RESEARCH ARTICLE

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Shifts in risk sensitivity and resource availability alter fat stores for a large mammal following extreme winter conditions

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Abstract

1. For species that inhabit environments where resource availability may be unpredictable, balance of resource allocation to life-history traits can have heightened consequences for survival, reproduction, and ultimately, fitness. Acquisition and allocation of energy to maintenance, capital gain and reproduction should be in tune with the landscape an animal inhabits—environmental severity, food availability and population size all influence the resources animals have and dictate the ways they should be allocated.

2. In seasonal environments, animals that experience periods of extreme resource limitation (e.g. harsh winters) may favour allocation of resources to body reserves to secure their survival at the cost of reproduction (i.e. risk averse). In contrast, the same accumulation of body reserves may not be necessary to survive in relatively benign landscapes where instead, allocation to reproduction is favoured (i.e. risk prone).

3. According to the theory of risk-sensitive allocation of resources, when animals are exposed to unprecedented or life-threatening conditions, they may shift resource allocation to favour building capital over allocation in reproduction to preempt against encountering another life-threatening event in the future.

4. Using data from a long-term project on a highly site-faithful and long-lived species, mule deer (*Odocoileus hemionus*), we evaluated how a life-threatening winter and the associated changes in resource availability resulting from a population

reduction influenced how animals acquired and allocated energy to survival (i.e. fat accumulation).

5. Per capita precipitation, and the associated reduction in population abundance after the severe winter, had a positive influence of accrual of fat over summer. After the extreme physiological stress of a hard winter, deer starting spring with low body reserves accumulated 2.8 percentage points more fat over summer compared with before the experience of a bad winter and had an increased probability of recruiting fewer offspring. Fat stores can interact with environment, life history and behaviour to influence survival during periods of resource scarcity.

6. For a long-lived herbivore, we documented shifts in risk tolerance associated with fat accrual in preparation for winter, supporting the notion that risk-sensitive allocation of resources may be plastic—an essential adaptation for animals to cope with rapidly changing landscapes.

1 | INTRODUCTION

Across taxa, animals optimize fitness by trading current reproduction against future survival (Clutton-Brock, 1984; Clutton-Brock & Sheldon, 2010; Stearns, 1992). For species with slow life histories, maternal investment in reproduction can be substantial, requiring a balance in allocation of energetic demands to reproduction with survival. For animals that live and reproduce for many years, the fitness value of survival and future reproductive efforts outweighs that of current reproduction; animals must successfully balance the energetic costs of reproduction with those of their own survival (Gaillard et al., 1998, 2000). For wild animals inhabiting environments with ephemeral, stochastic, or unpredictable resources, the effective balance of resource allocation to reproduction versus accrual of energy stores to promote survival must align with the vagaries of the environment to protect against mortality (Bårdsen et al., 2014; Stephens, 1981). Consequences of suboptimal allocation of energy to different life functions under variable conditions can have important, yet asymmetric, fitness costs. For example, allocating too much into somatic stores might not be warranted to improve survival beyond a certain point and could come at reductions to reproductive effort, whereas allocating too much energy to reproduction at the cost of body reserves can be fatal.

The allocation of energetic resources to life-history traits must be linked to the environment an animal lives in, through both its seasonality and predictability. Food availability and population density can strongly influence the resources animals have to allocate to survival (e.g. stored capital) and reproduction (Bowyer et al., 2014; Jorgenson et al., 1997; McCullough, 1999). In seasonal environments, animals often rely on stored capital to survive periods of resource limitation (Festa-Bianchet & Jorgenson, 1998; Jorgenson et al., 1997; McCullough, 1999; Stephens et al., 2014). For animals that invest

heavily in maternal provisioning and care, raising offspring may compromise stores of capital that are necessary to survive an upcoming period of resource scarcity. The amount of capital an animal accrues is not only dependent on the environment when resources are abundant, but also is influenced by the severity of the environment during periods of resource scarcity (Bårdsen et al., 2014; Monteith et al., 2013). If animals do not enter a period of resource limitation with sufficient stored reserves, they face a greater risk of mortality (LaSharr et al., 2023). Animals that spend their winters in harsh landscapes or summers in areas with frequent and extensive droughts, may need to secure or maintain more capital going into those seasons compared with animals that inhabit ranges that are more benign (Bårdsen et al., 2008; Caughley & Gunn, 1996). Yet, it is not only the severity of an environment that influences how animals allocate resources to reproduction and survival, but also the predictability of landscapes during periods of resource limitation.

Predictability of conditions during periods of resource scarcity can shape how animals accumulate capital during periods of resource abundance (Bårdsen et al., 2014). Even among conspecifics, animals that experience unpredictable environments (i.e., large variation in severity of conditions) may be sensitive to the risk associated with that uncertainty—allocating too many resources to reproduction could come at the cost of survival if conditions are particularly severe in a given year. Animals cannot predict the severity of conditions that will occur in a coming season, thus, animals that live in stochastic environments may operate in a risk-averse manner—favouring the buildup of capital resources instead of allocating to reproduction—to buffer themselves against potentially encountering a harsh winter (Bårdsen et al., 2014). Alternatively, if animals consistently are exposed to predictable and benign conditions during winter, they may be more risk-prone, investing high amounts of energy into reproduction at the cost of stored capital, which comes at

a relatively low risk to their own survival in a predictable landscape (Figure 1a; Bårdsen et al., 2014).

Even in environments with seasonal conditions that typically are consistent across years, animals still cannot predict the severity or intensity of a coming period of resource limitation. Stochastic and severe winters, and summers with prolonged droughts, are becoming more common as climate change affects ecosystems around the globe (Bårdsen et al., 2008; Convey & Smith, 2006; Grosbois et al., 2008; Parmesan, 2006). Populations that have adopted risk-prone strategies of reproduction that are in tune with
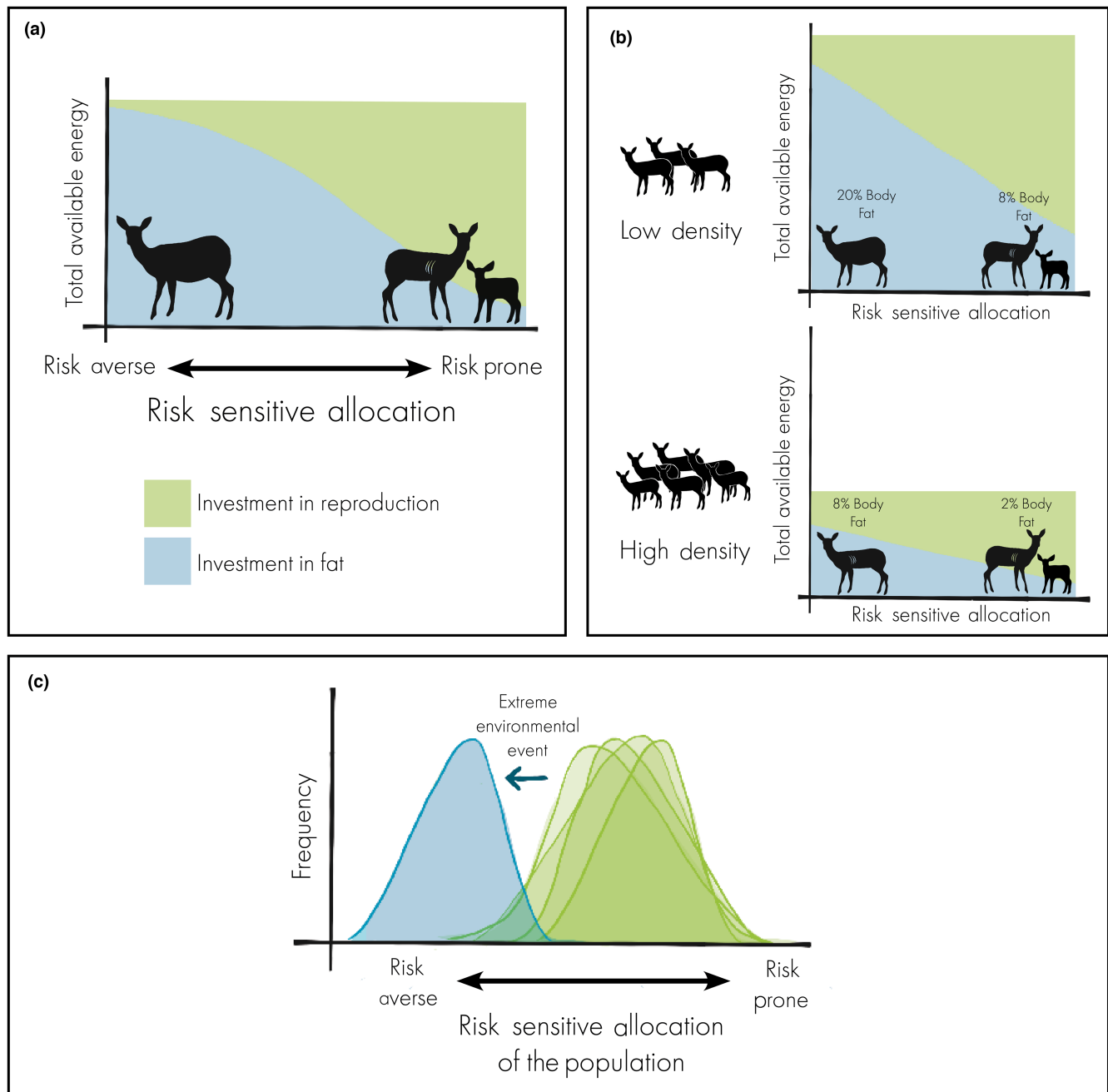
FIGURE 1 The risk-sensitive allocation of animals in seasonal environments should be dependent on the predictability and availability of resources on the landscape. Animals that are risk-averse should allocate relatively more in securing capital resources (i.e. fat) and relatively less in reproductive efforts compared to animals that are more risk-prone (a). The density of the population, and consequently, resources available to individuals influence the total energy that animals have to allocate in reproduction or fat accumulation. At high densities, a risk-averse animal may end a period of resource abundance with 8% body fat by prioritizing allocation to fat accumulation over raising offspring. At low densities with higher resource availability, however, a risk-prone animal may also end a period of resource abundance with 8% fat despite prioritizing the available energy into rearing offspring (b). During predictable years (green distributions), animals in a population may employ risk-prone behaviours. In the year following an extreme environmental event (e.g. a very harsh winter; blue distribution), surviving animals may shift their reproductive strategy to be more risk-averse to mitigate the chance of encountering another bad winter (c).

historic conditions may face high costs of survival if they suddenly are exposed to unprecedented and severe conditions. Indeed, wild populations are experiencing changes in both the predictability of the environments they inhabit and the quality and distribution of resources (Van der Putten, 2012). Plasticity in risk-sensitive allocation of resources to survival and reproduction may be critical to population persistence as animals encounter rapidly changing landscapes. Resource allocation, however, is contingent upon resource acquisition, which is in turn determined by the environment and the physiological capabilities of an animal. Thus, even if animals are exposed to harsh or unpredictable environmental conditions, the nutritional constraints imposed by population density may prevent individuals from accruing enough resources to reach sufficient stores of capital (Figure 1b), even if they have sacrificed reproductive efforts through either physiological (e.g. reduced pregnancy rates or non-viable offspring; Garroway & Broders, 2005; Gerhart et al., 1997) or behavioural changes (e.g. suckling rejections; Scornavacca et al., 2016).

Even for animals that are plastic in their responses, they are still constrained by the realities of the habitats they live in. Animals in populations that are at or near nutritional carrying capacity can face limitations in the energy they can acquire from their environment (Nanney et al., 2018; Smythe et al., 2019; Stephenson et al., 2020). For populations near nutritional carrying capacity, competition for resources can be high; as resource quality or availability declines, how energy is allocated may be especially important in maintaining survival. Alternatively, population crashes coincident with severe events that reduce the density of animals on the landscape could provide a nutritional benefit through lowered competition for high-quality resources. If the nutritional benefits of reduced density are great enough, animals may accrue enough capital to enter winter without sacrificing reproductive efforts.

Plasticity of resource allocation to survival and reproduction has important implications for long-lived and iteroparous animals around the globe, and understanding how animals are able to cope with seasons that are becoming increasingly stochastic and severe could have important implications for species conservation. We investigated how a life-threatening winter where mortality exceeded 30%, and the corresponding change in population density influenced risk sensitivity in acquisition and allocation of energy to survival and reproduction. Our dataset comprised a long-term, longitudinal study of mule deer (*Odocoileus hemionus*), a long-lived, iteroparous herbivore, wherein we measured seasonal changes in nutritional condition and reproduction over 9 years. We tested two complementary hypotheses to evaluate how animals accrue and allocate resources in a variable environment. If animals reflect risk-sensitive allocation following a near death experience, we expected that experiencing a harsh winter that jeopardized survival would result in a relative increase in allocation towards accumulation of capital (i.e., body fat) and a decrease in recruitment of young. Given environmental contributions to acquiring energy and how much capital an animal can accumulate, we expected resource availability per animal to affect accumulation of capital—when per capita resources were low, animals would accrue less body fat than when resources were more abundant.

2 | MATERIALS AND METHODS

As part of a long-term, longitudinal study of mule deer in western, Wyoming, USA, we repeatedly sampled individuals each spring and autumn from March 2013 to December 2021 to evaluate how their nutritional condition (i.e., fat levels) during different seasons relate to a suite of life history and environmental characteristics. During this study, the population experienced unprecedented and harsh winter conditions during the 2016–17 winter, a winter much more severe than anything animals had experienced in nearly two decades (LaSharr et al., 2023). During this winter, animals were exposed to high snowpack and extended periods of low temperatures; and consequently, adult survival dropped substantially from what is typical for large ungulates (from survival of ~90% to 70%; LaSharr et al., 2023). Population density dipped significantly (~30%), providing us with a unique opportunity to test how density and severe winter conditions influence acquisition and allocation of resources by individuals (Figure 2).

All field work that involved capture and handling of animals was done under compliance with a protocol approved by an Institutional Animal Care and Use Committee at the University of Wyoming (Wyoming Range 20131111KM00040, 20151204KM00135, 20170215KM00260, 20200305KM00412) and the Wyoming Game and Fish Department (Chapter 33 permit; #33–985), and were in accordance with guidelines of the American Society of Mammalogists (Sikes, 2016). No additional permitting was required to complete field work.

2.1 | Study area

Our study took place in the Wyoming and Salt River mountain ranges in western Wyoming, USA (42°250 N, 110°420 W). The Wyoming Range mule deer herd inhabits two distinct winter ranges, the North Wyoming Range (611 km², 42°23′ N, 110°16′ W) was located northwest of LaBarge, Wyoming and the South Wyoming Range (1904 km², 41°49′ N, 110°31′ W) was located 25 km west of Kemmerer, Wyoming. The primary vegetation types on winter range were sagebrush species (*Artemisia* spp.) with additional mountain-shrub communities (*Juniperus* spp., *Cercocarpus* spp., *Amelanchier* spp. and *Symphoricarpos* spp.). Elevations on winter range for mule deer in this system ranged from 2000 to 2300 m. The Wyoming Range Mule Deer herd inhabited the Wyoming and Salt River mountain ranges during the summer. Vegetation types on summer range were typically a mixture of sagebrush steppe, tall forb, mixed-mountain shrub, aspen and conifer communities. Elevations on summer range for mule deer in this system ranged from 2300 to 2750 m.
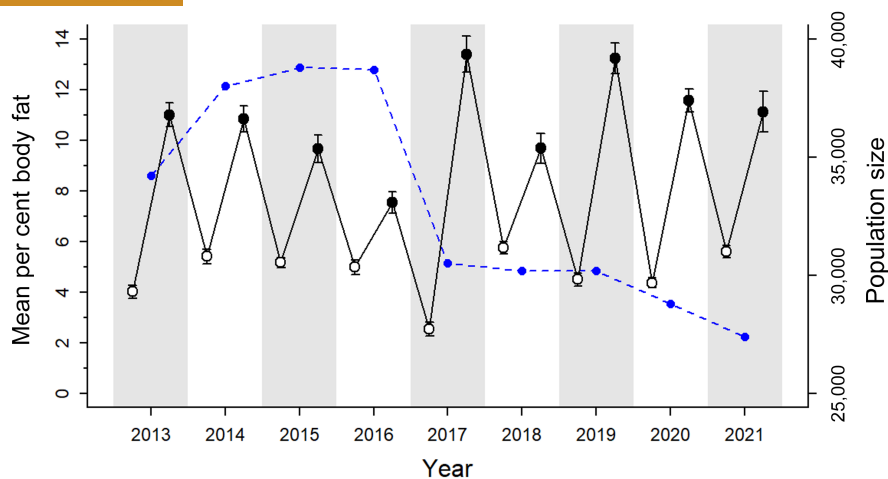
FIGURE 2 Nutritional condition and population estimates of mule deer in the Wyoming Range population in western Wyoming, USA. Estimates (blue) of the population from 2013 to 2021. Mean and standard deviation of fat estimates of adult, female mule deer captured in spring (white) and autumn (black) from March 2013 to December 2021. A harsh winter during the spring of 2017 in both winter ranges resulted in extremely poor nutritional condition of mule deer across the population and a substantial decrease in population size.

2.2 | Animal capture and handling

In March 2013, we captured 70 adult, female mule deer using helicopter net gunning. Each year following that initial capture event, we recaptured surviving individuals and captured new individuals to maintain a sample size of 70 animals in mid-March (i.e., spring) and early December (i.e., autumn) until December 2021. At the initial capture of any new animal, we extracted one incisiform canine to estimate age using cementum annuli (LaSharr et al., 2023). At each capture event, we collected data on nutritional condition, measured body mass and fit all animals with a GPS radiocollar programmed to take satellite fixes every 5 h from 2013 to Mar 2015, every 2 h from Mar 2015 to Mar 2018 and every 1 h from March 2018 to the end of the study (Advanced Telemetry Systems, Isanti, Minnesota, USA; Telonics, Mesa, Arizona, USA; and Vectronic Aerospace, Berlin, Germany). GPS radiocollars weighed ≤2 kg (~3.0% of adult body mass in spring and ~2.6% of adult body mass in autumn). We measured nutritional condition using protocols for mule deer which include measuring subcutaneous rump fat via ultrasonography and body palpation to estimate a body condition score (Cook et al., 2007; Stephenson et al., 2002). Using body mass, body condition score, and maximum thickness of rump fat via ultrasonography, we then estimated ingesta-free body fat (hereafter, 'body fat'; Cook et al., 2010). We calculated over summer change in body fat by subtracting the body fat of each animal in autumn from their body fat in spring. Each spring capture, we determined pregnancy and foetal number of each animal via ultrasonography (Aikens et al., 2021).

2.3 | Survival and recruitment monitoring

To account for the energetic cost of raising offspring, we determined recruitment status of radiomarked females each autumn. We determined presence and number of dependent young for collared

females each autumn (mid–late November). In 2013 and 2014, all recruitment was evaluated using visual observations. We watched marked females for 5–10 minutes using binoculars or spotting scopes to identify recruitment status based on maternal behaviour (Monteith et al., 2014). Maternal behaviours included close association, suckling or attempted suckling, and any other evidence of maternal care. Each observation was classified with a confidence level of 'low', 'medium' or 'high' based on evidence of maternal behaviours and group dynamics. For observations considered 'low' or 'medium' confidence, we returned to the site at a later day to make additional observations until the confidence level was 'high'. No 'low' or 'medium' observations were included in our analyses. Additionally, during autumn captures, we validated our observational data by confirming evidence of lactation by palpating the udder (Monteith et al., 2014; Stephenson et al., 2020).

During 2015–2021, we collared neonates of collared females each spring as an additional component of the long-term research project. Detailed methodology on capture and handling of neonates can be found elsewhere (Aikens et al., 2021). In instances where all neonates of a marked female were captured and collared (i.e., if a female was pregnant with two foetuses and two neonates were captured and collared), we used known fate from the juvenile collars to determine recruitment status of adult females each autumn. For any animals in which we were not successful in capturing all neonates in a litter, we used the aforementioned protocol to determine recruitment status.

2.4 | Environmental covariates and population estimates

To determine the role of population density and habitat on accumulation of capital over summer, we evaluated the influence of moisture, vegetative biomass, and metrics of greenness from NDVI. First, we

estimated seasonal home ranges of each animal using Brownian Bridge movement models (Sawyer et al., 2009). We estimated 95% summer home ranges for each animal in each summer from 1 June to 30 August.

We used the normalized difference vegetation index (NDVI) from remotely sensed data from the MOD09Q1 MODIS terra satellite to derive metrics of spring green-up. We estimated the start and end of spring for each individual home range by calculating the first and second derivatives of the instantaneous rate of green-up within a home range (Merkle et al., 2016). We then calculated the length of spring by subtracting the start of spring from the end of spring.

Compared with other large herbivores in North America, mule deer are selective in their foraging behaviour (Berry et al., 2019; Zimmerman et al., 2006) and biomass of all forage at the landscape scale may not represent the true availability of forage for deer—mule deer select for both specific plants and specific parts of those plants (Kie et al., 2003), thus we used moisture as a proxy for forage. Precipitation directly influences production of food availability (Lai et al., 2022; Lauenroth & Sala, 1992; Patton et al., 2007) and snowpack from the previous winter can have important influences on forage and body fat accrual for large herbivores (Monteith et al., 2013). We extracted daily values of precipitation from DAYMET (Daymet, 2022) and calculated cumulative precipitation during summer by summing all values from 1 May to 30 August at each cell in a given year. We calculated the mean cumulative precipitation by taking the average cumulative precipitation for each home range. We extracted daily values of snow water equivalent from SNODAS (National Operational Hydrologic Remote Sensing Center, 2004) during April. We calculated peak snowpack by extracting the maximum snow water equivalent value from a deer's home range in a given year (Monteith et al., 2013).

We used estimates of abundance for Wyoming Range mule deer from Wyoming Game and Fish Department. Estimates were developed using a time-specific juvenile, constant adult survival spreadsheet model inputted with post-season herd composition data gathered during helicopter surveys, and juvenile survival estimated based on winter severity (Wyoming Game and Fish Department, 2021). Using population estimates and cumulative summer precipitation and peak snow water equivalent for individuals, we derived an estimate of per capita precipitation and per capita snow water equivalent. Notably, estimates of population abundance by itself are not meaningful in variable environments where the resources available to a population can vary from year to year (Monteith et al., 2014). We divided cumulative precipitation on summer range and peak snow water equivalent during April for each individual by the population estimate to derive per capita precipitation and

per capita snow water equivalent respectively. These metrics represent density-dependent metrics of food availability (using moisture as a proxy), high values represent abundant resources available per animal on the landscape and low values represent scarce resources available per animal on the landscape in a given year (Monteith et al., 2014).

2.5 | Statistical analyses

We evaluated the effects of indices of food availability, a severe winter and life history on fat accrual and recruitment of female mule deer across 9 years. The scale of inference was among individuals in the population before ($n = 179$) and after ($n = 193$) a severe winter (Table 1).

First, we evaluated seasonal changes in nutritional condition over summer of mule deer as a function of spring body fat, age (continuous), recruitment status (0–2), if the population had experienced a bad winter (binary pre/post-bad winter; data collected from 2013 to 2016 were considered 'pre-bad winter', data collected from 2017 to 2021 were considered 'post-bad winter'), per capita precipitation, per capita snow water equivalent, length of spring, herbaceous biomass and an interaction between spring body fat and the binary pre/post-bad winter using Bayesian hierarchical models. Changes in risk-sensitive resource allocation should be represented by a significant interaction between spring body fat and bad winter, indication that the state-dependent accrual of fat over summer has changed since the experience of a bad winter. We included a random intercept for each deer.

For our first model, we assumed $y_{ij} \mid \mu_{ij}, \sigma_W^2 \sim N(\mu_{ij}, \sigma_W^2)$, where y_{ij} denotes the seasonal change in body fat at time j for animal i.

$$\begin{aligned} \mu_{ij} \mid \delta_{0i} = {}& \alpha_{\text{bad winter}} + \beta_1 X_{\text{post bad winter } (i)} + \beta_2 X_{\text{spring fat}(i)} + \beta_3 X_{\text{age}(i)} \\ & + \beta_4 X_{\text{recruitment}(i)} + \beta_5 X_{\text{per capita precipitation}(i)} \\ & + \beta_6 X_{\text{per capita snow water equivalent}(i)} + \beta_7 X_{\text{length of spring}(i)} \\ & + \beta_8 X_{\text{herbaceous biomass}(i)} + \beta_9 X_{\text{spring fat}(i)} X_{\text{bad winter}(i)} + \delta_{0i} \end{aligned}$$

where $\alpha_{\text{bad winter}}$ denotes the expected change in body fat of animals before or after the population had experienced a bad winter. $\beta 1 – \beta 8$ denote population averaged effects of a bad winter, spring fat, age, recruitment status, per capita precipitation, per capita snow water equivalent, length of spring and herbaceous biomass, respectively, on the seasonal change in body fat. The interaction of spring body fat and the experience of a bad winter is represented by $\beta 9$.

Second, we evaluated recruitment of juvenile offspring in the autumn as a function of age, change in body fat over summer, if the animal had experienced a bad winter and an interaction of changes in body fat

TABLE 1 Scale of inference of this study, identifying the relative role of density and environment on fat accumulation of mule deer in western, Wyoming, USA from 2013 to 2021.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Individuals	pre/post-bad winter	Pre-bad winter: $n = 179$ animal years; 69 animals; 4 years Post-bad winter: $n = 193$ animal years; 73 animals; 5 years

and the experience of a bad winter. For this model, we used ordinal logistic regression where the conditional response, $y_{ijk} \mid \delta_{0i}$, is assumed to be multinomial $(\pi_{ijk} \mid \delta_{0i})$ and denotes the observed recruitment status category ($k = 1, 2, 3$) at time j for animal i. The response categories are the recruitment of no offspring ($k=1$), 1 offspring ($k=2$) and 2 offspring ($k=3$) in the autumn. We assume that $\pi_{ijk} \mid \delta_{0i} = Pr(y_{ijk} \mid \delta_{0i} \leq k)$ denotes the true cumulative probability that the response for animal i at time j falls into category k or below. Using the logit link, we have

$$\pi_{ijk} \mid \delta_{0i} = \frac{exp(\gamma_{0k} + \eta_{ij})}{1 + exp(\gamma_{0k} + \eta_{ij})}, \text{for } k = 1, 2. \quad (1)$$

The link function in (1) links the conditional cumulative probabilities, $\pi_{ijk} \mid \delta_{0i}$, to the model unknowns in the γ_{0k} and $\eta_{ij} \mid \delta_{0i}$. The model unknowns correspond to the response category intercepts denoted by the γ_{0k} and the fixed and random effect regression coefficients in the conditional linear predictor (the $\eta_{ij} \mid \delta_{0i}$). The conditional linear predictor is given by

$$\eta_{ij} \mid \delta_{0i} = \beta_1 X_{\text{post bad winter}_{ij}} + \beta_2 X_{\text{change in body fat}_{ij}} + \beta_3 X_{\text{age}_{ij}} + \beta_4 X_{\text{change in body fat}_{ij}} X_{\text{post bad winter}_{ij}} + \delta_{0i}.$$

We denote the population-averaged (marginal) linear predictor as

$$\eta_{ij} = \beta_1 X_{\text{post bad winter}_{ij}} + \beta_2 X_{\text{change in body fat}_{ij}} + \beta_3 X_{\text{age}_{ij}} + \beta_4 X_{\text{change in body fat}_{ij}} X_{\text{post bad winter}_{ij}}.$$

Here, $\beta 1$ denotes population averaged effects of the experience of a bad winter, $\beta 2$ denotes population averaged effects of over summer change in fat and $\beta 3$ denotes population averaged effects of age. The interaction of change in body fat and the and the experience of a bad winter is represented by $\beta 4$. In both models, the δ_{0i} represents the random intercepts for each animal. The random intercepts are assumed to be distributed as N(0, σ_B^2).

Model parameters were estimated using the JAGS software in program R (R Core Team, 2021) with the 'R2Jags' package (Su & Yajima, 2021). We generated 110,000 posterior draws for each model parameter (using three separate chains) and used a burn-in of 1000 draws to insure convergence. We considered parameters as convergent if they had unimodel posteriors, R values <1.1 and even mixture of their respective MCMC chains. We selected every 10th posterior draw to prevent auto-correlation. In summary, the posterior distributions of each model parameter were estimated using 10,000 of the original 110,000 posterior draws. We evaluated parameter importance using 90% credible intervals. We report the median of the posteriors and 90% credible intervals for all parameters. Model formulation and corresponding code used for our Bayesian analyses are located in the Supplementary Materials.

3 | RESULTS

We estimated the effects of density, bad winters, environment, and life history on over summer change in body fat and recruitment

for 116 adult, female mule deer across 372 animal-seasons between spring 2013 and autumn 2021 (Table 1). All models converged based on even mixture of the MCMC chains and unimodal posteriors, $\hat{R}$ values <1.1. Range, 90% quantiles and median values for all covariates in the model are reported in the Supplementary Materials (Table S1).

3.1 | Change in fat over summer

Herbaceous biomass, per capita snow water equivalent and length of spring did not influence the amount of fat an animal accumulated over summer (Table S2). For all results and interpretations reported in the remainder of the manuscript, we used the median values for those variables in any predictions. Per capita precipitation, age, recruitment, experiencing a bad winter, and the interaction between the amount of body fat an animal started spring with and experiencing a bad winter affected the amount of body fat an animal accumulated over summer (Figure 3; Table S2).

Animals that lived in areas with the highest per capita precipitation (0.84 mm of precipitation/100 animals) accumulated 3.62 percentage points more fat than animals that lived in areas with the lowest per capita precipitation (0.03 mm of precipitation/100 animals). Both age and recruitment had an important effect on the amount of fat animals accrued over summer. The cost of reproduction over the summer was 2.6 percentage points of fat for every 1 offspring raised. With every 1-year increase in age, an animal gained 0.4 percentage points less fat over summer—a 10-year-old animal would have gained 3.1 percentage points less fat than a 2-year-old animal over summer.

Having experienced a bad winter interacted with spring body fat, indicating the relationship between spring body fat and fat gain over summer shifted following the experience of a bad winter (Figure 3). The experience of a bad winter had the greatest effect on how much fat an animal accrued over summer when animals started spring following the bad winter with low body fat levels. For example, before the experience of a bad winter, an animal in poor shape (1% spring fat, 7 y/o, recruited two offspring and average per capita precipitation [0.27 mm of precipitation/100 animals]), would accumulate 5.63 percentage points of fat over summer. In the summers after the population experienced a bad winter, an animal that started spring in the same condition would have accumulated 8.21 percentage points.

3.2 | Recruitment

The amount of fat an animal accumulated over summer and the experience of a bad winter influenced recruitment of adult, female mule deer, but age did not influence recruitment (Table S3). The experience of a bad winter reduced the probability of recruiting two offspring and increased the probability of recruiting a single offspring, particularly for animals that gained little fat over summer. For example, an animal that gained 1 percentage point of fat over
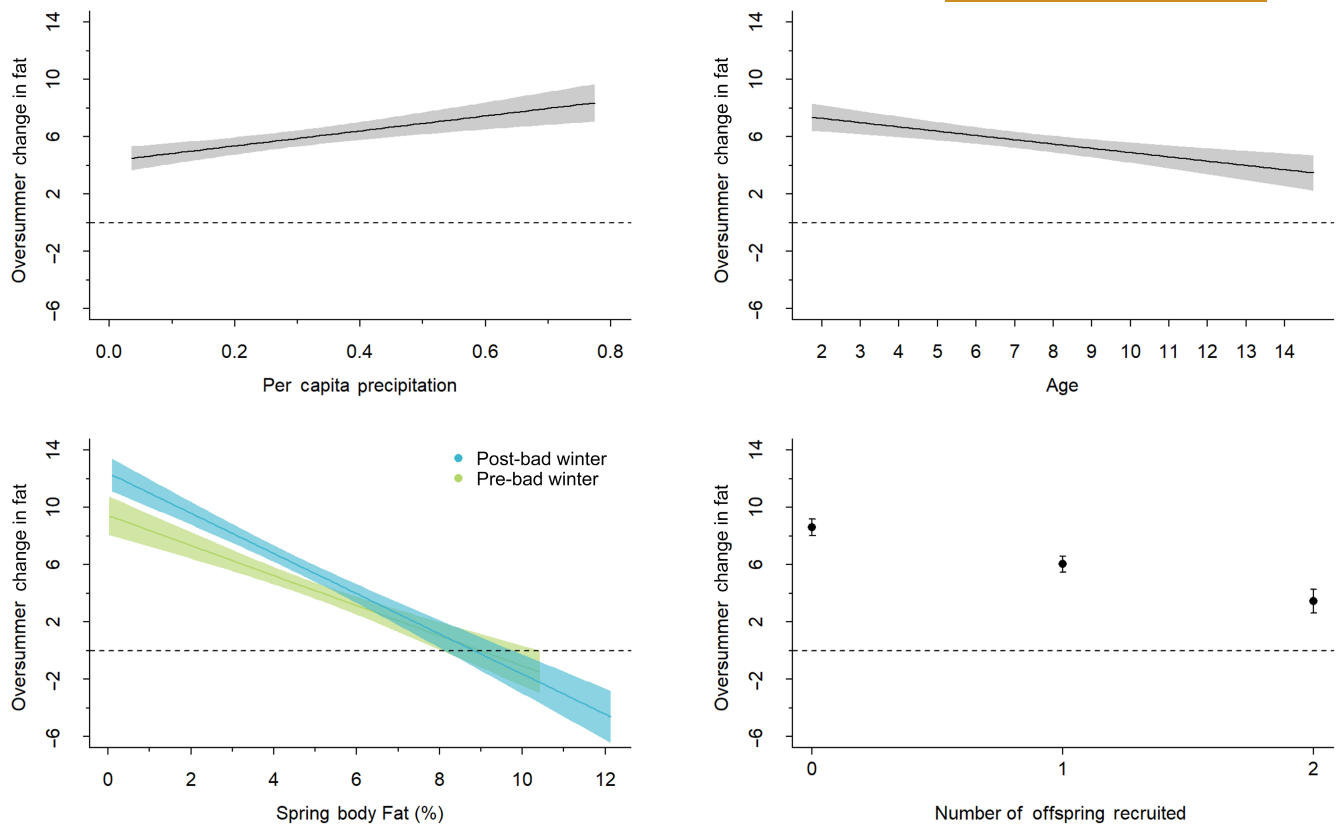
FIGURE 3 Effect of per capita precipitation, the interaction between the experience of a bad winter and the condition an animal started spring in, age, and number of offspring recruited on seasonal change in body fat of adult, female mule deer in western Wyoming, USA from 2013 to 2021.

summer had a 31% probability of recruiting two offspring before the experience of a bad winter, but that dropped to 21% following a bad winter (Figure S1).

4 | DISCUSSION

Effectively balancing allocation of energy across life-history traits is critical to lifetime fitness, particularly in the face of shifting risks (Bengston et al., 2017; Boggs, 1992; Stearns, 1992). Both past (harsh winters) and current experiences (resource availability per animal and habitat) influenced how a long-lived, highly faithful animal allocated energy to reproduction and survival (Figure 3). Mule deer changed risk-sensitive allocation following the experience of a harsh winter, as evidenced by a shift in the state-dependent relationship of fat gain favouring greater gain in fat reserves over summer and probability of recruiting offspring decreased following life-threatening winter conditions (Figure 3; Figure S1). Furthermore, the amount of capital that an animal began winter with was influenced strongly by the resources that were available per animal—regardless of whether they had experienced a harsh winter, as per capita precipitation increased, so did the amount of fat that animals had at the onset of winter (Figure 3). Plasticity in how animals allocate, store, and use energy for life-history traits under

rapidly changing conditions is likely critical to species persistence as climates, landscapes, and environments continue to change around the globe.

The balance between ensuring survival and raising offspring can be tenuous; especially given unpredictable shifts in environmental conditions can quickly upset that balance (Bårdsen et al., 2011). For animals that experience but survive unanticipated and life-threatening conditions, plasticity in resource allocation following that experience may be critical to their survival in subsequent years (Aguiar et al., 2023; Fischer et al., 2009). During harsh winters, animals that begin winter with insufficient stored capital face high risks of mortality (LaSharr et al., 2023). Mule deer retained the physiological memory of unprecedented winter conditions and adopted a shift in risk-sensitive allocation following that experience—after experiencing a harsh winter animals accumulated 1.4x as many capital stores over summer and were less likely to recruit offspring (Figure 3; Tables S2 and S3). Modification of risk-sensitive allocation indicate that environmental changes can have important implications for how wild animals allocate energy—particularly given many species of large herbivores in seasonal environments demonstrate strategies of risk-sensitive allocation, including reindeer (*Rangifer tarandus*; Bårdsen et al., 2014), elk (*Cervus elaphus*; Morano et al., 2013), mule deer (Figure 3; Monteith et al., 2013), white-tailed deer (*Odocoileus virginianus*; Simard et al., 2014) and chamois (*Rupicapra rupicapra*;

Morin et al., 2016). Flexibility in risk-sensitive strategies in the face of extreme environmental change may be especially important given the potential costs to reproduction that may come with increased allocation in capital accumulation following extreme and unpredictable environmental events.

For species that reproduce repeatedly and live numerous years, navigating the risks associated with investing energy in survival and reproduction can be a delicate balance because of an asymmetry between the cost and benefits associated with improved and worsened environmental conditions. In temperate environments, wild animals have evolved to cope with landscapes and resources that change seasonally (Boutin & Lane, 2014). The amount of stored capital an animal has at the onset of periods of resource scarcity can influence survival directly (Bright Ross et al., 2021; LaSharr et al., 2023; Miller et al., 2003). Consequently, the condition in which animals begin a season of resource limitation should be aligned with the conditions they will experience during those seasons. Unpredictable winter conditions favour animals that accumulate large amounts of fat (Monteith et al., 2013), and fat accumulation may be a requisite to population persistence in those systems (LaSharr et al., 2023). Indeed, the predictability or uncertainty in environmental conditions and resultant factors associated with periodic harsh winters can influence the acquisition, expenditure and allocation of energetic reserves (Bårdsen et al., 2014), and deer accumulated more fat following the experience of a harsh winter while recruiting fewer offspring (Figure S1). Animals that operate at the extreme of risk-aversion may secure their survival effectively each year, but it may come at a high cost to fitness if they are incapable of raising offspring to adulthood (Gaillard & Yoccoz, 2003; Oteyza et al., 2021). Alternatively, animals that employ extremely risk-prone strategies may be much more likely to succumb to mortality early in their life, sacrificing many years of potential reproduction (Orzack & Tuljapurkar, 2001).

Shifts in the risk-sensitive strategies of animals following an extreme event demonstrate the potential for wild populations to endure with rapidly changing environments, and the risks associated with those new environments (Bårdsen, 2017; Bårdsen et al., 2011). Yet, the response of animals to extreme environmental events might have lasting effects on population dynamics. Changes along the risk-prone–risk-averse gradient can have direct implications for reproduction (Oteyza et al., 2021), and survival at the extreme (Aguiar et al., 2023), which ultimately can influence population growth over time. The risk associated with different strategies, however, may vary immensely across a species distribution; the energetic reserves necessary to survive winter could be much greater in an alpine landscape with deep snow compared with a desert landscape with pulses of green-up throughout winter. Thus, the capital that animals accrue during periods of resource abundance is influenced by both the annual cycle of resources on their landscape, and the landscape itself—even if animals are physiologically programmed to enter winter with a certain amount of capital, their ability to reach that point is dependent on the conditions they experience on summer range (Monteith et al., 2013). Exposure to high per capita precipitation on

summer ranges allowed deer to enter winter with sufficient fat reserves (Figure 3); animals exposed to the highest per capita precipitation were able to accumulate over 3.5 percentage points more fat compared with animals at the lowest per capita precipitation. For mule deer in temperate environments, starting winter with sufficient fat reserves can be critical to survival (e.g. a difference in 10% and 20% body fat increased survival from 19.5% to 84.3% in mule deer; LaSharr et al., 2023), thus, an additional 3.5 percentage points of fat could be the difference between living and dying over winter.

The environment that animals inhabit throughout the year can have important, and additive influences on how animals accumulate, use and store capital for reproduction and survival (Boutin & Lane, 2014). Increased population density elevates competition for limited resources and can restrict an animal's ability to accumulate capital (i.e. density dependence; Gaillard et al., 2000). Alternatively, unprecedented environmental conditions during periods of resource scarcity can alter how animals allocate energy to reproduction and survival (i.e. risk sensitivity; Bårdsen et al., 2011; Monteith et al., 2013). If animals demonstrate a change in risk tolerance strategies following extreme events, populations may reflect rapid rebounds in abundance several years following harsh winters with above average mortality of adults and associated density reductions, given that resources on the landscape are abundant in the years following that winter and subsequent winters are of average to below average severity. Yet, if animals have shifted their allocation towards capital accumulation at the cost of reproductive effort, rebounds in the population may not occur rapidly if recruitment of juvenile animals is depressed. With rapidly changing landscapes and climates, maintaining stable populations may become increasingly challenging (Malhi et al., 2020). Managing populations below nutritional carrying capacity can enhance the nutritional buffer needed to survive periods of resource scarcity (Monteith et al., 2015; Stephenson et al., 2020). Reductions in population size through female harvest and targeted management of seasonal ranges—particularly summer and transitional ranges—to promote high quality and abundant forage and reduced competition may increase the relative amounts of fat that animals can accumulate over summer and be effective in increasing the stability of populations.

Flexibility in the amount of capital animals accrue and observations of changes in risk-sensitive reproductive allocation may be a necessary physiological adaptation for populations of species around the world to cope with rapidly changing landscapes. Populations that cannot appreciably change their relative allocation and thus, accrual of capital, in the face of rapid environmental change may face extirpation or extinction if a balance is not met and investment in reproduction comes at the cost of survival. Abundant resources during summer—resulting from reductions in population size—reduced energetic allocations to reproduction and measured changes in risk-sensitive allocation following the experience of a harsh winter led to accumulation of abundant fat reserves in mule deer as they entered winter. For a highly faithful, long-lived animal—both past and current conditions affected measured energy allocation to survival and reproduction.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data (LaSharr, 2023) are available on Dryad at https://doi.org/10.5061/dryad.bnzs7h4gm.

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REFERENCES

Aguiar, O., Sonnega, S., DiNuzzo, E. R., & Sheriff, M. J. (2023). Playing it safe; risk-induced trait responses increase survival in the face of predation. *Journal of Animal Ecology*, 92, 690–697. https://doi.org/10.1111/1365-2656.13880

Aikens, E. O., Dwinnell, S. P. H., LaSharr, T. N., Jakopak, R. P., Fralick, G. L., Randall, J., Kaiser, R., Thonhoff, M., Kauffman, M. J., & Monteith, K. L. (2021). Migration distance and maternal resource allocation determine timing of birth in a large herbivore. *Ecology*, 102(6), 1–12. https://doi.org/10.1002/ecy.3334

Bårdsen, B. J. (2017). Evolutionary responses to a changing climate: Implications for reindeer population viability. *Ecology and Evolution*, 7(15), 5833–5844. https://doi.org/10.1002/ece3.3119

Bårdsen, B. J., Fauchald, P., Tveraa, T., Langeland, K., Yoccoz, N. G., & Ims, R. A. (2008). Experimental evidence of a risk-sensitive reproductive allocation in a long-lived mammal. *Ecology*, 89(3), 829–837. https://doi.org/10.1890/07-0414.1

Bårdsen, B. J., Henden, J. A., Fauchald, P., Tveraa, T., & Stien, A. (2011). Plastic reproductive allocation as a buffer against environmental stochasticity—Linking life history and population dynamics to climate. *Oikos*, 120(2), 245–257. https://doi.org/10.1111/j.1600-0706.2010.18597.x

Bårdsen, B. J., Næss, M. W., Tveraa, T., Langeland, K., & Fauchald, P. (2014). Risk-sensitive reproductive allocation: Fitness consequences of body mass losses in two contrasting environments. *Ecology and Evolution*, 4(7), 1030–1038. https://doi.org/10.1002/ece3.1010

Bengston, S. E., Shin, M., & Dornhaus, A. (2017). Life-history strategy and behavioral type: Risk-tolerance reflects growth rate and energy allocation in ant colonies. *Oikos*, 126(4), 556–564. https://doi.org/10.1111/oik.03527

Berry, S., Shipley, L., Long, R., & Loggers, C. O. (2019). Differences in dietary niche and foraging behavior of sympatric mule and white-tailed deer. *Ecosphere*, 10(7), e02815.

Boggs, C. L. (1992). Resource allocation: Exploring connections between foraging and life history. *Ecology*, 6(5), 508–518.

Boutin, S., & Lane, J. E. (2014). Climate change and mammals: Evolutionary versus plastic responses. *Evolutionary Applications*, 7(1), 29–41. https://doi.org/10.1111/eva.12121

Bowyer, T., Bleich, V., Stewart, K., Whiting, J., & Monteith, K. (2014). Density dependence in ungulates—A review of causes and concepts. *California Fish and Game*, 100(3), 550–572.

Bright Ross, J. G., Newman, C., Buesching, C. D., Connolly, E., Nakagawa, S., & Macdonald, D. W. (2021). A fat chance of survival: Body condition provides life-history dependent buffering of environmental change in a wild mammal population. *Climate Change Ecology*, 2, 100022. https://doi.org/10.1016/j.ecochg.2021.100022

Caughley, G., & Gunn, A. (1996). *Conservation biology in theory and practice*. Blackwell Science.

Clutton-Brock, T., & Sheldon, B. C. (2010). Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution*, 25(10), 562–573. https://doi.org/10.1016/j.tree.2010.08.002

Clutton-Brock, T. H. (1984). Reproductive effort and terminal investment in iteroparous animals. *The American Naturalist*, 123(2), 212–229.

Convey, P., & Smith, R. I. L. (2006). Responses of terrestrial Antarctic ecosystems to climate change. *Plant Ecology*, 182(1–2), 1–10. https://doi.org/10.1007/s11258-005-9022-2

Cook, R. C., Cook, J. G., Stephenson, T. R., Myers, W. L., McCorquodale, S. M., Vales, D. J., Irwin, L. L., Hall, P. B., Spencer, R. D., Murphie, S. L., Schoenecker, K. A., & Miller, P. J. (2010). Revisions of rump fat and body scoring indices for deer, elk, and moose tools and technology article revisions of rump fat and body scoring indices for deer, elk, and moose. *Journal of Wildlife Management*, 74, 880–896. https://doi.org/10.2193/2009-031

Cook, R. C., Stephenson, T. R., Myers, W. L., Cook, J. G., & Shipley, L. A. (2007). Validating predictive models of nutritional condition for mule deer. *Journal of Wildlife Management*, 71(6), 1934–1943. https://doi.org/10.2193/2006-262

Daymet. (2022). Daily surface weather data on a 1-km grid for North America. Version 4 R1. https://doi.org/10.3334/ORNLDAAC/2129

Festa-Bianchet, M., & Jorgenson, J. T. (1998). Selfish mothers: Reproductive expenditure and resource availability in bighorn ewes. *Behavioural Ecology*, 9(2), 144–150. https://doi.org/10.1093/beheco/9.2.144

Fischer, B., Taborsky, B., & Dieckmann, U. (2009). Unexpected patterns of plastic energy allocation in stochastic environments. *The American Naturalist*, 173(3), E108–E120. https://doi.org/10.1086/596536

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, 13(2), 58–63. https://doi.org/10.1016/S0169-5347(97)01237-8

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, 31, 367–393.

Gaillard, J. M., & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: A case of environmental canalization? *Ecology*, 84(12), 3294–3306. https://doi.org/10.1890/02-0409

Garroway, C. J., & Broders, H. G. (2005). The quantitative effects of population density and winter weather on the body condition of white-tailed deer (*Odocoileus virginianus*) in Nova Scotia, Canada. *Canadian Journal of Zoology*, 83(9), 1246–1256. https://doi.org/10.1139/z05-118

Gerhart, K. L., Russell, D. E., Van DeWetering, D., White, R. G., & Cameron, R. D. (1997). Pregnancy of adult caribou (*Rangifer tarandus*): Evidence for lactational infertility. *Journal of Zoology*, 242(1), 17–30. https://doi.org/10.1111/j.1469-7998.1997.tb02926.x

Grosbois, V., Gimenez, O., Gaillard, J. M., Pradel, R., Barbraud, C., Clobert, J., Møller, A. P., & Weimerskirch, H. (2008). Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews*, 83(3), 357–399. https://doi.org/10.1111/j.1469-185X.2008.00047.x

Jorgenson, J. T., Festa-Bianchet, M., Gaillard, J.-M., & Wishart, W. D. (1997). Effects of age, sex, disease, and density on survival of Bighorn sheep. *Ecology*, 78(784), 1019–1032.

Kie, J., Bowyer, T., & Stewart, K. (2003). Ungulates in western coniferous forests: Habitat relationships, population dynamics, and ecosystem processes. In C. Zabel & R. Anthony (Eds.), *Mammal community dynamics: Management and conservation in the coniferous forests of Western North America* (pp. 296–340). Cambridge University Press. https://doi.org/10.1017/CBO9780511615757.010

Lai, Z., Shen, Y., Wang, Z., Ma, J., Yang, X., & Ma, L. (2022). Impact of precipitation variation on summer forage crop productivity and precipitation use efficiency in a semi-arid environment. *European Journal of Agronomy*, 141, 126616.

LaSharr, T. (2023). Movement and nutritional data of mule deer in Western Wyoming (December 2013–December 2021) (Version 2) [Data set]. Dryad. https://doi.org/10.5061/DRYAD.BNZS7H4GM

LaSharr, T. N., Dwinnell, S. P. H., Jakopak, R. P., Randall, J., Kaiser, R. C., Thonhoff, M., Scurlock, B., Fieseler, T., Hymas, N., Hymas, A., Roberts, N., Hobbs, J., Zornes, M., Brimeyer, D., Fralick, G., & Monteith, K. L. (2023). Behavior, nutrition, and environment drive survival of a large herbivore in the face of extreme winter conditions. *Ecosphere*, 14, e4601.

LaSharr, T. N., Dwinnell, S. P. H., Wagler, B. L., Sawyer, H., Jakopak, R. P., Ortega, A. C., Wilde, L. R., Kauffman, M. J., Huggler, K. S., Burke, P. W., Valdez, M., Lionberger, P., Brimeyer, D. G., Scurlock, B., Randall, J., Kaiser, R. C., Thonhoff, M., Fralick, G. L., & Monteith, K. L. (2023). Evaluating risks associated with capture and handling of mule deer for individual-based, long-term research. *Journal of Wildlife Management*, 87, e22333. https://doi.org/10.1002/jwmg.22333

Lauenroth, W. K., & Sala, O. E. (1992). Long-term forage production of North American shortgrass steppe. *Ecological Applications*, 2(4), 397–403.

Malhi, Y., Franklin, J., Seddon, N., Solan, M., Turner, M. G., Field, C. B., & Knowlton, N. (2020). Climate change and ecosystems: Threats, opportunities and solutions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1794), 20190104. https://doi.org/10.1098/rstb.2019.0104

McCullough, D. R. (1999). Density dependence and life-history strategies of ungulates. *Journal of Mammalogy*, 80(4), 1130–1146.

Merkle, J. A., Monteith, K. L., Aikens, E. O., Hayes, M. M., Hersey, K. R., Middleton, A. D., Oates, B. A., Sawyer, H., Scurlock, B. M., & Kauffman, M. J. (2016). Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20160456.

Miller, M. W., Aradis, A., & Landucci, G. (2003). Effects of fat reserves on annual apparent survival of blackbirds *Turdus merula*. *Journal of Animal Ecology*, 72(1), 127–132. https://doi.org/10.1046/j.1365-2656.2003.00678.x

Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Kie, J. G., & Bowyer, R. T. (2014). Life-history characteristics of mule deer: Effects of nutrition in a variable environment. *Wildlife Monographs*, 186, 1–62. https://doi.org/10.1002/wmon.1011

Monteith, K. L., Klaver, R. W., Hersey, K. R., Holland, A. A., Thomas, T. P., & Kauffman, M. J. (2015). Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. *Oecologia*, 178, 1137–1148. https://doi.org/10.1007/s00442-015-3296-4

Monteith, K. L., Stephenson, T. R., Bleich, V. C., Conner, M. M., Pierce, B. M., & Bowyer, R. T. (2013). Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. *Journal of Animal Ecology*, 82, 377–388. https://doi.org/10.1111/1365-2656.12016

Morano, S., Stewart, K. M., Sedinger, J. S., Nicolai, C. A., & Vavra, M. (2013). Life-history strategies of North American elk: Trade-offs associates with reproduction and survival. *Journal of Mammalogy*, 94(1), 162–172.

Morin, A., Rughetti, M., Rioux-Paquette, S., & Festa-Bianchet, M. (2016). Older conservatives: Reproduction in female Alpine chamois (*Rupicapra rupicapra*) is increasingly risk-averse with age. *Canadian Journal of Zoology*, 94, 311–321.

Nanney, J. S., Harper, C. A., Buehler, D., & Bates, G. E. (2018). Nutritional carrying capacity for Cervids following disturbance in hardwood forests. *The Journal of Wildlife Management*, 82, 1219–1228.

National Operational Hydrologic Remote Sensing Center. (2004). Snow data assimilation system (SNODAS) data products at NSIDC, Version 1.

Orzack, S. H., & Tuljapurkar, S. (2001). Reproductive effort in variable environments, or environmental variation is for the birds. *Ecology*, 82(9), 2659–2665. https://doi.org/10.1890/0012-9658(2001)082[2659:reiveo]2.0.co;2

Oteyza, J. C., Mouton, J. C., & Martin, T. E. (2021). Adult survival probability and body size affect parental risk-taking across latitudes. *Ecology Letters*, 24(1), 20–26. https://doi.org/10.1111/ele.13615

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37(1), 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Patton, B. D., Dong, X., Nyren, P. E., & Nyren, A. (2007). Effects of grazing intensity, precipitation, and temperature on forage production. *Rangeland Ecology and Management*, 60(6), 656–665.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Sawyer, H., Kauffman, M. J., Nielson, R. M., & Horne, J. S. (2009). Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications*, 19, 2016–2025. https://doi.org/10.1890/08-2034.1

Scornavacca, D., Lovari, S., Cotza, A., Bernardini, S., Brunetti, C., Pietrocini, V., & Ferretti, F. (2016). Pasture quality affects juvenile survival through reduced maternal care in a Mountain-Dwelling Ungulate. *Ethology*, 122(10), 807–817. https://doi.org/10.1111/eth.12530

Sikes, R. S. (2016). 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97, 663–688.

Simard, A., Huot, J., De Bellefeuille, S., & Côté, S. D. (2014). Influences of habitat composition, plant phenology and population density on autumn indices of body condition in a northern white-tailed deer population. *Wildlife Monographs*, 187(1), 1–28.

Smythe, S. E., Sanchez, D. M., & Epps, C. W. (2019). Contrasting winter moose nutritional carrying capacity models on a dynamic landscape. *Journal of Fish and Wildlife Management*, 10(1), 163–179.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.

Stephens, D. W. (1981). The logic of risk-sensitive foraging preferences. *Animal Behaviour*, 29(2), 628–629. https://doi.org/10.1016/S0003-3472(81)80128-5

Stephens, P. A., Houston, A. I., Harding, K. C., Boyd, I. L., & McNamara, J. M. (2014). Capital and income breeding: The role of food supply. *Ecology*, 95(4), 882–896. https://doi.org/10.1890/13-1434.1

Stephenson, T. R., Bleich, V. C., Pierce, B. M., & Mulcahy, G. P. (2002). Validation of mule deer body composition using in vivo and post-mortem indices of nutritional condition. *Wildlife Society Bulletin*, 30(2), 557–564.

Stephenson, T. R., German, D. W., Frances Cassirer, E., Walsh, D. P., Blum, M. E., Cox, M., Stewart, K. M., & Monteith, K. L. (2020). Linking population performance to nutritional condition in an alpine ungulate. *Journal of Mammalogy*, 101(5), 12441256. https://doi.org/10.1093/jmammal/gyaa091

Su, Y., & Yajima, M. (2021). R2jags: Using R to run 'JAGS'. R package version 0.7-1. https://CRAN.R-project.org/package=R2jags

Van der Putten, W. H. (2012). Climate change, aboveground-belowground interactions, and species' range shifts. *Annual Review of Ecology, Evolution, and Systematics*, 43, 365–383.

Wyoming Game and Fish Department. (2021). Pinedale job completion report 2021.

Zimmerman, T. J., Jenks, J. A., & Leslie, D. M., Jr. (2006). Gastrointestinal morphology of female white-tailed and mule deer: Effects of fire, reproduction, and feeding type. *Journal of Mammalogy*, 87(3), 598–605.

SUPPORTING INFORMATION

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

Table S1. Range, 90% quantiles and median of all covariates used to model over summer change in fat of adult, female mule deer in western Wyoming, USA from 2013 to 2021.

Table S2. Alpha and beta estimates from the Bayesian model for seasonal change in body fat of adult, female mule deer in western Wyoming, USA from 2013 to 2021 using 90% credible intervals. We report the median and the lower and upper 90% credible intervals. Pd is the probability of direction, with 1.00 meaning there is a 100% probability that the parameter falls in the direction of the median estimate.

Table S3. Alpha and beta estimates from the Bayesian model for recruitment by adult, female mule deer in western Wyoming, USA from 2013 to 2021 using 90% credible intervals. We report the median and the lower and upper 90% credible intervals. Pd is the probability of direction, with 1.00 meaning there is a 100% probability that the parameter falls in the direction of the median estimate. Recruitment [0 offspring] and recruitment [1 offspring] represents the difference in the intercept for recruiting 0 or 1 offspring, respectively, compared to recruiting 2 offspring.

Figure S1. Predicted probability of recruiting 0, 1 or 2 offspring in the fall before (black) and after (red) a bad winter depending on the amount of fat accumulated over summer by adult, female mule deer in western Wyoming, USA from 2013 to 2021.