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ARTICLE

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Heterogeneity in risk-sensitive allocation of somatic reserves in a long-lived mammal

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Abstract

Food quality and availability, when combined with energetic demands in seasonal environments, shape resource acquisition and allocation by animals and hold consequences for life-history strategies. In long-lived species with extensive maternal care, regulation of somatic reserves of energy and protein can occur in a risk-sensitive manner, wherein resources are preferentially allocated to support survival at the cost of investment in reproduction. We investigated how Rocky Mountain bighorn sheep (*Ovis canadensis*), an alpine mammal in a highly seasonal environment, allocates somatic reserves across seasons. In accordance with the hypothesis of risk-sensitive resource allocation, we expected accretion and catabolism of somatic reserves to be regulated relative to preseason nutritional state, reproductive state, and variation among populations in accordance with local environmental conditions. To test that hypothesis, we monitored seasonal changes in percent ingesta-free body fat (IFBFat) and ingesta-free, fat-free body mass (IFFFBMass) in three populations of bighorn sheep in northwest Wyoming between 2015 and 2019 through repeated captures of female sheep in December and March of each year in a longitudinal study design. Regulation of somatic reserves was risk-sensitive and varied relative to the amount of somatic reserves an animal had at the beginning of the season. Regulation of fat reserves was sensitive to reproductive state and differed by population, particularly over the summer. In one population with low rates of recruitment of young, sheep that recruited offspring lost fat over the summer in contrast to the other two populations where sheep that recruited gained fat. And yet, all populations exhibited similar changes in fat catabolism and risk sensitivity over winter. The magnitude of body fat and mass change across seasons may be indicative of sufficiency of seasonal ranges to meet energetic demands of survival and reproduction. Risk-sensitive allocation of resources was pervasive, suggesting nutritional underpinnings are foundational to behavior, vital rates, and, ultimately, population dynamics. For species living in alpine environments, risk-sensitive resource allocation may be essential to balance investment in reproduction with ensuring survival.

KEYWORDS

bighorn sheep, ingesta-free body fat, life history, nutritional condition, *Ovis canadensis canadensis*, recruitment, seasonal carry-over effects

INTRODUCTION

Spatial and temporal patterns of nutrient availability shape the life-history evolution of wild animals (Monteith et al., 2014; Parker et al., 2009) and often dictate species distributions and movements (White et al., 1975), foraging behavior (Penczykowski et al., 2014), timing of reproduction (Aikens et al., 2021; Peláez et al., 2020), and capacity to fight disease (French et al., 2007). Nutrition is the backbone of population regulation, via integral links with life-history characteristics, including pregnancy, age at first reproduction, size and number of offspring, adult and juvenile survival, and recruitment (Cook et al., 2004; Gustafsson et al., 1994; Meijer & Langer, 1995; Sand, 1996; Stearns, 1992). Because nutrition underpins behavior across foraging hierarchies, landscapes, and population processes (Bailey et al., 1996; Senft et al., 1987), the way resources are subsequently allocated reflects a fundamental adaptation that links animals with their environment.

Nutritional dynamics, or the patterns of nutrient acquisition and allocation, drive life-history strategies of animals in seasonal environments (Mautz, 1978). Temperate environments undergo marked seasonal cycles of resource availability and quality. To facilitate survival and reproduction in seasonal environments, many species accrete somatic reserves of energy and protein (McNamara & Houston, 2008; Stephens et al., 2014) during periods of resource abundance (Cook et al., 2013; Monteith et al., 2014). Somatic reserves can then be mobilized during periods of resource limitation (e.g., winter) to finance survival and reproduction (Mautz, 1978). Patterns of resource acquisition and allocation, however, can be variable and influenced by environmental conditions (Bårdsen et al., 2008). Model-based approaches have evaluated the influence of environmental variation on resource allocation and population dynamics (e.g., Desforges et al., 2021). Nevertheless, the longitudinal studies necessary to provide insights into factors underpinning the acquisition and allocation of fat and protein reserves of animals living in seasonal environments are few.

Variability in available nutritional resources coupled with high energetic costs of reproduction (primarily from lactation; Clutton-Brock et al., 1989) often forces a trade-off between survival and reproduction (Hamel et al., 2010; Hamel et al., 2011). For long-lived iteroparous animals, the fitness value of survival and future reproduction is generally greater than that of current reproduction (Stearns, 1992). Life-history theory predicts that when somatic reserves and nutritional income cannot support nutritional demands for both survival and reproduction, individuals should adopt a risk-sensitive strategy of resource allocation. Risk-sensitive resource allocation seeks to secure immediate survival and opportunities for future reproduction by sacrificing allocation to current reproductive efforts (Festa-Bianchet et al., 1998; Gaillard et al., 2000; Stearns, 1992). Capital breeders are reliant on somatic reserves to finance reproduction (Stearns, 1992). In a risk-sensitive framework, somatic reserves should be conserved relative to risk (i.e., reproductive and nutritional state) to promote the maintenance of sufficient reserves for survival and future reproduction in capital breeders (Monteith et al., 2013). Therefore, under the risk-sensitive framework of resource allocation, animals will use and gain resources according to the amount that they possess: An animal with fewer somatic reserves in the spring should gain more somatic reserves over summer—often at the cost of reproductive allocation—than an animal with greater levels of somatic reserves in spring (Monteith et al., 2013). Similarly, to avoid the risk of starvation, an animal with fewer somatic reserves in autumn should lose fewer somatic reserves over winter than an animal with more somatic reserves in autumn (Monteith et al., 2013). Capital breeders that experience highly stochastic environmental conditions or uncertainty in nutrient availability may be more prone to risk sensitivity in resource allocation (Bårdsen et al., 2008, 2010). Understanding how an individual allocates somatic resources to finance reproduction and survival depends upon an understanding of the nutritional state and the factors that determine resource allocation.

Alpine environments are highly seasonal, characterized by relatively cold and short growing seasons and low primary productivity (Pettorelli et al., 2007). Mountain ungulates (subfamily *Caprinae*) are capital-breeding, alpine species that are expected to exhibit conservative reproductive tactics relative to resource allocation (Toïgo et al., 2002). On alpine summer ranges, females attempt to rear offspring and replenish somatic reserves needed to buffer themselves against sparse nutritional resources on winter ranges. Thus, their nutritional dynamics must be fine-tuned to the extreme variation in resource availability they experience year-round. Further, mountain ungulates provide high levels of maternal investment during the summer for successful recruitment of juveniles into the population (Shackleton et al., 1999), which comes at the cost of gain in body mass in summer (Festa-Bianchet et al., 1998). Thus, allocation of somatic reserves, while likely important for the survival and growth of young, should occur in a risk-sensitive manner to ensure the survival of the mother.

To better understand nutritional dynamics in a capital-breeding mammal that is exposed to seasonal extremes, we evaluated inter-seasonal changes in somatic reserves of three populations of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) in Wyoming, USA. We tested the hypothesis that accretion and catabolism of protein and fat are risk-sensitive, especially in these environments that are characterized by seasonal extremes of weather and forage availability. We predicted that (1) preseason nutritional state (fat and protein reserves measured before summer and winter via ingesta-free body fat and ingesta-free, fat-free body mass; Monteith et al., 2013) and (2) reproductive state (pregnancy in March and lactation status in December) would largely underpin seasonal changes in somatic reserves (Bårdsen et al., 2008, 2010; Monteith et al., 2013). Specifically, we predicted that accretion of somatic reserves during summer would be inversely related to spring levels of somatic reserves and that catabolism of somatic reserves during winter would be inversely related to autumn levels of somatic reserves. Additionally, we expected that recruitment of offspring and pregnancy would come at a cost to somatic reserves in the summer and winter, respectively. Further, we predicted that the state-dependent relationships may be (3) context-dependent (i.e., dependent upon prevailing environmental conditions; Bårdsen et al., 2008), and therefore vary among populations. Understanding how mountain sheep adjust their resource allocation in accordance with their environment will provide better insight into how capital breeders physiologically cope with stochastic environmental conditions.

MATERIALS AND METHODS

Study system

We conducted our study during 2015–2019 using adult female bighorn sheep from three populations in northwestern Wyoming, USA: the Whiskey Mountain population located in the Wind River Range (43.436447, −109.551299), the Jackson population in the Gros Ventre Range (43.573926, −110.586624), and the Upper Shoshone segment of the Absaroka population in the Absaroka Range (44.420117, −109.714750). The Upper Shoshone segment of the Absaroka population winters along the North and South Fork of the Shoshone River and consists of animals from several different herd units. All three populations are native and have never been augmented. The populations were spatially separated and genetically distinct (Love Stowell et al., 2020). Females in all three populations give birth between mid-May and mid-June annually.

All three populations had positive detections of bacterial pathogens associated with pneumonia, including *Mycoplasma ovipneumoniae*, during the study (Butler et al., 2018). Despite similar pathogen presence, population performance among the three populations has differed since the 1990s. The Whiskey Mountain population declined after 1991, when it experienced a pneumonia outbreak, and continued to decline during this study because of low recruitment (Paterson et al., 2021; Proffitt et al., 2021). The Jackson population experienced pneumonia outbreaks in 2001 and 2011, but the population increased during this study (Wyoming Game and Fish Department, 2020). The size of the Absaroka population was relatively stable, but experienced declines in 2015–2017 and was stable from 2018 to 2019, though there are no documented pneumonia outbreaks associated with mass mortality events (Wyoming Game and Fish Department, unpublished data).

All sheep in the study migrated seasonally along elevational gradients (Lowrey et al., 2020). Winter ranges for each population were 2000–2500 m in elevation and summer ranges were 2600–3600 m. All winter ranges were classified as sagebrush steppe, dominated by big sagebrush (*Artemisia tridentata*). Mean daily temperatures on winter ranges from December to March in 2015–2019 were −3.7°C for the Whiskey Mountain population (Dubois, WY; ACIS station 482715), −6.2°C for the Jackson population (Jackson, WY; ACIS station 484910), and −0.7°C for the Upper Shoshone segment of the Absaroka population, hereafter referred to as the Upper Shoshone population (Wapiti, WY; ACIS station 489467; High Plains Regional Climate Center [HPRCC], 2020). Mean annual snowfall varied across winter ranges during the study period, 2015–2019 (Whiskey Mountain: 33.8 cm; Jackson: 70.8 cm; and Upper Shoshone: 19.4 cm; HPRCC, 2020). During summers, June through August 2015–2019, mean daily temperatures of summer ranges were 5.9°C for the Whiskey Mountain population, 8.8°C for the Jackson population, and 12.3°C for the Upper Shoshone population (HPRCC, 2020). Mean annual precipitation on summer ranges was 18.8 cm for the Whiskey Mountain population, 13.3 cm for the Jackson population, and 6.8 cm for the Upper Shoshone population (HPRCC, 2020). The summer range of the Whiskey Mountain population was characterized by granitic outcrops, glaciers, permanent snowfields, and patches of short, dense vegetation among rocky outcrops. Predominant plant species in summer range of the Whiskey Mountain population were *Carex* spp., *Geum rossii*, and *Potentilla* spp. Limestone cliffs, conifer forests, and alpine meadows interspersed with more tall–forb communities characterized the summer range of the Jackson population. Predominant plant species in the summer range of the Jackson population were *Carex* spp., *Poa* spp., and *Lewisia pygmaea*. The summer range of the Upper Shoshone population was characterized by volcanic vent and alluvial facies and alpine vegetation. Predominant plant species were *Carex* spp., *Phlox pulvinae*, and *Deschampsia* spp.

Sampling

Beginning in December 2015, we captured adult females using helicopter net-gunning (Whiskey Mountain and Jackson populations; Krausman et al., 1985; Wagler et al., 2022) or ground-darting and chemical immobilization (Upper Shoshone population) and fitted each with an individually identifiable GPS collar (various models, Advanced Telemetry Systems, Isanti, MN, USA; Vectronics Aerospace, Berlin, Germany). Every animal collared was assigned a unique identifier (animal ID). Each subsequent March and December 2015–2019, we recaptured collared females whenever possible and captured uncollared females to maintain sufficient sample sizes (25 in Whiskey Mountain, 20 in Jackson, and 15 in Upper Shoshone populations). We programmed GPS collars to record locations 2–24 times/day.

Upon the first capture, we estimated age using a combination of horn annuli and tooth eruption and wear (Dekelaita et al., 2020; Geist, 1966; Rubin et al., 2000). Each March, we determined pregnancy status using ultrasonography (Stephenson et al., 1995). Each December, we determined lactation status (a proxy for recruitment) by palpating the udder and attempting to express milk (Monteith et al., 2014). At each capture event, we measured nutritional condition using ultrasonography to measure subcutaneous rump fat (5-MHz transducer; Ibex Pro, E.I. Medical Imaging, Loveland, CO, USA) according to methods described in Stephenson et al. (2020). If there was no measurable subcutaneous rump fat, we used manual palpation to assign a body condition score (BCS; Stephenson et al., 2020). We used the ultrasonography measurements and BCS to estimate percent ingesta-free body fat (% IFBFat) using equations developed and validated for bighorn sheep (Stephenson et al., 2020). To measure body mass, we weighed each sheep using a platform or hanging scale to the nearest 0.1 kg. We subtracted 2 kg from pregnant sheep in March to account for fetal mass and products of conceptus (Cook et al., 2010; Monteith et al., 2013). We calculated ingesta-free body mass using the following equation (Stephenson et al., 2020):

$$\begin{aligned}&\text{Ingesta-free body mass (in kilograms)}\\&\quad=0.668(\text{body mass; in kilograms})+6.418.\end{aligned}\tag{1}$$

We calculated ingesta-free, fat-free body mass (IFFFBMass; in kilograms) using the following equation for animals with no measurable subcutaneous rump fat (MAXFAT; Stephenson et al., 2020):

$$\text{IFFFBMass (in kilograms)}=\text{IFBMass}-2.11(\text{BCS})-1.46.\tag{2}$$

We calculated IFFFBMass using the following equation for animals with measurable subcutaneous rump fat (MAXFAT; Stephenson et al., 2020):

$$\begin{aligned}\text{IFFFBMass (in kilograms)}=\text{IFBMass}-6.85(\text{MAXFAT})\\+3.28.\end{aligned}\tag{3}$$

Spatial data and statistical analysis

We completed all data analyses in Program R (R Core Team, 2020). We defined summer as June through

August because it is the primary growing season in the alpine zone and thus the primary period for nutrient acquisition and potential accumulation of somatic reserves. We defined winter as December through March because most sheep were on their winter ranges and most snowpack accumulated during these months. We randomly selected 2 locations/day for each sheep to create a balanced sample size across individuals. We excluded sheep with fewer than 30 GPS locations during a season (Street et al., 2021). We calculated seasonal home ranges as 75% kernel density utilization distributions using a 250-m resolution for each sheep using the adehabitatHR package (Calenge, 2006). We chose a 75% utilization distribution to include the core home range and the primary area that sheep are using while excluding areas that sheep likely are not using (Clapp & Beck, 2015; Downs & Horner, 2008) that may bias spatial variable estimates (e.g., heavily forested areas on the edge of escape terrain that may inflate biomass estimates). We extracted spatially explicit data for mean snow depth (in meters) at a 1-km resolution (National Operational Hydrologic Remote Sensing Center, 2004) of each winter home range and herbaceous biomass estimates (Rangeland Analysis Platform; in kilograms per hectare; annual temporal resolution) for summer and winter home ranges at a 30-m resolution as an index of forage availability on seasonal ranges (Jones et al., 2020; Robinson et al., 2019). We extracted the spatial data for December through March for winter home ranges and June through August for summer home ranges. We used these spatial data on snow depth and biomass to assess the effects of weather and forage conditions on seasonal changes in fat and lean body mass of sheep. Annual estimates of biomass on winter range were used as an estimate of relative forage availability that was available following the primary growing season.

To evaluate whether the allocation of somatic reserves by bighorn sheep was risk-sensitive, we used generalized linear mixed models to determine whether changes in somatic reserves over the summer and winter were related to reproductive status, population, and somatic reserves from the previous season. We used four model sets to evaluate overwinter and oversummer changes in IFBFat (change in percentage points [ppt]) and IFFFBMass (change in kilograms). For oversummer changes in reserves, we evaluated combinations of oversummer change in IFBFat or IFFFBMass (i.e., the difference between December and the previous March) with fixed effects of percent IFBFat or IFFFBMass in March, population, age, vegetation biomass, and lactation status in December with a random intercept for animal ID. For overwinter change in IFBFat and IFFFBMass (i.e., the difference between March and the previous December), we used the same model structure as in oversummer models, and evaluated combinations of variables including fixed effects of percent IFBFat or IFFFBMass in December, population, age, vegetation biomass, snow depth, IFBFat for change in IFFFBMass model, and pregnancy status in March with a random intercept for animal ID.

We included population as a covariate to test for differences among populations (i.e., context dependence). We tested for interactions between preseason somatic reserves and population, as well as recruitment and population separately. Interactions between preseason somatic reserves or recruitment and population would indicate different relationships across populations. We tested separately for the inclusion of squared terms for age and vegetation biomass to assess for a curvilinear relationship with those terms, and the natural log of age to assess an asymptotic effect of that term. We tested for a quadratic and natural log relationship with age because of previous observations of nonlinearity in relationships between age and physiological characteristics in bighorn sheep (Nussey et al., 2011). We tested for a quadratic relationship with biomass to allow for the detection of an influence of intermediate values of biomass to account for potential trade-offs between forage quantity and quality because net intake rates are maximized at intermediate biomass levels (Hebblewhite et al., 2008). We retained interactions in the global model if they differed from zero and improved model fit. Over winter, there were no animals with seasonal transitions of IFFFBMass that were not pregnant in the Upper Shoshone population, so we could not include population and pregnancy status in the same model. We developed two global models for overwinter change in IFFFBMass, one including pregnancy and one including population along with the other covariates. We used the Akaike information criterion adjusted for small sample size ($\mathrm{AIC_c}$) to determine which global model to further test (Burnham & Anderson, 2002).

We evaluated all possible combinations of covariates because each corresponded to our hypotheses or were factors known to influence changes in somatic reserves in other ungulates (Arnold, 2010; Monteith et al., 2013). We used $\mathrm{AIC_c}$ to rank competing models (Burnham & Anderson, 2002). When population was included in the top model, we calculated estimated marginal means (Searle et al., 1980) using the emmeans package (Length, 2022) to evaluate population-level differences in seasonal change in somatic reserves.

RESULTS

Between 2015 and 2019, we obtained 79 seasonal transitions (i.e., two sequential captures) of 49 female bighorn sheep over the summer, and 93 seasonal transitions of 57 female bighorn sheep over the winter. The number of seasonal transitions for animals ranged from 1 to 8, with a mean of 2.57 seasonal transitions. We were unable to obtain mass measurements during several of the captures, so sample sizes for models of change in IFFFBMass were smaller than for models of change in IFBFat (Table 1). In December, mean IFBFat in the Whiskey Mountain population was an average of 3.58 percentage points (ppt) lower than in the Jackson and Upper Shoshone populations (Table 1). In March, the mean percent IFBFat was more similar among populations than in December (Table 1), ranging from 8.27% in the Jackson population to 8.61% in the Upper Shoshone population (Table 1). Both in December and March, mean IFFFBMass was lower in the Whiskey Mountain population than in the Jackson and Upper Shoshone populations (Table 1). Mean pregnancy rates were relatively high in all three populations, with 88.23 ± 8.05% pregnant in Upper Shoshone, 90.70 ± 4.48% in Whiskey Mountain, and 87.88 ± 5.77% in Jackson populations.

The Whiskey Mountain summer ranges had the lowest mean biomass value of 121.27 ± 8.10 kg/ha, followed by Upper Shoshone with 167.95 ± 19.23 kg/ha, and Jackson summer ranges had the greatest biomass with 243.57 ± 6.30 kg/ha. At the individual level, biomass did not correlate with change in IFBFat or IFFFBMass. Biomass on winter ranges was lowest for the Upper Shoshone population with 406.63 ± 14.83 kg/ha, followed by Whiskey Mountain with 422.40 ± 9.41 kg/ha and Jackson with 558.43 ± 17.94 kg/ha. The Jackson populations experienced the most snow over winter, with a mean depth of 0.70 ± 0.04 m on home ranges. The Upper Shoshone population experienced a mean depth of 0.17 ± 0.04 m on winter home ranges, and the Whiskey Mountain population experienced a mean depth of 0.26 ± 0.03 m. At the individual level, biomass and snow depth did not correlate with change in IFBFat or IFFFBMass over winter.

Seasonal changes in fat

No interactions among preseason somatic reserves or recruitment status with population improved model fit, which would have indicated a different relationship across populations and, thus, were not included in global models. Accretion of fat over summer was affected negatively by recruitment, varied across populations (Figure 1), and occurred as a function of fat levels in March (Table 2). The amount of fat change over summer was an inverse function of IFBFat in March; sheep with less fat in March accumulated more fat over summer (Figure 2). Sheep that recruited young to autumn accumulated less fat than those that did not recruit (Figure 1). In the Whiskey Mountain population, sheep gained 5.86 fewer ppt of IFBFat than in the Jackson population ($p < 0.001$) and 5.08 fewer ppt of IFBFat than in the Upper Shoshone population ($p < 0.01$) over the summer (Table 2). In 12 of 79 seasonal transitions, sheep lost fat over the summer; 10 of the 12 sheep that lost fat over the summer recruited young.

On average, females that recruited young in the Whiskey Mountain population lost 1.15 ± 0.50 ppt of IFBFat over summer, whereas females that recruited young in Upper Shoshone and Jackson populations gained 0.82 ± 1.28 and 4.46 ± 0.91 ppt of IFBFat, respectively. Mean recruitment rates were similar in Upper Shoshone and Jackson populations at 57.14 ± 13.73% and 51.43 ± 8.57%, respectively; the Whiskey Mountain population had a lower mean recruitment rate of 20.00 ± 7.42%.

Fat loss over winter was affected by snow depth on winter range, age, and population, and as an inverse function of fat in December (Table 3). Sheep with less fat in December lost less fat overwinter than their counterparts with more fat in December (Figure 3). Fat loss over winter differed between populations, with the Upper Shoshone population losing 1.81 more ppt of IFBFat than the Whiskey Mountain population ($p < 0.05$) and 2.19 more ppt of IFBFat than the Jackson population ($p < 0.05$; Table 3).

Seasonal changes in lean mass

Seasonal changes in IFFFBMass did not vary by population and were thus not context-dependent. Sheep gained a mean of 1.79 ± 0.28 kg of lean mass over summer, but

TABLE 1 Sample sizes and seasonal means of somatic reserves of bighorn sheep captured in northwest Wyoming between 2015 and 2019.

	December IFBFat			March IFBFat			December IFFFBMass			March IFFFBMass		
Population	*N*	Mean	SE	*N*	Mean	SE	*N*	Mean	SE	*N*	Mean	SE
Upper Shoshone	14	14.89	1.23	17	8.61	0.94	8	45.98	1.01	9	42.41	0.77
Jackson	30	15.14	0.74	33	8.35	0.50	35	45.82	0.71	33	42.98	0.60
Whiskey Mountain	30	11.49	0.74	43	8.27	0.38	30	42.15	0.45	42	40.71	0.33

Abbreviations: IFBFat, ingesta-free body fat; IFFFBMass, ingesta-free, fat-free body mass.

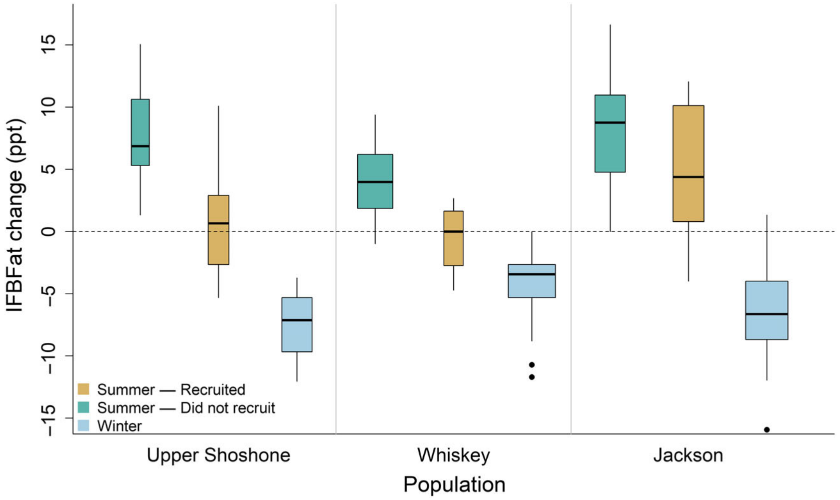

FIGURE 1 Median change in percentage points (ppt) of ingesta-free body fat (IFBFat) in summer and winter of 67 individual bighorn sheep throughout 172 concurrent observations in northwest Wyoming between 2015 and 2019.

TABLE 2 Model outputs, including non-standardized beta estimates, from oversummer change ($N = 79$ seasonal transitions, 49 animals) in percent ingesta-free body fat (IFBFat) in bighorn sheep in northwest Wyoming between 2015 and 2019. The Upper Shoshone population is the reference population.

Parameter	Estimate	SE	df	95% CI
Intercept	15.28	2.03	73.08	11.11, 19.12
Recruit	−5.52	0.85	57.22	−7.07, −3.38
March IFBFat	−0.76	0.15	70.86	−1.04, −0.46
Whiskey Mountain population	−5.08	1.47	46.46	−7.82, −2.09
Jackson population	0.78	1.42	43.66	−1.93, 3.50

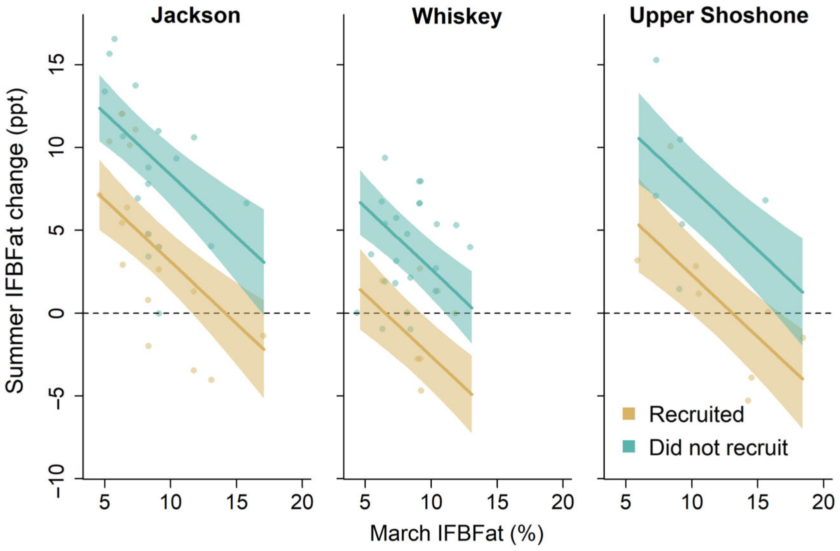

FIGURE 2 Relationship between preseason (March) ingesta-free body fat (IFBFat) and change in percentage points (ppt) of IFBFat over the summer in female bighorn sheep in northwest Wyoming between 2015 and 2019.

this change ranged from −3.74 to 6.96 kg. Sheep lost a mean of 1.79 ± 0.28 kg of lean body mass over winter, but this change ranged from a loss of 8.51 to a gain of 4.20 kg. Seasonal change in lean body mass was related negatively to March lean body mass over summer (Table 4, Figure 4) and negatively related to December lean body

TABLE 3 Model outputs, including non-standardized beta estimates, from overwinter change ($N = 93$ seasonal transitions, 57 animals) in percent ingesta-free body fat (IFBFat) in bighorn sheep in northwest Wyoming between 2015 and 2019. The Upper Shoshone population is the reference population.

Parameter	Estimate	SE	df	95% CI
Intercept	3.86	1.20	83.28	1.45, 6.15
December IFBFat	−0.55	0.05	85.48	−0.65, −0.45
Age	−0.26	0.12	65.01	−0.48, −0.03
Whiskey Mountain population	1.81	0.65	55.40	0.56, 3.05
Jackson population	2.19	0.88	81.86	0.52, 3.87
Snow depth	−4.26	1.09	55.96	−6.34, −1.98

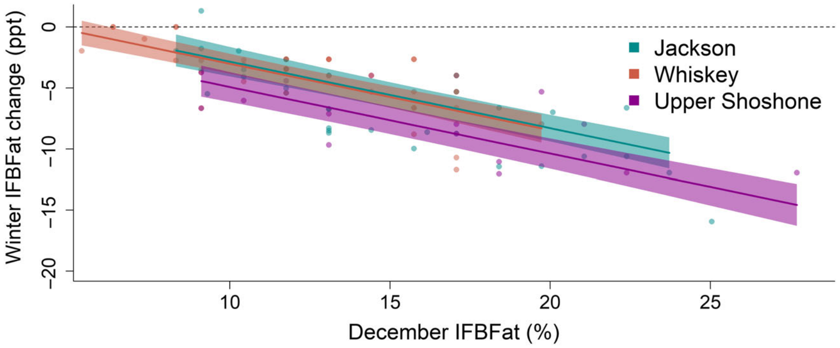

FIGURE 3 Relationship between preseason (December) ingesta-free body fat (IFBFat) and change in percentage points (ppt) of IFBFat over the winter in female bighorn sheep in northwest Wyoming between 2015 and 2019.

TABLE 4 Model outputs, including non-standardized beta estimates, from oversummer change ($N = 73$ seasonal transitions, 45 animals) in ingesta-free fat-free body mass (IFFFBMass; in kilograms) in bighorn sheep in northwest Wyoming between 2015 and 2019.

Parameter	Estimate	SE	df	95% CI
Intercept	9.20	3.39	57.02	2.38, 16.24
March IFFFBMass	−0.28	0.08	65.59	−0.47, −0.11
March IFBFat	0.29	0.09	68.91	0.10, 0.47
Biomass	0.01	0.00	59.32	0.00, 0.02

Abbreviation: IFBFat, ingesta-free body fat.

mass in the winter (Table 5, Figure 5). Change in lean body mass was related positively to March IFBFat over summer and December IFBFat over winter (Tables 4 and 5, Figure 6). Female sheep with 5% body fat in December were predicted to catabolize 2.70 kg of lean mass during winter.

DISCUSSION

Seasonal dynamics in accretion and catabolism of body fat and lean mass were linked strongly to nutritional state in three populations of bighorn sheep. The relationship between change in fat and nutritional state exemplifies the fine-tuned regulation of nutritional reserves in line with the hypothesis of risk-sensitive allocation (Monteith et al., 2013). During winter, fat regulation relative to nutritional state was largely similar across all three populations; however, nutritional dynamics among the populations diverged over summer. Although fat accretion over summer remained strongly state-dependent, one population (Whiskey Mountain) gained less fat over the summer. In contrast to the other two populations, sheep in the Whiskey Mountain population that recruited offspring lost fat, indicating potential nutritional deficiencies in summer range. As expected, fat was consistently the labile source of energy that varied by population and reproductive status, whereas lean mass reserves were consistently conserved but were catabolized when fat reserves were lowest. Fine-tuned regulation of nutritional

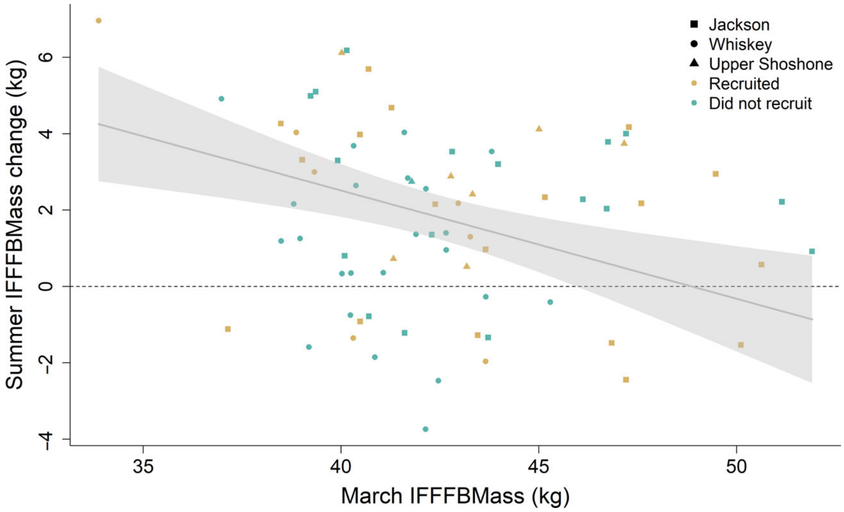

FIGURE 4 Relationship between preseason (March) ingesta-free, fat-free body mass (IFFFBMass) and change in IFFFBMass over the summer in female bighorn sheep in northwest Wyoming between 2015 and 2019.

TABLE 5 Model outputs, including non-standardized beta estimates, from overwinter change ($N = 84$ seasonal transitions, 52 animals) in ingesta-free fat-free body mass (IFFFBMass; in kilograms) in bighorn sheep in northwest Wyoming between 2015 and 2019.

Parameter	Estimate	SE	df	95% CI
Intercept	14.12	2.97	65.80	7.81, 20.63
December IFFFBMass	−0.45	0.06	65.95	−0.59, −0.31
Pregnant	2.24	0.77	71.62	0.71, 3.69
December IFBFat	0.12	0.05	77.96	0.02, 0.22

Abbreviation: IFBFat, ingesta-free body fat.

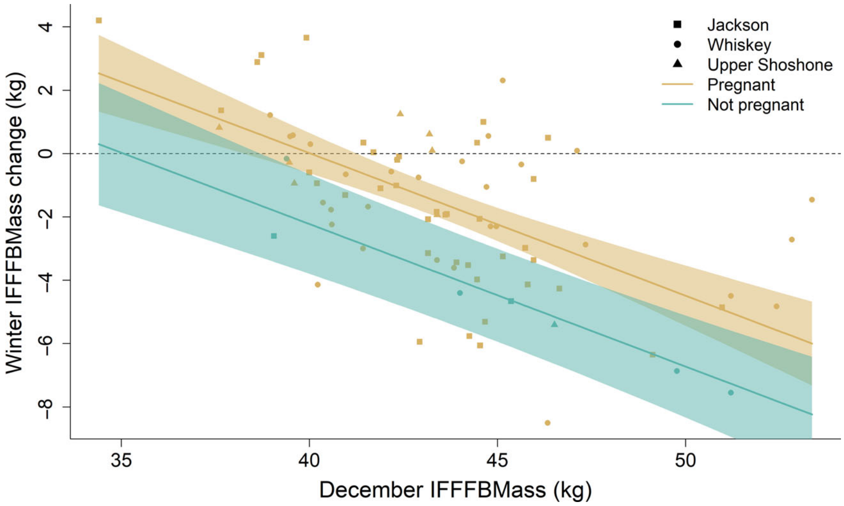

FIGURE 5 Relationship between preseason (December) ingesta-free, fat-free body mass (IFFFBMass) and change in ingesta-free, fat-free body mass (IFFFBMass) over the winter in female bighorn sheep in northwest Wyoming between 2015 and 2019.

reserves is necessary to finance survival and reproduction because of seasonal changes in resource availability. Ultimately, the allocation of resources to reproduction and survival influences population persistence, particularly for ungulates that inhabit environments with marked seasonal variation in resource quality and quantity

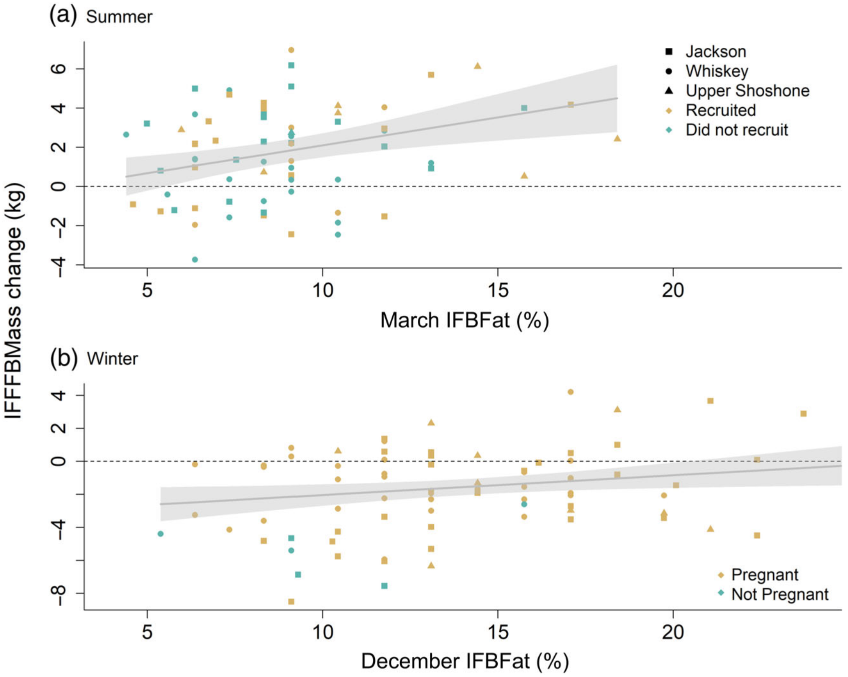

FIGURE 6 Relationship between preseason ingesta-free body fat (IFBFat) and change in ingesta-free, fat-free body mass (IFFFBMass) over the summer (a) and winter (b) in female bighorn sheep in northwest Wyoming between 2015 and 2019.

(Monteith et al., 2013; Parker et al., 2009). Alpine ungulates experience extreme variability in resource availability and, thus, must regulate somatic reserves conservatively to ensure survival and reproduction. In our three study populations, risk-sensitive resource allocation prevailed and likely holds implications for understanding the relative effects of the environment on demographic rates in mountain ungulates.

Fat and lean mass reserves both were regulated in a risk-sensitive manner relative to their availability at the beginning of a season in bighorn sheep. In contrast to protein reserves, fat reserves were sensitive to context (i.e., population) in both summer and winter and reproductive state in the summer, which supports that conservation of lean mass is prioritized over body fat. During both winter and summer, sheep that entered the season with higher fat levels gained relatively more lean mass over summer and lost relatively less lean mass over winter than animals that entered each respective season with lower fat levels. Protein conservation was largely prioritized over the conservation of fat, as was observed in mule deer (Monteith et al., 2013). Lean body mass is expensive to accumulate and maintain (Elia, 1992), is a less efficient energy source, and is critical for structural function and locomotion. Thus, changes in fat more readily demonstrate changes in nutritional condition through time compared with changes in protein.

Seasonal regulation of somatic reserves was dependent on nutritional state, but the magnitude of fat gain over summer was notably less in one population (Whiskey Mountain), which also had lower recruitment rates. Nevertheless, in winter, the magnitude of fat loss was more similar, and the populations had similar fat levels in March. Therefore, resources available to expend toward reproduction were limited by fat reserves and nutritional availability on summer range—both of which were likely inadequate in the Whiskey Mountain population and contributing to the observed low recruitment rates. Risk-sensitive allocation of resources ultimately may be underpinned by nutritional adequacy of available habitats. Although animals have flexibility to alter nutrient intakes by adjusting foraging behavior, nutrient balances ultimately are constrained by how well available nutritional resources support nutritional requirements of individuals and populations (Cook et al., 2013; Monteith et al., 2018). When nutrition is adequate, females may not be forced to sacrifice investment in reproduction for investment in survival (Cook et al., 2004); however, situations in which nutrient intake is entirely adequate may be rare in winter (Bishop et al., 2009; Hobbs et al., 1982) and summer–autumn (Cook et al., 2013; Denryter et al., 2022; Hurley et al., 2017; Post & Klein, 1999; Proffitt et al., 2016) for wild ungulates. Risk-sensitive allocation may be a critical adaptation to species living in seasonal environments where available resources cannot fully support reproduction and survival every year, necessitating reproductive pauses (e.g., Cameron, 1994) or other tactics to enhance lifetime reproductive success and fitness.

Myriad factors may influence the context dependence of nutritional dynamics in ungulate populations beyond what we could detect via remotely sensed environmental variables, including population density (McCullough, 1999; Oates et al., 2021), pathogen presence (Oliver-Guimerá et al., 2017), and behavior (Denryter et al., 2021). Though the Whiskey Mountain summer ranges host the lowest amounts of biomass relative to the other populations, biomass levels did not influence seasonal changes in fat. While we suspect forage quality and quantity heavily influence nutritional dynamics, remotely sensed indices of forage (i.e., biomass) were unable to explain population-level differences. Biomass did, however, explain some variation in seasonal change in IFFFBMass over summer. Snow depth did influence fat loss over winter, likely because costs of locomotion through snow are high (Parker et al., 1984) and increased snow depth makes forage more difficult to access. Remotely sensed environmental variables can be useful in detecting resource availability, but confounding factors, such as population density, can weaken their apparent influence (Oates et al., 2021). Environmental variables almost certainly contribute to population-level differences in nutrition, and though they may be difficult to measure at the scale and relevant to the animal, they are inherently integrated into measures of nutritional condition (Oates et al., 2021).

In summer when high-quality resources are available, large herbivores are faced with the trade-off between accumulating capital resources to finance their own survival through the coming winter and investing energy in the costs of raising offspring (Fauchald et al., 2004; Festa-Bianchet et al., 2019). Mountain sheep bear trade-offs in accumulation or maintenance of fat reserves for reproduction; sheep that successfully recruited offspring accumulated less body fat than those that did not. Successful reproduction came at a cost of about 6 ppt in body fat across all populations when lactating and non-lactating females were compared in autumn—a quantity of stored fat that provided 130.5 MJ of energy and could extend overwinter survival by 21 days (Stephenson et al., 2020). The differences in fat gain between non-lactating and lactating females over the summer provide evidence for an energetic cost of reproduction and nutritional trade-offs between survival and reproduction, which is fundamental to risk-sensitive reproductive allocation (Bårdsen et al., 2008).

According to the selfish mother hypothesis, females should invest more in their own survival and future reproduction than in current reproduction (Festa-Bianchet & Jorgenson, 1998). Mountain sheep mothers tend to transfer costs of reproduction to their offspring by prioritizing maintenance of their own mass over investment in mass gain of their offspring (Martin & Festa-Bianchet, 2010). Further, successful recruitment during the previous summer decreased reproductive effort during the subsequent summer (Martin & Festa-Bianchet, 2010). Reproductive expenditure in female elephant seals is primarily driven by their mass during parturition (Arnbom et al., 1997), indicating risk-sensitive resource allocation to reproduction. In all but one population of bighorn sheep in our study, females gained fat over summer while recruiting offspring. In one population, females that recruited offspring lost fat, implying that successive years of recruitment may not be sustainable when summer ranges fail to accommodate accretion of somatic reserves while reproducing. Thus, a lack of sufficient resources to support successive years of reproduction may limit recruitment rates and, consequently, population growth. Disentangling characteristics of landscapes and available habitats that influence population dynamics is critical for understanding how nutrition regulates populations of large herbivores.

There are potential nutritional limitations associated with living in alpine ranges. Ungulates inhabiting alpine environments can experience shorter periods of availability of high-quality forage than other temperate ungulates, especially during summers with early and rapid snowmelt (Pettorelli et al., 2007). Further, before giving birth, mountain sheep often migrate to high-elevation summer ranges or parturition sites before spring green-up begins (Festa-Bianchet et al., 1998). Because they move to high elevations before green-up has occurred, mountain sheep often experience the most energetically expensive period of lactation (Monteith et al., 2014; Parker et al., 2009) in areas with poor forage availability. In addition, bighorn sheep mothers are constrained to habitats close to escape terrain for predator avoidance and forego areas of better nutrient availability (Courtemanch et al., 2017). Selecting for escape terrain may limit their ability to maximize nutrient intake in summer. Thus, inhabiting and raising young in alpine environments may pose a nutritional limitation when compared with other ungulates that occupy more productive areas during summer. Reliance on somatic reserves to finance reproduction reinforces the importance of seasonal carryover of somatic reserves and risk-sensitive allocation of reserves.

All three populations in our study, possess pneumonia-associated pathogens and displayed risk-sensitive resource allocation; yet the popoulations have different population trajectories. Pneumonia has plagued mountain sheep populations and conservation efforts for decades (Cassirer et al., 2018), and a growing body of work connects pneumonia pathogens to population dynamics (Butler et al., 2018; Dekelaita et al., 2020). In the presence of pathogens, females may use somatic reserves to finance immune function, pathogen tolerance, and/or pathogen resistance; the added costs of mounting an immune response may incur trade-offs between competing nutrient demands in the presence of nutritional limitations (Gustafsson et al., 1994; Hasselquist & Nilsson, 2012; Plowright et al., 2008). Lactating females, for example, had higher parasite loads compared with non-lactating females in Soay and bighorn sheep (Leivesley et al., 2019; Pelletier et al., 2005), indicating an energetic trade-off associated with immune function and reproduction. Despite the persistent presence of pathogens in our focal populations, strong state-dependent relationships with resource allocation prevailed (Figures 2 and 3). Therefore, even in the presence of disease, risk sensitivity in nutritional dynamics is fundamental to the life history of mountain sheep with cascading implications on demography and potential immunological processes of coping with pneumonia pathogens or disease.

Understanding nutritional dynamics and resource allocation is fundamental to understanding how the environment shapes a species' life history. Importantly, patterns of somatic reserve losses and gains are not widely generalizable, as we observed differences between populations. Deviations from expected nutritional dynamics (e.g., the inability of mothers who recruit offspring to gain fat reserves over summer) may reflect the adequacy of the environment to support both survival and reproduction. The populations we studied have distinct trajectories, and strong risk-sensitive allocation of reserves across seasons indicates that nutrition likely plays an underpinning role in variation of demographic rates. We did not explicitly test the relationship between nutrition and demographic rates because of the potential confounding role of pneumonia in survival and recruitment. In the absence of pneumonia, nutrition does indeed underlie demographic rates (Dekelaita et al., 2020; Proffitt et al., 2021; Stephenson et al., 2020) and good nutrition is important to population productivity, even where disease or other limiting factors are present. While our results support the growing body of evidence of risk-sensitive allocation of reserves in long-lived mammals, we further the notion that risk-sensitive allocation is itself a component of life history that is a requisite for understanding of the contextual underpinnings of the environment and its consequences on fitness.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Smiley et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.qrfj6q5jh.

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