

## RESEARCH ARTICLE

# Contrasting seasonal effects of climate change influence density in a cold-adapted species

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## Abstract

Many ecological processes are profoundly influenced by abiotic factors, such as temperature and snow. However, despite strong evidence linking shifts in these ecological processes to corresponding shifts in abiotic factors driven by climate change, the mechanisms connecting population size to season-specific climate drivers are little understood. Using a 21-year dataset and a Bayesian state space model, we identified biologically informed seasonal climate covariates that influenced densities of snowshoe hares (*Lepus americanus*), a cold-adapted boreal herbivore. We found that snow and temperature had strong but conflicting season-dependent effects. Reduced snow duration in spring and fall and warmer summers were associated with lowered hare density, whereas warmer winters were associated with increased density. When modeled simultaneously and under two climate change scenarios, the negative effects of reduced fall and spring snow duration and warmer summers overwhelm the positive effect of warmer winters, producing projected population declines. Ultimately, the contrasting population-level impacts of climate change across seasons emphasize the critical need to examine the entire annual climate cycle to understand potential long-term population consequences of climate change.

## KEYWORDS

climate change, climate scenarios, population dynamics, population projections, snow cover, snowshoe hare, state-space model, temperature

## 1 | INTRODUCTION

In the northern hemisphere, predominant climate change outcomes include increased temperatures (Bintanja & van der Linden, 2013; Screen & Simmonds, 2010; Williams et al., 2015) and reduced snow cover (Kunkel et al., 2016; Pederson et al., 2011; Zhu et al., 2019). Both snow and temperature can have substantial effects on wild plant and animal phenology (Kumar et al., 2020; Martin, 2007; Rickbeil et al., 2019; Zimova et al., 2020), species interactions (Huggard, 1993; Murray & Boutin, 1991; Sirén

et al., 2022; Stenseth et al., 2004), and physiological processes (Sheriff et al., 2009, 2017; Ton & Martin, 2017). However, the multifaceted ways in which snow and temperature can contribute to changes in species density are still being elucidated, even in well-known systems (Williams et al., 2015). Furthermore, recent studies show that the demographic and physiological mechanisms connecting these abiotic changes to population dynamics may be season specific (Cordes et al., 2020; Loe et al., 2021; Paniw et al., 2019). Therefore, field-based demographic studies that test for season-specific effects are required to form the basis for

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general predictive frameworks of how climate change will affect population dynamics (Yoccoz, 2020).

Here, we focus on a species whose phenology, physiology, and population dynamics are profoundly affected by seasonal climate covariates including snow, temperature, and rain (Keith et al., 1984; Krebs et al., 2002; Mills et al., 2018; Zimova et al., 2016). Snowshoe hares (*Lepus americanus*) are a cold-adapted boreal species (Boonstra et al., 2016) that provides a crucial food resource for a diverse array of carnivores (Boutin et al., 1995). Along with 20 other species globally, snowshoe hares undergo biannual coat color molts to retain camouflage against seasonally transient snow cover (Mills et al., 2013, 2018; Zimova et al., 2018). Although snow presence can modify molt phenology in snowshoe hares (Kumar et al., 2020), this plasticity is insufficient to prevent increasing camouflage mismatch (Kumar et al., 2020; Zimova et al., 2020) or its negative fitness costs (Wilson et al., 2019; Zimova et al., 2016) occurring with shorter snow duration (Mills et al., 2013).

In addition to snow, temperature and rain can also affect hare vital rates and, consequently, hare density. Temperatures above 38°C, the upper critical temperature, and below -5°C, the lower critical temperature (Hart et al., 1965) may increase resting energy demand (Speakman, 1996, 1999), subsequently reducing hare bone marrow fat and body mass (Hodges et al., 2006; Meslow & Keith, 1971) and increasing predator-induced mortality (Hodges & Sinclair, 2003; Keith et al., 1984; Murray, 2002). Thus, warmer winters (i.e., reductions in the number of days below -5°C) may increase hare survival. In summer, hares can tolerate warm temperatures through evaporative cooling via respiration (Hart et al., 1965), but the costs of increased evaporative cooling may lower foraging efficiency, decrease body condition, and ultimately reduce survival (Du Plessis et al., 2012; Gardner et al., 2016). Furthermore, juvenile hares (leverets) may experience higher mortality due to exposure during particularly hot summers or wet springs (Krebs et al., 2002).

To quantify the effects of snow, temperature, and rain on snowshoe hare density, we analyzed a 21-year time series of summertime capture-mark-recapture data from approximately 2,000 live-trapped hares across 14 sites in two study areas in western Montana (Mills et al., 2020). We further refined hare density estimates using a Bayesian state space model consisting of both an observation model and a process model to separate nuisance measurement error (variability due to sampling) from process noise (fluctuations caused by environmental variability) (Dennis et al., 2006; Rotella et al., 2009). Using this modeling framework, we evaluated three non-mutually exclusive hypotheses by which changing climate covariates could impact snowshoe hare density in summer: (a) if shorter snow cover duration (via later snow onset and/or earlier snow melt) increases hare mismatch and decreases adult survival, we predict lower summer hare density following winters with shorter snow cover duration; (b) if warmer winter temperature increases adult survival, we predict higher hare summer density following years with fewer extremely cold winter days and/or higher winter minimum temperatures; and (c) if increased climate severity (warmer summer temperatures and/or wetter

springs) reduces adult and/or leveret survival, we predict lower adult hare summer density in the year following warmer summers and/or wetter springs. Finally, as climate change is expected to alter future temperature and precipitation regimes (Bintanja & van der Linden, 2013; Pederson et al., 2011; Zhu et al., 2019), we incorporated climate projections into our Bayesian modeling framework to explicitly project future hare density under climate change.

## 2 | METHODS

### 2.1 | Study areas

We collected snowshoe hare summer (May–August) density data from 1998 to 2018 at 14 trapping grids in two areas (Seeley Lake and Tally Lake) in western Montana, USA (Mills et al., 2005). All sites are managed by the U.S. Forest Service (USFS) with a history of multiple use including timber production. Seeley Lake (Lat. = 47.2°, Long. = -113.4°) and Tally Lake (Lat. = 48.5°, Long. = -114.8°) are approximately 175 km apart and span similar elevations (approximately 1500–1900 m.a.s.l.). Both areas are dominated by moist, coniferous forests of Douglas fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and Ponderosa pine (*Pinus ponderosa*) with a herbaceous understory.

### 2.2 | Capture/handling

Snowshoe hares were trapped during the summer (May–August) using live-traps (51×18×18 cm, Tomahawk Live Trap Company) baited with alfalfa cubes and apples, spaced approximately 50 m apart (Mills et al., 2005). Each of the seven Seeley Lake hare trapping grids consisted of approximately 50 traps, whereas the seven Tally Lake trapping grids had approximately 80 traps each. Each grid was trapped for 3–5 days each summer (May–August), ensuring population closure. We marked all hares >500 g with a unique numbered ear tag. We weighed all hares, determined sex, and measured right hind foot length. Hares were considered adults if they weighed ≥700 g and if their right hind foot length was ≥10 cm. Only adults were used to estimate hare density. All capture and handling procedures were approved by the University of Montana Animal Care and Use Committee (various permits over 21 years).

### 2.3 | Climate data

We derived past temperature data from Daymet, which provides daily temperature and precipitation at 1 km resolution based on modeling and interpolating meteorological station data (Thornton, Thornton, Mayer, et al., 2018). In a cross-validation of Daymet predictions, mean absolute error for single day predictions for 2010 maximum temperature was less than 1°C for western Montana (Thornton, Thornton,

& Vose, 2018). Specific temperature derived covariates we initially considered included: number of days each year with minimum temperature below  $-5^{\circ}\text{C}$ , yearly minimum winter temperature (i.e., coldest temperature on the coldest day each year), number of days each year with maximum temperature above  $38^{\circ}\text{C}$  and yearly maximum summer temperature. The yearly maximum summer temperature was strongly correlated ( $r = 0.79$ ) with the average daily maximum temperature from June to September in our study. Summer was defined as June–August, winter was December–March. Total spring precipitation was calculated as the sum of daily precipitation from May 15 to June 15. This period captures the window when leverets are most likely to succumb to heavy precipitation induced hypothermia (0–5 days old (Krebs et al., 2002; O'Donoghue, 1994)), as determined by live-trapping weights and growth curves (Keith et al., 1968). Since we hypothesized spring precipitation only affected juveniles, we only considered an effect on adult hare density the following year, when juveniles reached adulthood, producing a lag of ~14 months between when the covariate was measured and when it affected hare density (e.g., spring 2010 precipitation affects summer 2011 adult hare density). Summer covariates included ~12-month lags and winter covariates included ~6-month lags.

We derived past snow data from the NOAA National Weather Service's National Operational Hydrologic Remote Sensing Center (NOHRSC) Snow Data Assimilation System (SNODAS) (Barrett, 2003). SNODAS provides estimates of snow cover and associated parameters at 1 km resolution from 2003 to 2018 (Barrett, 2003). SNODAS combines modeling with data assimilation from a variety of sources (ground based, airborne, and satellite) with varying temporal resolution to produce an output with daily temporal resolution (Barrett, 2003). Although SNODAS can exhibit some bias in New England (Sirén et al., 2018), SNODAS accurately predicted snow depth in the Rocky Mountains (Clow et al., 2012), and has been used to approximate western Montana snow depth (Holbrook, Squires, Olson, DeCesare, & Lawrence, 2017; Holbrook, Squires, Olson, Lawrence, & Savage, 2017). For years prior to 2003, we relied on the Livneh et al. (2015) hydrometeorological dataset, which provides estimates of snow cover and associated parameters at ~6 km resolution (Livneh et al., 2015). We defined snow presence as snow water equivalent  $> 0\text{mm}$  to approximate daily snow cover and defined snow cover duration as the number of days per year when snow was present.

Finally, we used climate covariates projected under different greenhouse gas concentration scenarios to examine how future changes in important climate covariates might influence hare densities. Future monthly minimum and maximum temperatures were calculated from climatic surfaces provided by the Rocky Mountain Research Station, USDA Forest Service that considered an ensemble of 17 different climate models from the Coupled Model Intercomparison Project Phase 5 (CMIP5) under two representative concentration pathways (RCPs) including medium-low (RCP4.5) and high (RCP8.5) greenhouse gas concentration scenarios (Rehfeldt et al., 2006). Snow cover was also projected using an ensemble of CMIP5 models downscaled to our study region under both RCP4.5 and RCP8.5 (for detailed methods on downscaling analyses see Mills et al., 2013).

## 2.4 | Statistical analysis

### 2.4.1 | Density

We estimated adult snowshoe hare density with a spatially explicit capture–mark–recapture (SECR) model using the Package SECR (Borchers & Efford, 2008; Efford, 2004; Efford & Fewster, 2013) in Program R (version 3.5.3, R Development Core Team 2019) following the methods of Kumar (2020). In brief, we built models varying  $g_0$ , the probability of detection given the individual's activity center is at the detector (trap location), and  $\sigma$ , the spatial scale over which the detection probability declines. We ranked models using AICc and used AICc differences ( $\Delta\text{AICc}$ ) and Akaike weights ( $w_i$ ) to evaluate model support. The best model included the effects of sex and heterogeneity (used to account for individual variation) on  $g_0$  and heterogeneity on  $\sigma$  (Kumar, 2020).

### 2.4.2 | Snow and temperature effects on density

We used a state space model-based framework (Rotella et al., 2009) to determine the effects of snow and temperature on summer hare density. State space models consist of both an observation model and a process model, and can separate measurement error from process noise (Dennis et al., 2006; Rotella et al., 2009). In this context, we use measurement error to refer to variability in the data that arises purely as a result of the sampling process and process noise to refer to fluctuations caused by environmental variability (Humbert et al., 2009). The observation model used hare density estimates and the associated measurement error to approximate the unknown true hare density. The process model then estimated process variance and covariates on density with measurement error removed. Our observation model linked estimated density to true density with the following relationship:  $\hat{D}_t \sim N(D_t, se_t^2)$ , where  $\hat{D}_t$  is the time-specific density estimates obtained from the SECR model,  $D_t$  is the true density, and  $se_t^2$  is the squared estimate of measurement error obtained from the SECR model. Our process model was as follows:  $\log(D_t) = \mu + y_t$  with  $\mu$  being the equilibrium value of the logarithm of true density and  $y_t \sim N(\alpha_t, \sigma_{pr}^2)$  where  $\sigma_{pr}^2$  is process variation. Finally,  $\alpha_t = \beta_1(\text{cov1}) + \beta_2(\text{cov2}) + \beta_3(\text{cov3}) \dots$  where  $\beta$  represented the coefficient relating the covariate to  $\alpha_t$ . We assumed that process variation and measurement errors were independent.

We implemented the model in a Bayesian framework (Rotella et al., 2009) to accommodate years when we did not trap (~18% of all grid-year combinations). We considered the following covariates: number of days with minimum temperature below  $-5^{\circ}\text{C}$  (lower critical temperature for hares; Hart et al., 1965), minimum winter temperature, maximum summer temperature, total precipitation from May 15 to June 15, and snow cover duration. There were no days with maximum above  $38^{\circ}\text{C}$  (upper critical temperature for hares (Hart et al., 1965)) so we omitted that covariate. All covariates required a lag of 6–14 months between when the covariate was measured and when it affected hare density, so that

we could consider the effects of previous springs (~14-month lag), winters (~6-month lag), or summers (~12-month lag) on current summer hare densities. We standardized all covariates to have a mean of 0 and a standard deviation of 1 to ease interpretation and expedite convergence. Finally, we ensured all covariates were not strongly correlated ( $\rho < 0.6$ ).

We fit models with Markov Chain Monte Carlo (MCMC) in JAGS using the R package `jagsUI` (Kellner, 2018), with uninformative priors, except in the case of snow data pre-2003 (pre-SNODAS). Priors for snow cover duration for those years were informed by Livneh data, which was correlated with SNODAS ( $\rho = 0.64$ ). The informative priors had a normal distribution with a mean equal to the standardized Livneh snow cover duration and a precision (1/variance) of 0.1. We used a gamma distribution as a prior for  $\sigma_{pr}^2$  with both hyperparameters set to 0.001. We specified the prior for  $\mu$  as a normal distribution with a mean of 0 and a precision of 0.01. We used a normal distribution with a mean of 0 and a precision of 0.01 as a prior for all the betas. These priors represent a stationary distribution of 1 hare/ha and no effects of any covariate on density. We ran all models with five chains of at least 110,000 iterations, discarding the first 10,000 as burn-in. We assessed convergence by visually examining the trace and density plots for the beta coefficients and with the Gelman–Rubin statistic ( $\hat{R} < 1.1$ ). We used the 95% credible intervals as well, as the probability that the beta coefficient does not equal 0, to determine the importance of the covariates.

### 2.4.3 | Effects of climate change

In order to examine the effects of climate change, we used future climate covariate values estimated for our study area under two greenhouse gas concentration scenarios (RCP4.5 and RCP8.5). Specifically, for temperature we used the future mean maximum temperature in the warmest month (mmax) and mean minimum temperature in the coldest month (mmin) for each grid for both mid (2056–2065) and late century (2086–2095). We first calculated current values for mmax and mmin using the Daymet data. Specifically, we calculated trapping grid and year specific values for mmax and mmin from 1995 to 2018 and averaged them to represent the average value of mmax and mmin that the hares experienced. We then calculated the future proportional change in both mmax and mmin using the current and projected values. Finally, we applied those proportional changes in mmax and mmin to our modeled summer and winter climate covariates, respectively, yielding future estimates of our climate covariates of interest. We followed a similar approach for snow cover duration whereby we used current snow cover duration and mid- and late-century projections (Mills et al., 2013) to estimate the proportional change in snow cover duration mid and late century under RCP4.5 and RCP8.5 (see [Supplemental Methods](#) for more details).

We used all combinations of present and future climate covariates to estimate hare density in the Bayesian state space model separating out nuisance measurement error. For estimates where

only one future climate covariate was considered, we used the study-level average for all other covariates. These density estimates were then compared to  $\mu$  (the equilibrium value of the logarithm of true density for all sites and years) converted to the original scale. Estimates outside of the 95% Bayesian credible interval were deemed significantly different.

## 3 | RESULTS

### 3.1 | Snow and temperature effects on density

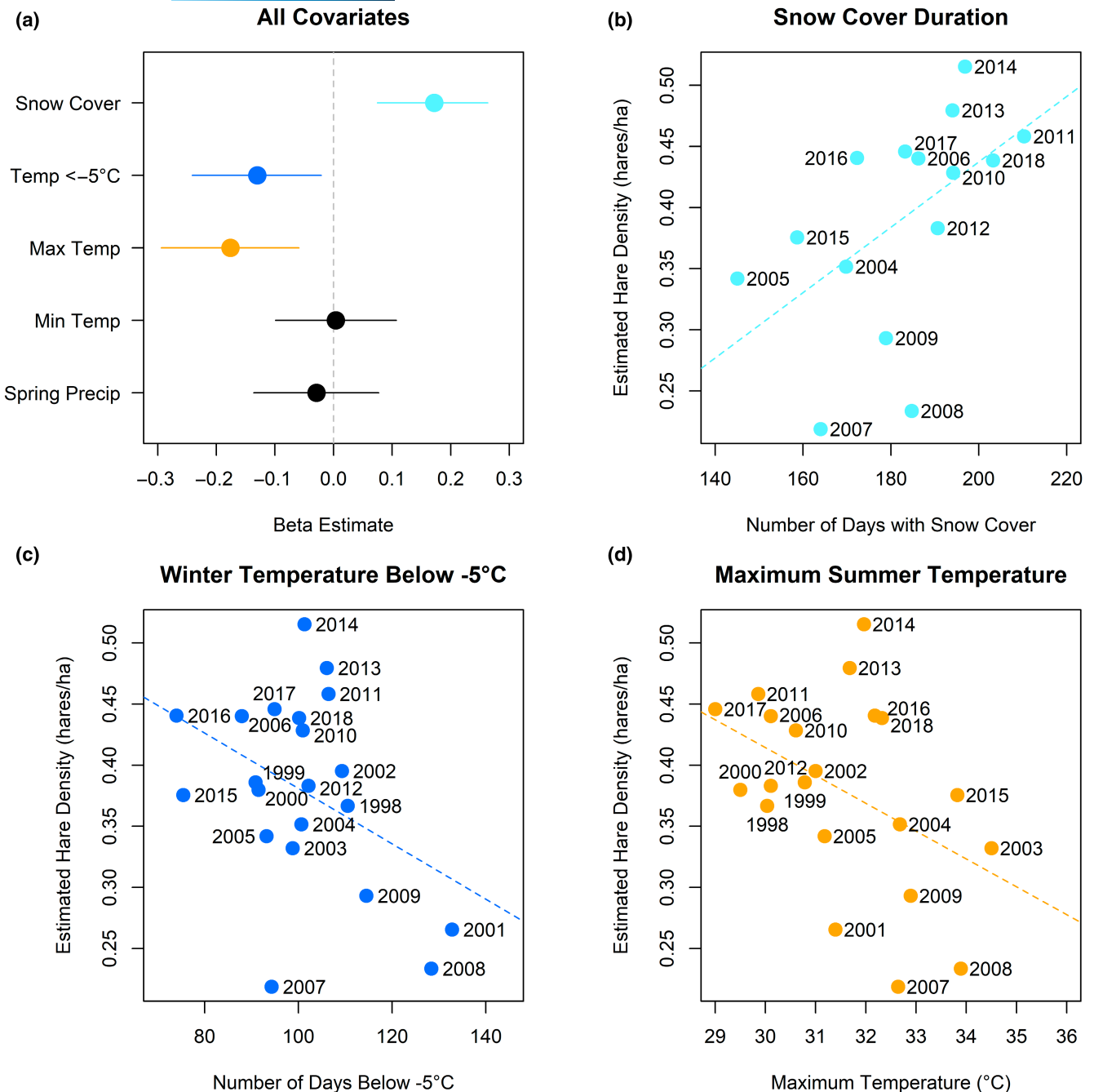
We found support for all three hypothesized relationships between climate covariates and summer snowshoe hare densities during the study period (1998–2018). Seasonal snow duration had a strong positive association with hare density, whereas temperature had strong effects that varied depending on seasonal context. Specifically, a reduction in the number of days with snow cover was associated with decreased hare densities in the subsequent summer (Figures 1 and 2; Table S1). Contrastingly, a decrease in the number of days with minimum temperature below  $-5^{\circ}\text{C}$  (i.e., warmer winters) was strongly associated with increased hare densities, whereas warmer maximum summer temperature was strongly associated with reduced hare densities (Figures 1 and 2; Table S1). Spring precipitation and winter minimum temperature did not have significant effects on hare density.

### 3.2 | Effects of climate change

At our sites, baseline projected summer hare density fluctuated around a stationary distribution ( $\mu$ , see Methods) of 0.30 hares/hectare (95% CI = [0.27–0.33]) (Figure 3). Based on the observed winter temperature effects projected in isolation, hare density would be expected to significantly increase under all climate scenarios and timeframes, with potential >50% increases by late century under RCP8.5 (Figure 3; Table S2). Conversely, increased summer temperature or reduced snow duration projected in isolation led to significantly decreased predicted future hare density only under the longest projection (late century) and RCP8.5 scenario (Figure 3; Table S2). However, after accounting for simultaneous cross-season effects, including reduced snow cover in fall/spring, fewer extremely cold winter days and warmer summers, hare density would likely decrease significantly under most timeframes and climate scenarios (Figure 3; Table S2). Most notably, late-century estimates of hare density decrease significantly by approximately 15% (RCP4.5) or 40% (RCP8.5).

## 4 | DISCUSSION

Despite rapid changes in climate, ecologists know little about how specific climate covariates interact to affect densities of wild species. We

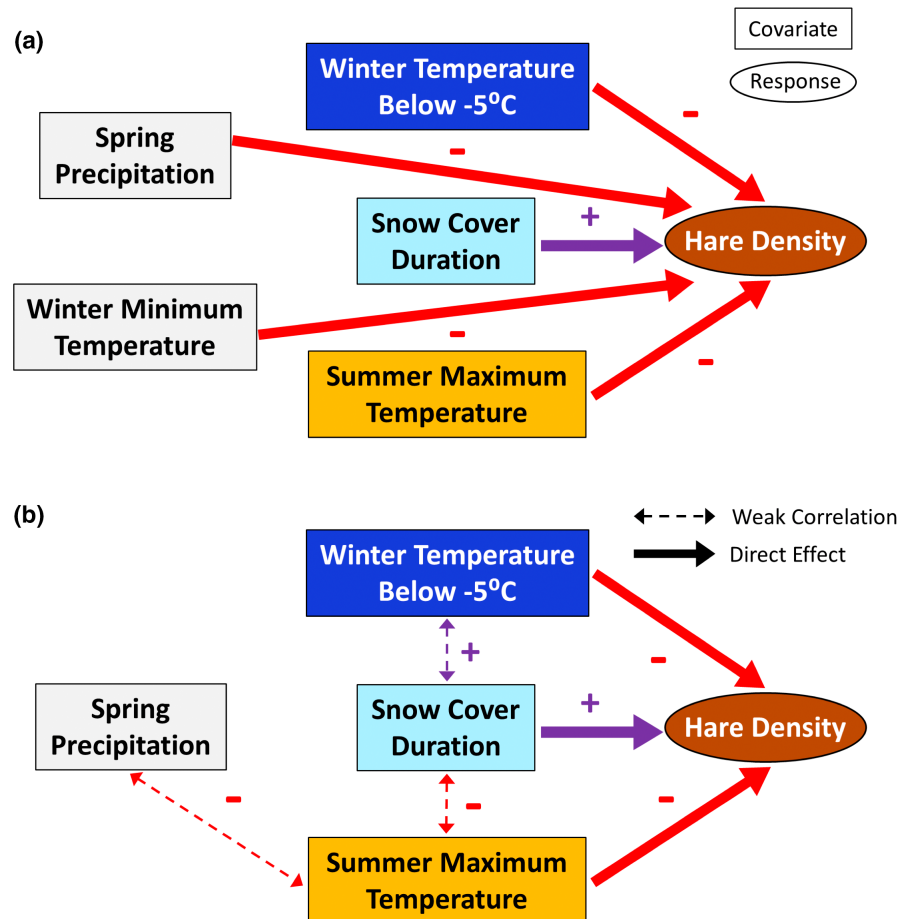


**FIGURE 1** Effects of seasonal climate covariates on snowshoe hare densities in western Montana from 1998 to 2018. (a) Beta estimates of the effects of climate covariates on hare density. Horizontal lines indicate 95% credible intervals. Snow cover is the total number of days of snow cover per year from the previous winter. Temp < -5°C is the number of days per year where the daily minimum temperature is below -5°C during the previous winter. Max temp is the absolute maximum temperature during the preceding summer. Min temp is the absolute minimum temperature during the previous winter. Spring precip is the total precipitation from May 15 to June 15 of the previous year. (b) Isolated effect of snow cover duration on hare density. (c) Isolated effect of winter temperature below -5°C on hare density. (d) Isolated effect of maximum summer temperature on hare density.

used a 21-year time series and a unified data-driven modeling framework to understand how climate affects density of snowshoe hares, a keystone species whose life history and behaviors are directly shaped by climate. We found significant effects of snow and temperature on hare density. Decreased snow duration reduces density in the subsequent summer and warmer winters were associated with increased

density, whereas warmer summers were associated with decreased density. Future projections reveal that the negative effects of reduced fall and spring snow cover and warmer summers will likely overwhelm the positive effect of fewer cold winter days. Although this projection only considers a few of the myriad effects of climate change, it underscores the value of considering biologically informed, simultaneous

**FIGURE 2** Hypothesized (a) and observed (b) effects of climate covariates on snowshoe hare densities. Three abiotic effects (winter temperature below  $-5^{\circ}\text{C}$ , snow cover duration and maximum summer temperature) have direct (positive or negative) effects on density. These effects are also weakly correlated ( $0.25 < \rho < 0.5$ ) among themselves. Spring precipitation does not directly affect density but is weakly correlated with summer maximum temperature, which affects density. Minimum winter temperature did not directly affect density nor was it weakly correlated with any abiotic effects.



and potentially opposing effects on vital rates when considering climate change outcomes on population dynamics.

Reduced snow cover duration can decrease hare density by increasing camouflage mismatch of white hares on snowless backgrounds (Mills et al., 2013, 2018), thereby decreasing survival (Wilson et al., 2019; Zimova et al., 2016). Furthermore, snow itself influences the molt phenology such that hares can lengthen the duration of the white winter molt when snow is present, although this effect is insufficient to reduce mismatch (Kumar et al., 2020; Zimova et al., 2020). In addition to influencing mismatch, changes in snow may affect hare predator evasion, as coyotes in the Yukon are more successful hare predators in shallow snow (Peers et al., 2020). However, snow depth was not associated with changes in hare density in this system (Kumar, 2020) possibly because mean snow depth across all our sites was almost twice as high as the 35cm snow depth threshold below which Yukon hare mortality increased (Peers et al., 2020).

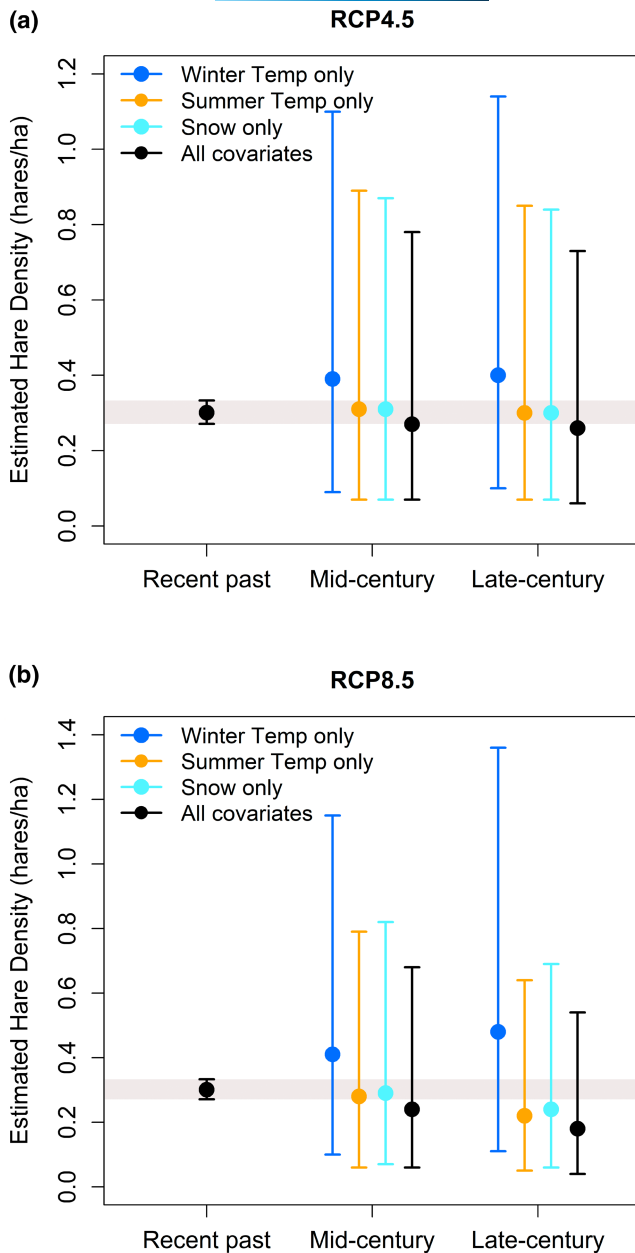
Possible consequences of changing frequencies of very cold winter temperatures on hare densities have not been examined previously. Our finding of increased densities with fewer days below  $-5^{\circ}\text{C}$  may reflect reduced predation-induced hare mortality during warmer winter weather, as predation accounts for  $>90\%$  of hare mortality (Hodges, 2000). We did not find support that the minimum winter temperature affected hare densities emphasizing that prolonged durations below a biologically relevant threshold

are more predictive than an index of extreme winter temperature. Lower temperatures, especially below the thermal neutral zone ( $-5^{\circ}\text{C}$  in hares), increase energy demand (Speakman, 1996; Williams et al., 2015) and may encourage hares to forage in habitats and microsites with higher predation risk (Griffin & Mills, 2009; Keith et al., 1984). Therefore, climate change-driven decreases in very cold days may reduce the negative impacts of cold winter temperatures on hare populations.

The possible contrasting impact of winter versus summer climate on populations has been largely neglected. Here we demonstrate that despite the positive association of warmer winters with hare density, increased maximum summer temperatures were associated with lower hare densities in the subsequent summer. We chose to focus on maximum instead of mean temperature values because temperature extremes are most likely to impact demography (Chitwood et al., 2015; Du Plessis et al., 2012). Moreover, yearly maximum summer temperature can index longer warming trends (Alexander et al., 2006) and was strongly correlated (see Methods) with the average daily maximum temperature from June to September in our study. Ultimately, maximum summer temperature indicated an important influence on density and raises an important new avenue for future research on demographic constraints of climate.

Although temperatures were not above the upper critical temperature of hares ( $38^{\circ}\text{C}$ ; Hart et al., 1965), this value is based on animals at rest. Activity and reproductive effort quickly generate





**FIGURE 3** Observed and projected snowshoe hare densities in western Montana under two climate change scenarios considering various climate covariates. Observed densities (recent past) are based on annual density estimation during 1998–2018 using a spatially explicit capture–mark–recapture framework incorporated into a Bayesian state space model to separate measurement error from process noise. Future projections were modeled using two representative concentration pathways (RCPs) from an ensemble of 17 Coupled Model Intercomparison Project Phase 5 models: (a) medium-low (RCP4.5) and (b) high (RCP8.5). Vertical lines indicate 95% credible intervals; estimates outside the gray bands are significantly different from the recent past.

heat such that temperatures below the upper critical temperature of the thermoneutral zone may still generate significant negative impacts (Król et al., 2007). In birds, hot temperatures can reduce juvenile survival (Cunningham et al., 2013) and lower body condition as the costs of increased evaporative cooling lowers foraging

efficiency (Du Plessis et al., 2012; Gardner et al., 2016). Resulting reductions in hare body condition can increase susceptibility to predation (Hodges et al., 2006; Keith et al., 1984). In addition, high temperatures may lower juvenile survival (e.g., white-tailed deer—Chitwood et al., 2015; African wild dogs—Woodroffe et al., 2017) possibly through reduced maternal milk provisioning as found in laboratory mice (Król et al., 2007) and dairy cattle (Rhoads et al., 2009).

At our study area, we predict winter temperatures to increase proportionally more than summer temperatures by late century under RCP8.5 (31% vs. 23%), consistent with other regions where winter warming outpaces summer warming (Bintanja & van der Linden, 2013; Screen & Simmonds, 2010). Although warmer winters considered in isolation would be expected to benefit hares, based on our modeling results, the cumulative effect of climate change drivers across seasons leads to expected reductions in hare density by the end of the century (Figure 3).

The demonstrated effects of snow cover and summer and winter temperatures may be intensified, weakened, or remain unchanged in other parts of the snowshoe hare range. Widespread population synchrony across geographic ranges for various taxa (Bjørnstad et al., 1999; Liebhold et al., 2004) including snowshoe hares (Cheng, 2010; Krebs et al., 2013) may imply spatially consistent effects of climate on populations dynamics (Grenfell et al., 1998; Hanski & Woiwod, 1993; Koenig, 2002; Moran, 1953; Post & Forchhammer, 2002). However, intraspecific variation in climate effects on species occupancy has been demonstrated in various taxa (Hällfors et al., 2016; Ikeda et al., 2017) including lagomorphs (Smith et al., 2019; Sultaire et al., 2022). The effects of snow cover on hare occupancy and survival are consistent in the central (Zimova et al., 2016) and southern extents of the hare range (Burt et al., 2017; Diefenbach et al., 2016; Sultaire et al., 2016, 2022; Wilson et al., 2019); however, male body size in snowshoe hares in the northern part of the range is affected more by snow depth, whereas growing degree days drive body size variation in the southern range (Gigliotti et al., 2020). Furthermore, average yearly temperature has been shown to have opposing effects within the southern range extent, with increased temperature reducing occupancy probability at the southern range terminus and increasing occupancy probability at slightly higher latitudes within the southern range extent (Sultaire et al., 2022). How these findings scale to the entire range and are affected by considering seasonally opposing effects of temperature remains unclear. Overall, further research will be required to determine how generalizable our findings are across the snowshoe hare range.

As is true with all studies that project expected population dynamic shifts in a changing climate, a necessary caveat of our inferences is the assumption of no adaptive shifts in fitness-relevant seasonal traits. For snowshoe hares, climate-relevant, genetically based adaptive shifts have been demonstrated in the winter molt color (Jones et al., 2018; Mills et al., 2018). Adaptive shifts in plasticity, for example in molt timing and in behaviors to avoid mismatch or its consequences, are also possible but have not yet been detected

at meaningful levels (Kumar et al., 2020; Zimova et al., 2014, 2020). In short, the quantitative magnitude of effects of climate change on population trajectory will depend in part on the as-yet-unknown scope for local adaptation.

The contrasting and cumulative impacts of seasonal differences in climate change on demographic rates are only beginning to be considered. For example, under climate change, yellow-bellied marmots are expected to experience lower winter survival but higher summer survival (Cordes et al., 2020), and meerkats are predicted to have reduced fecundity in the breeding season but increased survival in the nonbreeding season (Paniw et al., 2019). Delayed autumn snow cover was associated with increased spring body mass in caribou, providing a mechanism to counteract the negative effects of warming winters (Loe et al., 2021). Additionally, contrasting effects of climate change on demographic rates can occur throughout a species range, exemplified by southern plant populations having lower survival and recruitment but higher growth than northern populations (Doak & Morris, 2010). Finally, the climate effects that we identified drive hare population dynamics, namely warmer summers, colder winters and snowpack reduction also influence pika range contraction (Beever et al., 2011). Thus, our study adds to the small number of empirical studies required to begin forming a general framework for predicting species-specific demographic responses to climate change across seasons (Yoccoz, 2020).

Our 21-year time series and unified data-driven modeling framework illuminate the context-dependent effects of multiple climate drivers on wild populations. Our future projections further reveal that negative effects of reduced snow cover duration and warmer summers would likely overwhelm the positive effect of fewer cold winter days. These findings highlight the need to critically examine the particular life-history strategies and attributes of focal species and identify climate metrics directly informed by these attributes. Additionally, our results underscore the value of considering the many and possibly opposing season-specific effects of climate in a unified framework to predict cumulative population outcomes for wild species.

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## CONFLICT OF INTEREST

The authors have no competing interests to declare.

## DATA AVAILABILITY STATEMENT

The snowshoe hare data that support the findings of this study are openly available at the Environmental Data Initiative at <https://doi.org/10.6073/pasta/180be476a353cf9969076e332dd1cddb>. The climate data were derived from the following resources available in the public domain: <https://daymet.ornl.gov/>, <https://nsidc.org/data/g02158>, <https://charcoal2.cnre.vt.edu/climate/>, and <https://doi.org/10.1073/pnas.1222724110>.

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## SUPPORTING INFORMATION

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

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