convergence using traceplots for each estimated parameter, as well as the Gelman-Rubin convergence diagnostic (Gelman and Rubin 1992).

### Competing models

We developed 6 competing pregnancy models that included the early and late precipitation and NDVI covariates, body fat, and age class based on plausible biological hypotheses as to how these covariates may influence pregnancy (Table 2). These pregnancy models share many structural components and differ only in two respects: the index of growing season conditions (NDVI or precipitation) and the timing of the growing season covariate (early, late, or

cumulative). We hypothesized that higher precipitation and integrated NDVI during the previous summer may result in better forage resources and increase pregnancy the following fall; however, we were uncertain as to the relative importance of early summer, late summer, or cumulative summer conditions on pregnancy, so we evaluated models for each period. Last, we hypothesized that animals entering the winter with more body fat were more likely to be pregnant.

For survival, we developed 12 competing models that used a combination of indices for seasonal growing conditions, age class, winter severity, and predation risk (Table 2). Similar to pregnancy, these models share many structural components. These survival models differ in two respects: the complexity of the models (main effects only, interactions between either NDVI and SWE or PREC and SWE, or interactions between both NDVI and SWE and PREC and SWE) and the timing of the covariates (early, late, or cumulative). We predicted that accumulated snow water equivalence and mountain lion risk would affect winter survival and included these two covariates in all survival models. We predicted that low summer precipitation and NDVI followed by severe winters may result in lower overwinter survival rates. However, we were uncertain as to which portion of the summer season was influential in determining animal condition entering winter, or if precipitation, NDVI, or the combination of precipitation and NDVI most affected survival. Therefore, we competed 12 models that included the main effects of early summer, late summer, and cumulative summer precipitation and NDVI and the

interactive effects of precipitation and NDVI with winter severity on overwinter survival (Table 2).

### Model selection

Our two key goals were to estimate the distribution of bighorn sheep survival and pregnancy rates and evaluate the effects of covariates on variation in pregnancy and survival rates. To accomplish both goals, we used the Bayesian predictive information criterion (BPIC, Link and Sauer 2016) to estimate the predictive ability of our models. For pregnancy models, we approximated the conditional predictive ordinate (CPO) for each individual pregnancy test by estimating the model using the rest of the data set (omitting the individual test) and evaluating the density of the predictive distribution for the omitted test at the value of the covariates observed for the test sample. For survival models, it was computationally impractical to do a full leave-one-out cross-validation due to model run times. A large body of empirical research suggests that adult ungulates, including bighorn sheep, maintain high survival rates (Gaillard et al. 2000, Conner et al. 2018), which is consistent with the relatively few deaths seen in our data set ( $n = 155$ ). Therefore, the more rigorous test of model fit is to assess the power of the model to predict the rare case of death. To reduce the computational requirements of full leave-one-out cross-validation and at the same time provide a rigorous assessment of predictive power, we chose to focus on the ability of these models to predict the fates of animals that died. We evaluated the ability of each survival model to predict an individual's fate categorized as dead (dead at the end of the study) when all data for that animal were left out. The BPIC for an entire model (BPIC<sup>m</sup>) was calculated as follows:

$$\text{BPIC}^m = \sum_j \log(\text{CPO}_j^m) \quad (21)$$

where  $j = 1, \dots, j$  denotes the held-out records of individual  $j$ , and  $\text{CPO}_j^m$  is the mean of the posterior distribution for the conditional predictive ordinate for held-out record  $j$  and model  $m$ . In contrast to the Akaike information criterion or

similar deviance-based metrics for model selection, a higher BPIC score indicates a better predictive model. Therefore, we ranked models ranked from lowest BPIC score to highest BPIC score with the interpretation of increasing predictive power.

### Goodness of fit

We used posterior predictive checks to assess the adequacy of model fit for both pregnancy and survival models (Gelman et al. 1996). For each sample of the approximate posterior distribution, we generated a replicated data set and then compared the replicated data set to the observed data set using a discrepancy statistic. Better-fitting models have p-values closer to 0.50, and grossly inadequate models have p-values close to 0 or 1 (Gelman et al. 1996). Given the evidence for overall high pregnancy rates in bighorn sheep (Festa-Bianchet 1988), we wanted to ensure that our models could replicate the rarer case of nonpregnancies. Therefore, we compared the number of nonpregnancies in simulated data to the observed data and calculated a Bayesian p-value as the mean proportion of simulations where the replicated number of nonpregnancies was less than the observed number of nonpregnancies. For survival models, we assessed the goodness of fit of our top model by focusing on mortalities in the data set. For those individuals that died, we compared the observed failure time to the failure times in replicated data sets and generated a Bayesian  $P$ -value as the mean proportion of simulations, where the replicated failure time was less than the observed failure times. Differences in goodness-of-fit metrics derived from posterior predictive checks do not have as simple an interpretation as BPIC scores (e.g., it is not clear what the practical difference is between a model with a Bayesian p-value derived from a posterior predictive check of 0.4 and one with a value of 0.35). Rather, they are used as a check to make sure that the models can at least approximate the data-generating mechanism, that is, to make sure that the top model chosen using BPIC is still a biologically reasonable model (a point that the relative score of BPIC cannot address). We estimated goodness-of-fit metrics on the top-performing models for both pregnancy and survival to assess this approximation.

RESULTS

We sampled a total of 703 individuals from 19 populations during biological years 2011–2018 for some combination of pregnancy, survival, and/or movement monitoring through GPS collaring. Populations ranged in size from approximately 36–466 animals (Appendix S2: Table S1). The pregnancy data set included 669 samples collected from 576 individual animals in 17 populations over 8 yr (Fig. 2). The overall mean pregnancy rate (number of positive tests divided by the total number of tests) was 0.89. Annual

population mean pregnancy rates ranged from 0.42 in the Jackson population during 2012 to 1.0 (multiple cases of populations in which every animal tested positive for pregnancy) across populations and years (Fig. 2). In the pregnancy data set, we had repeat pregnancy tests ( $\geq 2$  samples) from 69 individuals from 7 populations (SouthMadison, Jackson, Wapiti, FrancsPeak, CastleReef, LostCreek, Whiskey) with a median number of two repeated samples from these 69 individuals (min = 2, max = 4). Of the 669 samples, 42 were from yearlings, 560 were from prime-aged animals, 59 were from old animals,

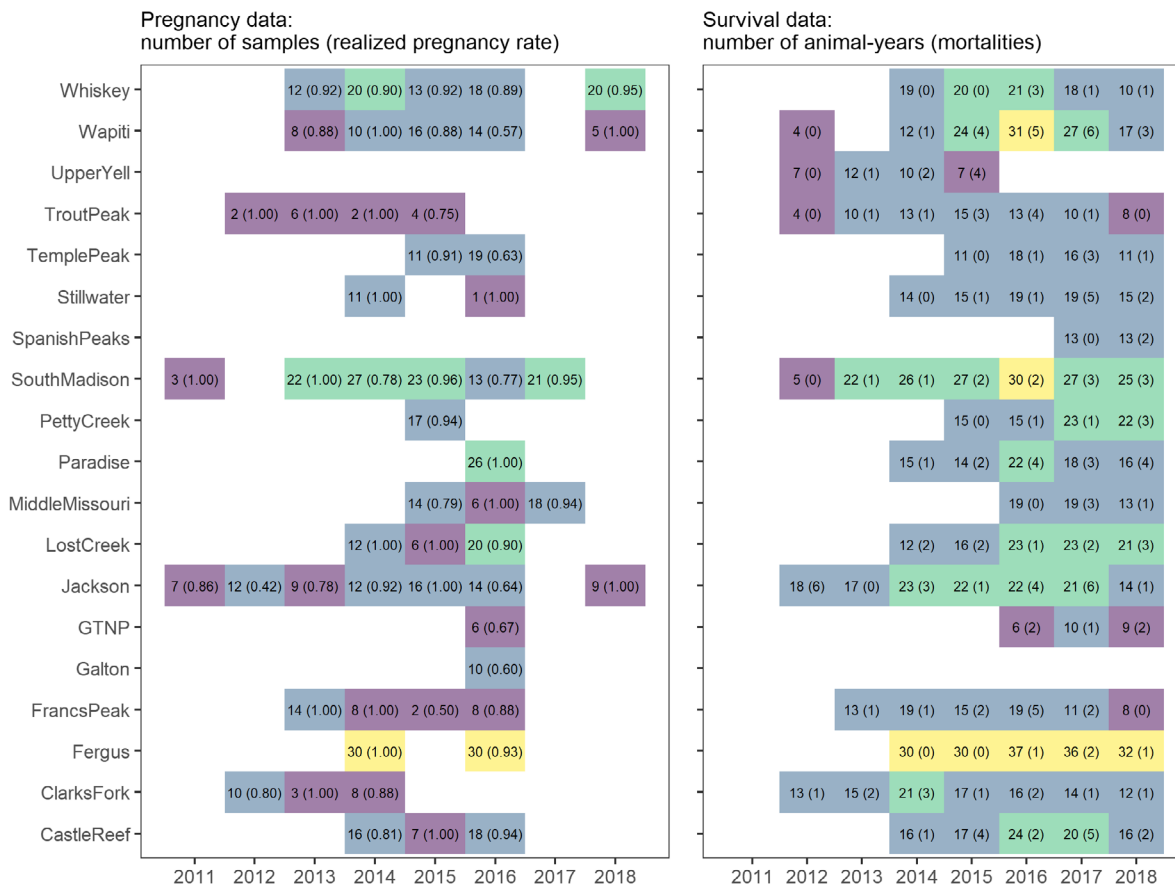


Fig. 2. Summary of pregnancy and survival data from 19 populations of bighorn sheep during the 2011–2018 biological years. Biological years correspond to the period of 1 June–31 May and reference the year of birth (i.e., the 1 June year). The values in the left panel represent the number of animals sampled for pregnancy and realized pregnancy rate (in parentheses) for each population in each biological year. The values in the right panel represent the number of animal-years included in the survival data set and the number of mortalities (in parentheses) that occurred for each population in each biological year. Population-years with sample sizes of 1–9 are shown in purple, 10–19 are shown in blue, 20–29 are shown in green, and  $\geq 30$  are shown in yellow.



and 8 were missing age data. For the body fat data, we had a total of 297 samples from 278 individuals in 12 populations and repeated measurements on 19 individuals from 3 populations (SouthMadison, CastleReef, LostCreek, Appendix S4: Fig. S1).

The survival data set included information for 466 animals from 18 populations and 1557 animal-years (Fig. 2). At the time of capture, 24 were yearlings, 355 were prime-aged, 19 were old, and 68 were missing age-class information at capture. Of the 355 individuals that were prime-aged at capture, 122 were missing a numerical age; therefore, the age class in all subsequent years was treated as missing data. We had 155 mortalities over the course of the 7 years of survival data collection (Appendix S4: Fig. S8). Across population-years, the number of mortalities ranged from 0 ( $n = 52$ ) to 6 ( $n = 3$ ) with a median number of mortalities across all populations in each year of 26 (range from 6 to 30) and a median number of mortalities in each population across all years of 9.5 (range from 2 to 21).

We collected GPS data from a total of 455 individuals and 1080 animal-years (Appendix S3). Across the populations for which we had GPS data ( $n = 18$ ), the size of the annual, summer, and winter home ranges averaged 493 km<sup>2</sup> (range: 89–1376 km<sup>2</sup>), 409 km<sup>2</sup> (range: 67–1132 km<sup>2</sup>), and 258 km<sup>2</sup> (range: 72–699 km<sup>2</sup>), respectively. The values for the single population for which we only had home ranges derived from expert opinion were lower (101, 90, and 12 km<sup>2</sup>) but within the variation observed in GPS-collared populations for annual and summer ranges.

Mean covariate values across seasonal ranges are presented in Appendix S2: Table S1. Covariate values displayed considerable variation among populations and years (Appendix S4: Figs. S2–S5), and pairwise correlations between covariate values suggested collinearity was not a concern (Appendix S4: Figs. S6–S7).

### Pregnancy modeling results

BPIC scores were similar for all the models, which suggest that the competing models had similar predictive ability (Fig. 3a). This ambiguity in model selection was compounded by the lack of a guideline for how to interpret differences among BPIC scores. However, the biological inference across the models for the effects of age class and

body fat was consistent, and the only model that demonstrated a significant relationship between covariates and pregnancy was our top model (Appendix S5: Fig. S1). Given these results, we selected the single top model that included early-season NDVI for biological inference and predictions (model 1, Table 2). The top model had a Bayesian  $P$ -value of 0.495, which indicates that the model adequately fit the data.

The median estimated probability of pregnancy for each individual sample ranged from 0.484 (90% highest posterior density interval = 0.184, 0.777) to 0.987 (0.959, 1.00), with an overall (across all population-years and individuals) median value of the probability of pregnancy of 0.924 (0.902, 0.946; Fig. 4a). Early-season integrated NDVI was related positively to pregnancy ( $\hat{\beta}_{\text{NDVI}_{\text{early}}} = -0.691$  (0.27, 1.13); Fig. 5a). With all other covariates including population and year effects held to their mean values, this relationship translated into changes in predicted probabilities of pregnancy from 0.883 (0.774, 0.965) at minimum observed NDVI<sub>early</sub> value to 0.990 (0.968, 1.00) at the maximum observed value (Fig. 6a). We found suggestive but inconclusive evidence for a positive association between IFFB and the probability of pregnancy ( $\hat{\beta}_{\text{IFFB}} = 0.329$  (−0.021, 0.678); Fig. 5a). The predicted probabilities of pregnancy varied from 0.828 (0.608, 0.977) at the minimum observed value of IFFB to 0.978 (0.931, 0.999) at the maximum observed value of IFFB (Fig. 6a). The top model predicted the median IFFB value of non-pregnant individuals as 14.36 (6.474, 20.640) and the median IFFB value of pregnant individuals as 15.05 (8.243, 21.967). The pregnancy rate for yearlings was lower than that for prime-aged animals ( $\hat{\beta}_{\text{yearling}} = -1.653$  (−2.473, −0.858); Fig. 5a), which translated into a median pregnancy rate for yearlings of 0.731 (0.510, 0.917) compared with 0.933 (0.871, 0.981) for prime-aged animals (Fig. 7a). In contrast, we found no evidence that pregnancy differed between prime-aged and old animals. Pregnancy rates varied among years ( $\hat{\sigma}_{\text{year}} = 1.147$  (0.511, 1.978); Fig. 5a), with lower than expected pregnancy rates in winter 2012–2013 and 2016–2017 (Fig. 8 a). Finally, we found some evidence for among-population variation in pregnancy ( $\hat{\sigma}_{\text{pop}} = 0.637$  (0.177, 1.178)); however, each 90% highest posterior density interval for population-level

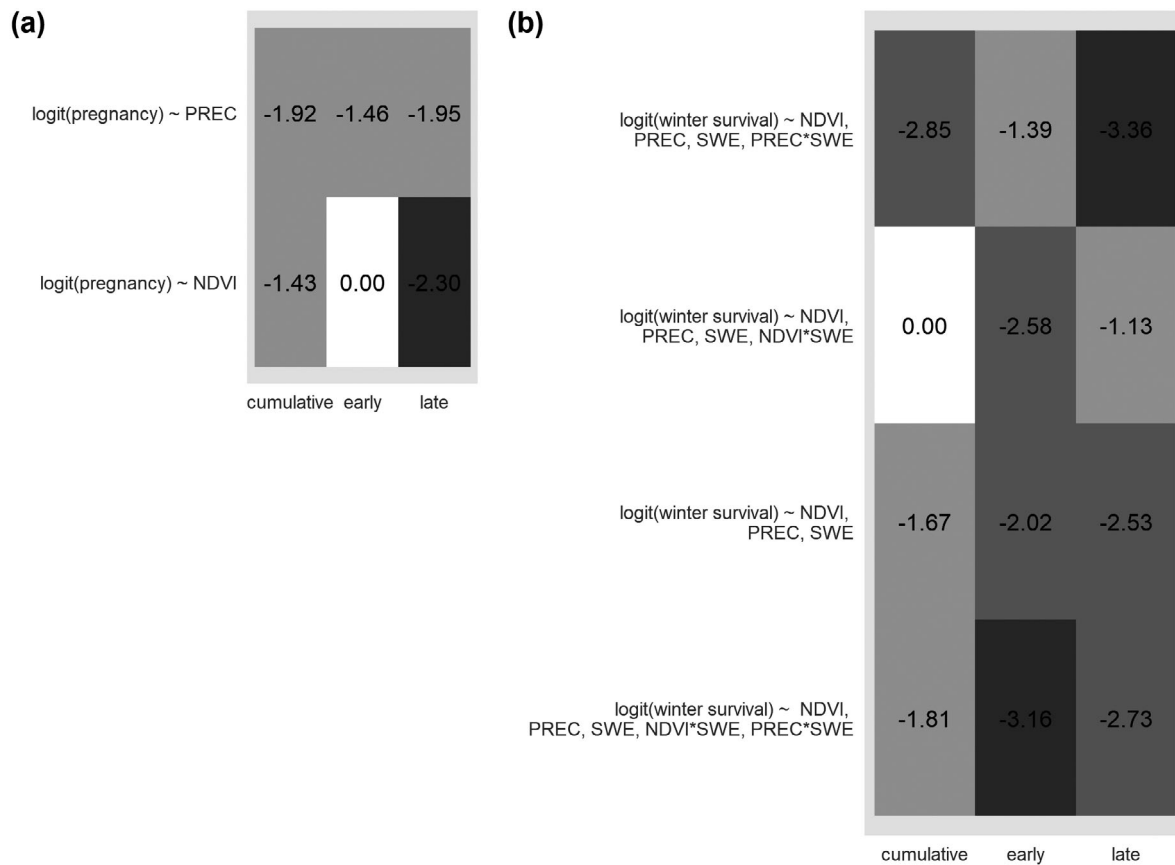


Fig. 3. Model selection results for bighorn sheep pregnancy and survival models of 19 populations of bighorn sheep during 2011–2018. The numbers denote the difference in Bayesian predictive information criterion (BPIC) values between each competing model and the top model (denoted with 0.00) for (a) pregnancy models and (b) survival models. Results are shown as a function of the model structure on the  $y$ -axis (e.g., NDVI, or PREC, or NDVI  $\times$  SWE; see Table 2) and timing of the covariate on the  $x$ -axis (cumulative, early, or late season). Better predictive models have higher BPIC scores and are represented by lighter values.

overlapped zero and prevented strong inference (Fig. 8b).

However, we note that these estimates were influenced by the additive structure of the model used to assess the strength of evidence for environmental effects on the probability of pregnancy. The estimated model parameters (the covariate model with additive random effects of population and year) were influenced by the unbalanced sample sizes (Fig. 2). Post hoc, we used the posterior distribution for the estimated probabilities of pregnancy for each individual sample within a population-year to calculate a population-year level probability of pregnancy and then compared that estimate to

one from a completely unpooled model with an independent probability of pregnancy for every population-year. Population-years with more data had a substantial impact on point estimates of the probabilities of pregnancy (Appendix S5: Fig. S3). For example, in the Trout Peak population in 2015 the estimated population-year probability of pregnancy from the covariate model was 0.922 (0.854, 0.994). This estimate was substantially different from the unpooled model (0.667 (0.394, 0.955)) and highlighted a pattern in the covariate model wherein population-years with little data were pulled upwards to the mean value for that year.

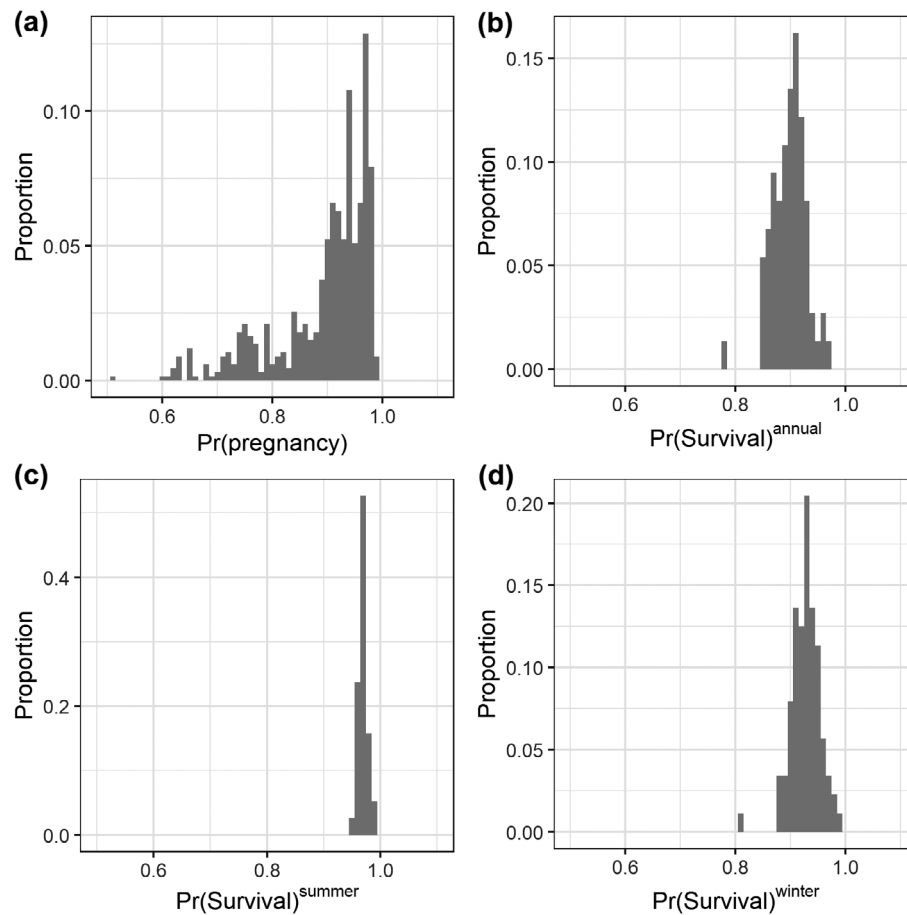


Fig. 4. The distribution of estimated median probabilities of pregnancy (a), and the distributions of estimated median population-year annual (b), summer (c), and winter survival rates (d) for 17 populations of bighorn sheep during 2011–2018. For each panel, we used the median of the approximate posterior distribution for each parameter (e.g., the probability of pregnancy for an individual, or the probability of summer survival for a population-year) as the point estimate, the distributions of which are shown below. These histograms represent the integrated result of observed variation in covariate values and estimated random effects of year and populations.

#### Survival modeling results

Model selection results from the survival analysis indicated that the model including cumulative metrics of growing season conditions and an interaction between  $NDVI_{cum}$  and  $SWE_{acc}$  (model 10, Table 2) was best supported by the data (Fig. 3b). Similar to the pregnancy analysis, the difference in BPIC scores was slight among all of the models (Fig. 3b). However, the strength and direction of covariate effects were similar in all of the competing survival models (Appendix S5). Given consistency across models, we used the single top model for biological inference. The

goodness of fit was adequate for the top model (Bayesian  $P$ -value = 0.573).

Seasonal and annual survival rates varied considerably. With all other covariates held to their mean values, predicted survival rates for prime-aged animals were lower in winter ( $\hat{S}_{winter} = 0.935$  (0.914, 0.955)) than summer ( $\hat{S}_{summer} = 0.971$  (0.959, 0.982); Fig. 4b). Summer survival rates for prime-aged animals across all population-years were high, with a range from 0.954 (0.926, 0.977) to 0.987 (0.977, 0.996) and an overall median across all population-years of 0.970 (0.960, 0.980). In contrast, estimated winter

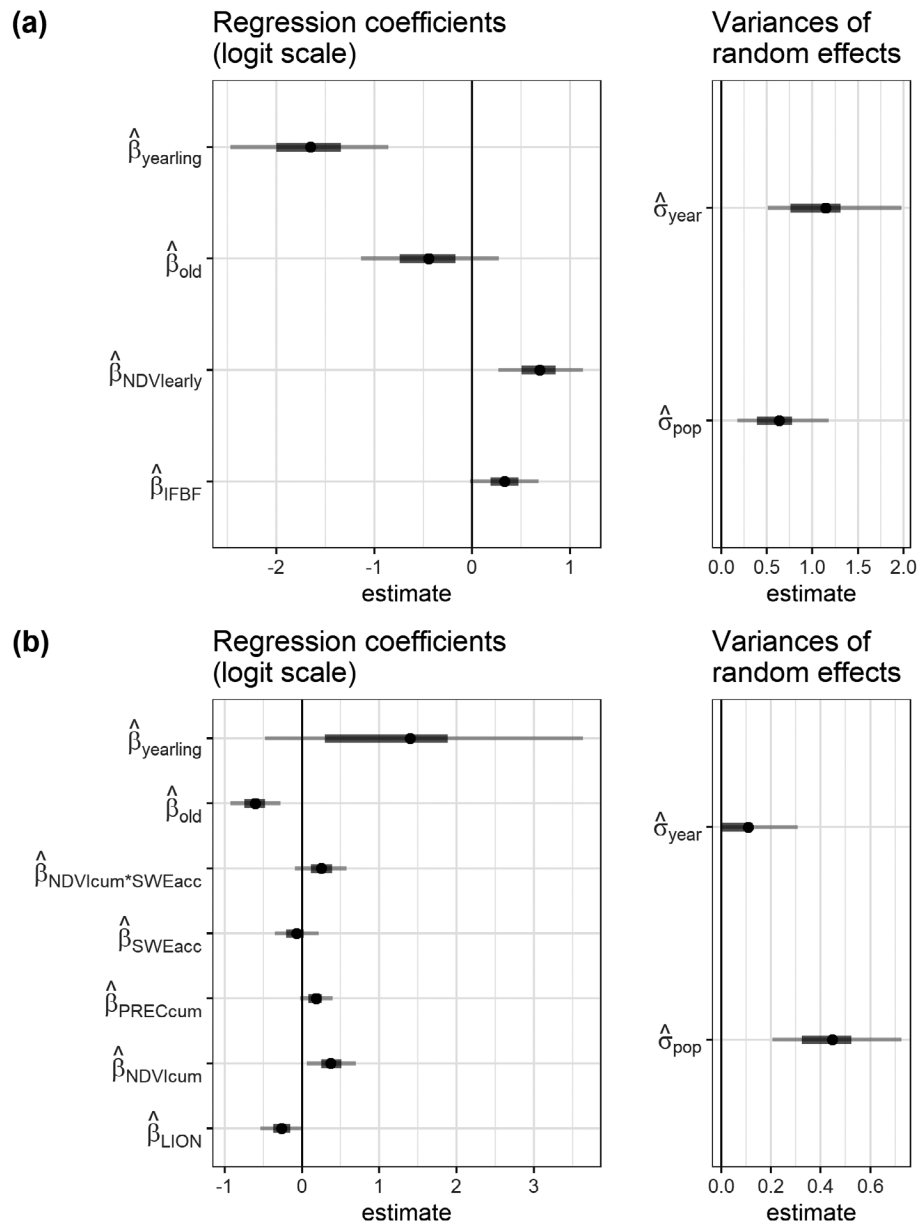


Fig. 5. Estimated coefficients from the top-ranked model for bighorn sheep pregnancy rates (a) and survival rates (b) in Montana and Wyoming. Pregnancy covariates include age class (yearling, prime, old), NDVI, and IFBF. Survival covariates include age class, precipitation (PREC), NDVI, mountain lion risk (LION), and accumulated winter snow water equivalence ( $\text{SWE}_{\text{acc}}$ ). The dot depicts the median estimate, the thick box represents the 50% highest posterior density interval, and the thin line represents the 90% highest posterior density interval.

survival rates tended to be lower with a range from 0.807 (0.637, 0.947) to 0.985 (0.969, 0.997) and an overall median value across all population-years of 0.930 (0.913, 0.947). Variation in seasonal rates translated into a distribution of

annual survival rates for prime-aged females with a range from 0.780 (0.614, 0.921) to 0.970 (0.948, 0.989) and a median value across all population-years of 0.901 (0.879, 0.923); however, we note the minimum value of annual is an outlier



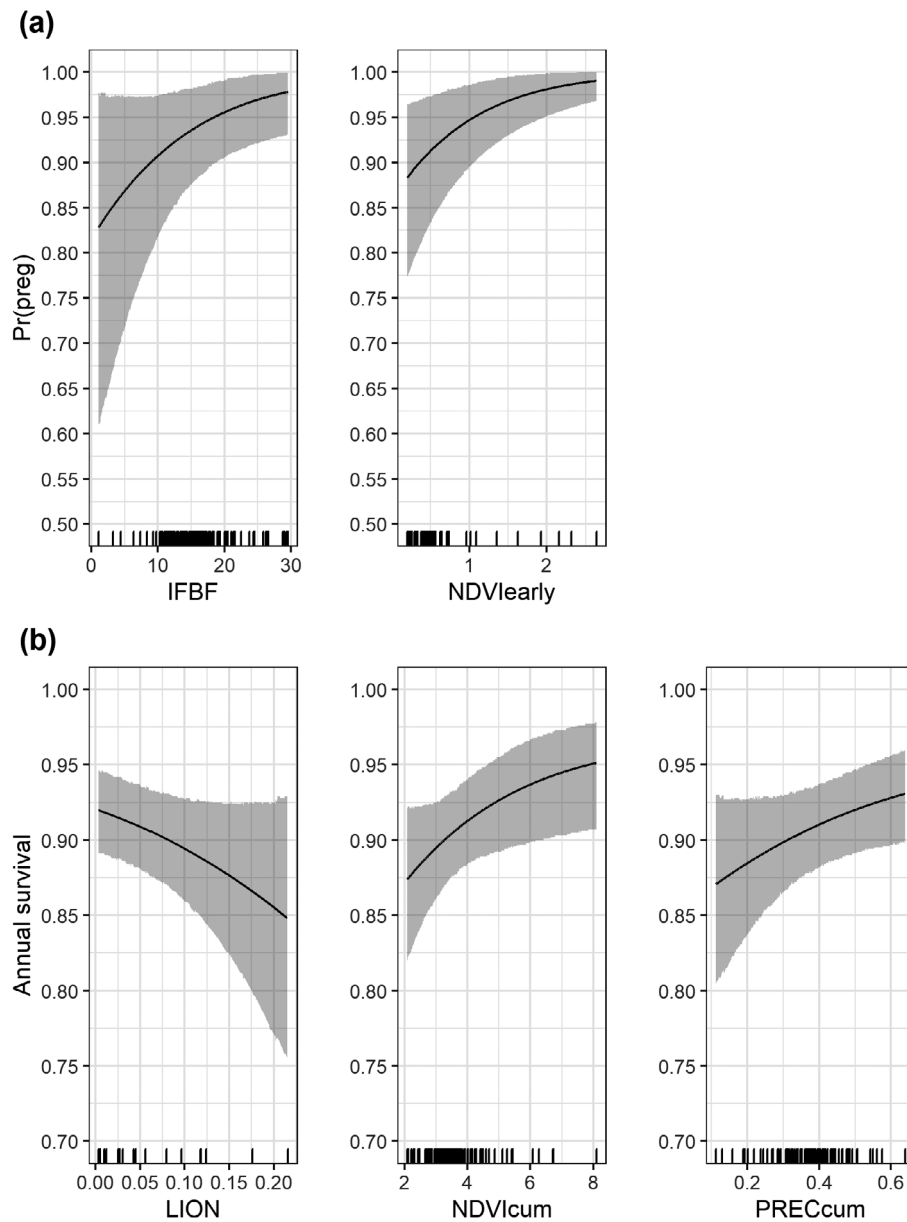


Fig. 6. The predicted relationships between covariates and vital rates for the top model from (a) pregnancy and (b) survival. Pregnancy covariates include age class, NDVI, and IFBF. Survival covariates include age class, precipitation (PREC), NDVI, mountain lion risk (LION), and accumulated winter snow water equivalence ( $SWE_{acc}$ ). Predictions are estimated from the top-ranked model for each rate for prime-aged animals with the random effect of population and year at zero and with all other covariates help to their mean value. The black line is the median, and the gray interval represents the 90% highest posterior density interval.

relative to the rest of the distribution of estimated annual survival rates (Fig. 4b). Annual survival rates of old-aged females were lower, with a median across all population-years of 0.830 (0.797, 0.863) and a range from 0.653 (0.433, 0.843) to 0.947 (0.907, 0.981).

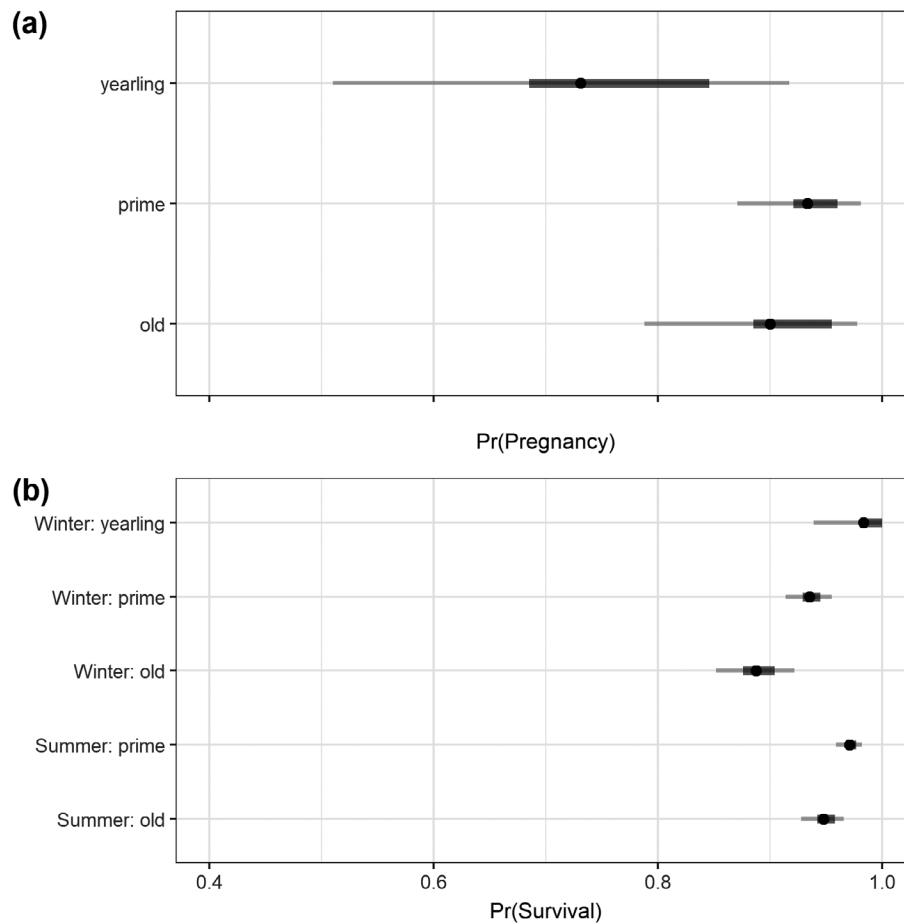


Fig. 7. Estimated overall median vital rates predicted from the top-ranked pregnancy model (a) and survival model (b), holding all covariates including the population and year effect to their mean values for yearling, prime, and old-aged bighorn sheep. The dot depicts the median, the thick box represents the 50% highest posterior density interval, and the thin line represents the 90% highest posterior density interval.

Winter survival was associated positively with an index of growing conditions the previous summer ( $\hat{\beta}_{\text{NDVI}_{\text{cum}}} = 0.371$  (0.063, 0.695); Fig. 5b). With all other covariates including population and year effects held to their mean values, this relationship translated into predicted differences in annual survival of 0.874 (0.819, 0.921) at the minimum observed  $\text{NDVI}_{\text{cum}}$  value to 0.951 (0.907, 0.978) at the maximum observed  $\text{NDVI}_{\text{cum}}$  value (Fig. 6b). We did not find evidence that winter survival varied in response to PREC or SWE values. We found weak evidence for a relationship between LION and winter survival ( $\hat{\beta}_{\text{LION}} = -0.263$  (-0.534, 0.013); Fig. 5b) that translated into a predicted large, yet uncertain, decline in annual survival with median

values of the mountain lion RSF on winter range from 0.920 (0.891, 0.946) at the lowest value of LION to 0.848 (0.755, 0.929) at the highest value (Fig. 6b). Animals in the old age class had lower survival rates than prime-aged animals ( $\hat{\beta}_{\text{old}} = -0.605$  (-0.927, -0.276)), but we did not find evidence for a difference in survival between prime-aged and yearling animals (Fig. 5b).

We found little evidence for otherwise unaccounted for variation among years ( $\hat{\sigma}_{\text{year}} = 0.109$  (0, 0.307); Figs. 5b, 8a). We found weak evidence for among-population variation in survival ( $\hat{\sigma}_{\text{pop}} = 0.448$  (0.206, 0.726); Fig. 5b). This estimated variation, however, did not result in substantial differences among the random effects for each population (Fig. 8b). With the exception of

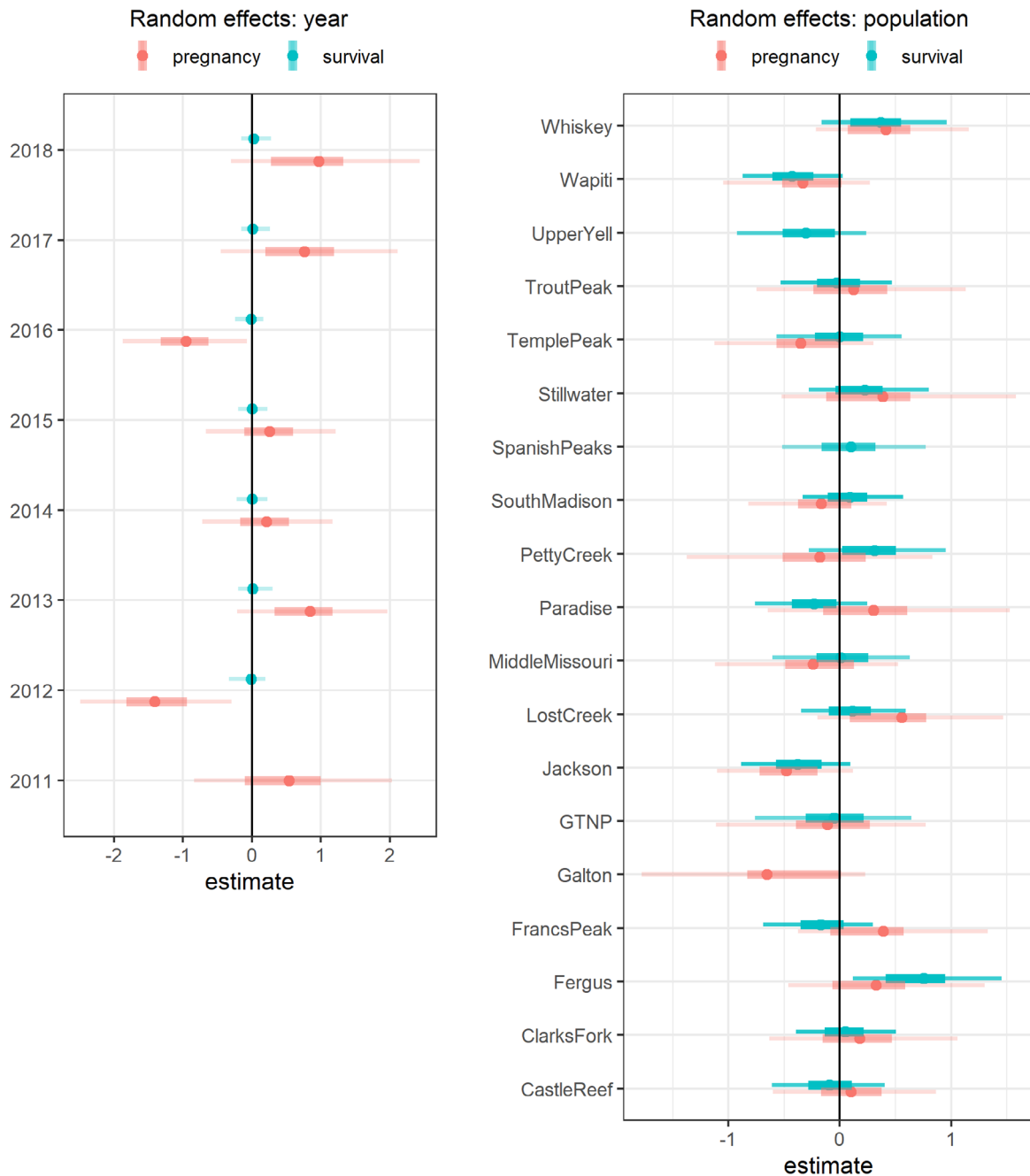


Fig. 8. Estimated random effects (on the logit scale) of year and population on the probability of bighorn sheep pregnancy and survival from the top-ranked models. The dot depicts the median, the thick box represents the 50% highest posterior density interval, and the thin line represents the 90% highest posterior density interval.

one population (Fergus), uncertainty in the resulting estimated random effects prevented strong inference as to differences among populations.

Similar to pregnancy, estimates of annual survival from the covariate model were strongly influenced by the unbalanced sample size of collars across populations and years (Fig. 2). We

compared the estimates of annual survival from the covariate model to the unpooled model that had independent season- and population-year-specific probabilities of seasonal survival. Population-years with more data had a substantial impact on point estimates of the probabilities of annual survival (Appendix S5: Fig. S4). For example, in the Trout Peak population in 2012 the estimated population-year probability of annual survival from the covariate model was 0.891 (0.828, 0.945). This estimate was substantially different from the unpooled model (0.405 (0.019, 0.772)), reflecting the fact that a single collar was deployed in that population from the first day of summer (2012-06-01) to February the following spring (2013-02-08).

## DISCUSSION

We characterized the distribution of the estimated probabilities of survival and pregnancy for 19 bighorn sheep populations in Wyoming and Montana during 2011–2018 and identified important factors driving regional variability in these key vital rates. Summer growing season conditions, as indexed by integrated NDVI, positively influenced probability of pregnancy and winter survival, highlighting the important relationship between summer growing season conditions, bighorn sheep physiological status, and the resulting effect on vital rates. Our results characterize the distribution and sources of variation of two important vital rates for bighorn sheep and broadly support the dominant paradigm of ungulate demography (Eberhardt 2002). Although we document nontrivial changes in both pregnancy and winter survival rates associated with environmental variation, our results are consistent with this paradigm insofar as adult female survival rates were higher and had less variation than pregnancy rates. Furthermore, after accounting for variation in environmental conditions, we found strong evidence for otherwise unaccounted for variation among years and populations in pregnancy rates, and essentially no evidence for similar variation in survival rates (Fig. 8).

Survival of prime age-aged females was relatively high and stable across years and populations, particularly during summer. Other studies have indicated that survival of adult bighorn may be severely reduced by disease outbreaks

(Jorgenson et al. 1997, Cassirer and Sinclair 2007) or cases of specialized predation by mountain lions (Festa-Bianchet et al. 2006, Conner et al. 2018). In our study, only 2 of 28 animals that died of known causes were classified as disease-related mortalities (although the cause of death was uncertain in 127 of 155 cases) and we expect our vital rate estimates to largely represent vital rates typical of populations in the absence of disease epizootics. In the absence of these sporadic instances, survival of prime-aged adult females in our study and elsewhere is relatively high and stable; estimates of annual survival from our top model, 0.901 (0.879, 0.923; based on average conditions), are similar to other estimates in the northern Rocky Mountain region of 0.94 (95% CI = 0.89–0.97, Yellowstone National Park; White et al. 2008), 0.94 (SE = 0.007, Ram Mountain, Alberta, based on periods without high levels of predation; Festa-Bianchet et al. 2006), and 0.92 (SE = 0.014, Sheep River, Alberta, based on periods without high levels of predation; Festa-Bianchet et al. 2006). Longitudinal studies of bighorn sheep survival provide strong evidence for senescence-related declines in survival after age 7 (Jorgenson et al. 1997, Festa-Bianchet et al. 2006). Our result demonstrating lower survival rates for old age-class animals is consistent with those results; however, our results related to senescent declines should be interpreted with caution as (1) our study was cross-sectional rather than longitudinal, (2) aging techniques were imperfect, and (3) sample sizes of old animals were small in some populations. Although our estimates of yearling survival were similar to adult survival, our yearling survival estimates were likely biased high because we captured animals in December or January and censored mortalities within 14 d of capture. This resulted in most yearlings being exposed to potential mortality for only 2–3 months toward the end of the winter period, rather than the entire winter period.

Survival of adult female bighorn sheep in our study varied across the 7 yr and 18 populations, and better summer growing season conditions, as indexed by higher NDVI<sub>cumv</sub>, were related to higher winter survival. NDVI<sub>cum</sub> provided an index of primary production within each populations' summer range during the growing season and is frequently interpreted as a proxy for annual forage productivity (Hamel et al. 2009,



Pettorelli et al. 2011). We infer that following summers characterized by high annual forage productivity, adult female bighorn sheep enter the energy-limited winter period in better physical condition to survive the winter period, as compared with survival following summers with lower forage productivity. This interpretation is broadly consistent with the documented effects of summer–fall nutrition on probability of overwinter survival from other ungulate species (Cook et al. 2004, Bender et al. 2008, Parker et al. 2009, Monteith et al. 2014), which confirms that individuals with greater fat reserves entering winter may have higher winter survival than individuals with lower reserves. Our body fat data set was incomplete across all 17 populations and did not allow for a reliable, individual-level evaluation of the relationship between body fat and overwinter survival as would have been ideal, and modeling results linking IFBF to survival were inconclusive. Our inference is therefore based on using NDVI as a proxy for annual variation in population-level forage productivity.

Our results demonstrate biologically relevant variation in the probabilities of winter survival ranging from 0.807 to 0.985 (Fig. 6b) in association with variable environmental conditions. This amount of variation is sufficient to impact population growth rates (Wittmer et al. 2005, Johnson et al. 2010, Bourbeau-Lemieux et al. 2011), which suggests winter survival may limit bighorn sheep populations. Indeed, although pneumonia epizootics are widely acknowledged to significantly reduce survival rates (Jorgenson et al. 1997), all-age die-offs are relatively rare and may not impact population abundance more than multiple years of adverse environmental conditions. In northern latitudes and alpine conditions, ungulates are often exposed to extreme winter conditions. Snow depth influences energy expenditure during locomotion (Parker et al. 1984, 1999) and may limit food acquisition (White et al. 2009). Winter is often critical because low temperatures, rain events, and strong winds may increase metabolic costs associated with thermoregulation (Parker and Robbins 1985). This combination of sparse nutrient availability and high metabolic costs has the potential to reduce winter survival and highlights the need for animals to accrue sufficient resources during the summer growing season to

buffer against the metabolic costs of the harsh winter period.

The aggregation of animals on winter ranges, combined with the effects of the winter period on animal condition, may predispose bighorn sheep to predation during winter. Although this study was not designed to evaluate the effects of predation on bighorn sheep, we did find weak evidence that an index of population abundance of mountain lions negatively influenced winter survival of bighorn sheep. The effects of mountain lion predation on bighorn sheep populations are well-documented, and mountain lion predation has the potential to influence trajectories of some bighorn sheep populations (Ross et al. 1997, Hayes et al. 2000, Rominger et al. 2004, Festa-Bianchet et al. 2006). Our index provided a coarse metric of regional variability in mountain lion abundance across a broad landscape of Montana and Wyoming. Due to difficulty accessing mortalities in remote winter ranges, we did not formally evaluate cause-specific mortality of bighorn sheep. However, when possible we did conduct mortality investigations to determine the cause of death. We estimated the cause of death for 28 of 155 mortality events and found mountain lion predation was an important source of mortality (i.e., 6 of the 28 mortalities were attributed to mountain lion predation, an additional 6 were attributed to predation with the predator species not identified, and an additional 2 were attributed to suspected but unconfirmed predation). We also found hunter harvest ( $n = 1$ ), avalanches and trauma potentially due to falls ( $n = 4$ ), and collisions with vehicles or trains ( $n = 6$ ) were sources of mortality. These results echo previous studies of bighorn sheep survival and suggest that predation may be a key limiting factor in some bighorn sheep populations and should be considered in management efforts to restore or increase bighorn sheep populations.

Bighorn sheep pregnancy rates showed substantially higher variability among years and populations compared with survival rates. Predicted median pregnancy rate for prime-aged animals was 0.933 (0.871, 0.981), similar to other studies reporting pregnancy rates of 0.91 (Singer et al. 2000b) and 0.94 (Berger 1991). Our results are unique from many other studies in that we included data from 8 yr and 17 populations, and we documented high among-population (see Fig. 8b) and within-population-years variability

in pregnancy rate, ranging from 0.42 in Jackson 2012 to 1.0 in multiple population-years. The low rates in Jackson 2012 may reflect the poor condition of bighorn sheep recovering from a documented disease event. Additionally, variability in this vital rate may result from annual and regional differences in weather and growing season conditions not captured in our covariates. We also found evidence for lower probability of pregnancy for yearlings than for prime-aged and old animals, with the predicted median pregnancy rate for yearlings of 0.731 (0.510, 0.917). Similarly, lower and variable probability of yearling pregnancy has been documented elsewhere, including Sheep Mountain, Alberta, where lactation rate for 2-yr-old animals averaged 52% across years, but annually ranged as low as 0% (Festa-Bianchet 1989). The wide predicted distribution of the probability of pregnancy across the population-years included in this study suggests this vital rate is sensitive to annual and population-level variability in resources.

Our analysis provides evidence that pregnancy rates were higher following summers with better growing season conditions during early summer, as indexed by higher NDVI<sub>early</sub>. The acquisition of high-quality nutritional resources during summer is an important driver of the level of body fat that ungulates accrue by the fall breeding period (Cook et al. 2013, 2016, Monteith et al. 2013, Proffitt et al. 2016) and can affect the subsequent probability of pregnancy (Cook et al. 2013, Stephenson et al. 2020). The positive relationship between probability of pregnancy and early summer NDVI suggests bighorn sheep accrue greater nutritional resources in summers characterized by high early summer NDVI, and the effect is biologically meaningful in translating into higher probability of pregnancy the following winter. Additionally, we found high levels of among year and among population variability in bighorn sheep body fat (Appendix S4: Fig. S1). Although other studies have documented a positive association between bighorn sheep body fat and pregnancy (Stephenson et al. 2020), we found only weak evidence that individuals with higher fall body fat levels had higher probability of pregnancy. Body fat was included in the top pregnancy model, and the coefficient relating body fat to probability of pregnancy was positive but narrowly overlapped zero. This less clear

relationship is not surprising, given body fat may be an imperfect predictor of pregnancy due to the variety of physiological mechanisms that influence ovulation and breeding (Gerhart et al. 1997, Cook et al. 2013). Additionally, a range of other individual and annual effects driving variation in body condition of ungulates may be of equal or greater importance to resultant body fat than spatial gradients in forage (Bergman et al. 2018), and thus, additional lines of inquiry are needed to fully understand the mechanisms relating nutritional resources to body fat and body fat to demography.

Together, our results regarding the distribution of the estimated probabilities of pregnancy and survival, and the identification of the important factors driving regional variability in these key vital rates, provide a foundation for understanding the dynamics of bighorn sheep populations in the Rocky Mountains, outside of documented pneumonia epizootic events. The influence of summer growing season conditions on these vital rates suggests management efforts should focus on maintaining and improving nutritional resources on bighorn sheep summer ranges, to enhance the condition of animals entering the breeding and nutrient-limited winter seasons. Additionally, future climate change has the potential to alter growing season timing and conditions, and these effects may be particularly pronounced in the alpine environment occupied by some summering bighorn sheep populations. Mountain ungulates in particular may be sensitive to changing climatic conditions (Jacobson et al. 2004, Aublet et al. 2009, White et al. 2011, 2018) as these species occupy extreme and highly seasonal environments that are predicted to experience changes in vegetation phenology and community composition in response to predicted climatic changes (Inouye 2008, Wipf et al. 2009, Gottfried et al. 2012). Within our study region, bighorn sheep populations occupy diverse landscapes from prairie populations occupying relatively arid landscapes of prairie badlands, to nonmigratory populations occupying low elevation mountain foothills, to seasonally migratory populations occupying alpine environments in summer and low elevation foothills in winter, to populations with a significant component of animals that remain year-round in high elevation alpine environments (Lowrey et al. 2020). Given

the wide diversity of regional environmental conditions experienced by the populations in our study, we would expect the impacts of climate change in the demographic performance of these populations to also be diverse. Our results suggest that climate-related changes that alter vegetation phenology and summer growing season conditions have the potential to impact bighorn sheep survival and pregnancy rates. Given this potential, we recommend careful monitoring of vegetation conditions on summer ranges to identify and mitigate potential influences of changing climatic conditions on bighorn sheep vital rates.

Additional research is necessary to understand how variability in reproduction and survival affects population growth rates and therefore shapes the population dynamics of bighorn sheep. The degree to which bighorn sheep population growth rates are influenced by variation in different vital rates is not well-understood. Moreover, for small populations, such as many of the populations included in our data set, there may be among-population variability in the relative influence of different vital rates on population growth rates such that generalizations need to be made with great care (Johnson et al. 2010). In spite of a relatively large sampling effort, we did not evaluate among-population differences in responses to environmental variation and instead our analysis revealed the important regional responses to environmental variations. Disease events may have influenced vital rates and partially explain some of the regional variance; however, uncertainty in when and where disease may have occurred prohibits a formal evaluation of these effects in our data. We found that vital rate estimates were very strongly influenced by unbalanced sample sizes among populations and years, with population-years with few individuals varying little from the overall mean values in pooled models. Given the relatively high survival and pregnancy rates, larger per-population sample sizes are needed to evaluate population-specific responses to environmental variation (i.e., evaluate random slopes, random intercept model) and design population-specific management actions to influence vital rates. Such a study would be extremely expensive and challenging to implement. A more practical option for evaluating population-specific demographic responses to environmental variation may be to combine the

best-available information on the distribution of vital rates garnered from smaller studies such as ours (used as priors) with routinely collected animal count and classification data to develop population models capable of estimating population-specific vital rates and among-population differences in the relationship of vital rates to environmental variation. The distribution of survival and pregnancy rates reported here (Fig. 7), together with animal count and classification data generated ideally from standardized survey approaches, may be used to develop integrated population models to better understand demography and manage populations.

Our study did not evaluate any density-dependent variation in vital rates, although populations are subject to a diverse set of density-dependent processes that can drive variation in probabilities of survival and reproduction. Negative density dependence is considered a ubiquitous feature of populations and has considerable empirical support (Brook and Bradshaw 2006, Bowyer et al. 2014); however, in populations of ungulates, evidence suggests it is primarily associated with declines in offspring survival and delayed primiparity (Festa-Bianchet et al. 2003), with less known about density dependence in adult survival. Positive density dependence (Allee effects) can also play a critical role in the dynamics of small or threatened populations as increasing density is associated with improved vital rates (Dennis 1989, Møller and Legendre 2001). For bighorn sheep, it is unclear how density dependence manifests as variation in the probabilities of adult survival and reproduction. There is some evidence for a positive association between yearling and adult female survival rates and population size for small populations subject to predation (Bourbeau-Lemieux et al. 2011), negative density dependence in survival for only some age classes (Jorgenson et al. 1997), a lack of density dependence in adult survival (Bonenfant et al. 2009), and confounding influences of negative density dependence and variable age structures in small populations (Festa-Bianchet et al. 2003). In light of these considerable uncertainties, we consider our assumption of density-independent processes governing variation in survival and pregnancy to be a reasonable simplification for our sampled populations (Beisinger and Westphal 1998), similar to other studies on this species (Johnson et al. 2010). However, we

acknowledge the likelihood of multiple density-dependent processes for these populations, and we suggest an improved understanding of density dependence in the probabilities of adult survival and reproduction in bighorn sheep is a key area of future work.

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