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Linking population performance to nutritional condition in an alpine ungulate

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Bighorn sheep (*Ovis canadensis*) can live in extremely harsh environments and subsist on submaintenance diets for much of the year. Under these conditions, energy stored as body fat serves as an essential reserve for supplementing dietary intake to meet metabolic demands of survival and reproduction. We developed equations to predict ingesta-free body fat in bighorn sheep using ultrasonography and condition scores in vivo and carcass measurements postmortem. We then used in vivo equations to investigate the relationships between body fat, pregnancy, overwinter survival, and population growth in free-ranging bighorn sheep in California and Nevada. Among 11 subpopulations that included alpine winter residents and migrants, mean ingesta-free body fat of lactating adult females during autumn ranged between 8.8% and 15.0%; mean body fat for nonlactating females ranged from 16.4% to 20.9%. In adult females, ingesta-free body fat > 7.7% during January (early in the second trimester) corresponded with a > 90% probability of pregnancy and ingesta-free body fat > 13.5% during autumn yielded a probability of overwinter survival > 90%. Mean ingesta-free body fat of lactating females in autumn was positively associated with finite rate of population increase (λ) over the subsequent year in bighorn sheep subpopulations that wintered in alpine landscapes. Bighorn sheep with ingesta-free body fat of 26% in autumn and living in alpine environments possess energy reserves sufficient to meet resting metabolism for 83 days on fat reserves alone. We demonstrated that nutritional condition can be a pervasive mechanism underlying demography in bighorn sheep and characterizes the nutritional value of their occupied ranges. Mountain sheep are capital survivors in addition to being capital breeders, and because they inhabit landscapes with extreme seasonal forage scarcity, they also can be fat reserve obligates. Quantifying nutritional condition is essential for understanding the quality of habitats, how it underpins demography, and the proximity of a population to a nutritional threshold.

Key words: adipose tissue, body composition, energetics, lambda, Sierra Nevada, vital rates

Landscapes differ in their capacity to meet the nutritional requirements of ungulates (Cook et al. 2013, 2018), which is determined in part, by the intrinsic capacity of the habitat to meet nutritional requirements of individuals (McLoughlin et al. 2007). Per capita availability of forage and its quality are determined by the interaction between intrinsic capacity of the habitat and animal density (McCullough 1999; Monteith et al. 2014). Fundamentally, the collective contributions of quantity and quality of forage and animal density define the ability of ranges to support population growth from the bottom up (Caughley 1970). Nevertheless, the role of the interaction of forage resources and animal density in affecting population growth is commonly underappreciated because of the masking effect of fat stores, which buffer animals against inadequate forage during seasons of forage scarcity or high energetic demands (Hempson et al. 2015). For example, as forage quality and quantity decline during lean seasons, ungulates with stored fat reserves may continue to balance their energy needs (Kohli et al. 2014). In addition, ruminants exhibit physiological adaptations to reduce metabolism and food intake for extended periods, which results in catabolism of somatic reserves to meet basal metabolic demands (Monteith et al. 2013). Subsequently, when food availability improves, they possess the ability to recover those reserves (Adamczewski et al. 1993; Chilliard et al. 1998). Thus, somatic reserves are recognized as an essential source of energy (Mautz 1978; Monteith et al. 2013) of which lipids are the primary energy currency to satisfy metabolic requirements when they are not met by current energy gains through forage (Robbins 1993).

The somatic reserves mobilized during periods of energetic needs ultimately are those that were maintained or acquired during the previous season, their impacts on individual nutritional status thus represent a lagged or carryover effect (Harrison et al. 2011) that if not measured directly can obscure relationships of seasonal contributions of forage resources to nutritional dynamics and ultimately, fitness (Monteith et al. 2013). Comprehensive and accurate efforts to model energetics of ungulates therefore require quantification of lipid reserves (Hobbs 1989; Miquelle et al. 1992; Moen et al. 1997). Traditional methods of assessing body fat of animals required that the individual be sacrificed, and subsequently, postmortem analyses were conducted to estimate percent body fat based on standard indices (Stephenson et al. 1998). Contemporary methods employ the use of body palpation and ultrasonography to estimate percent body fat of animals in vivo, thereby allowing the evaluation of carryover effects on behavior and fitness, and for the acquisition of longitudinal data. Equations to predict ingesta-free body fat via body palpation and ultrasonography have been developed for most North American cervids, including mule deer (*Odocoileus hemionus*), elk (*Cervus elephus*), caribou (*Rangifer tarandus*), and moose (*Alces alces*—Stephenson et al. 1998, 2002; Cook et al. 2001b, 2007, 2010; Parker et al. 2005). Development of standardized techniques to evaluate nutritional condition of live animals has led to marked advances in understanding the fundamental role of nutritional condition in behavioral and population ecology of large ungulates (Keech et al. 2000; Cook et al. 2001a, 2018; Bishop et al. 2009; Monteith et al. 2014).

Nutritional condition also is an essential metric for characterizing the complex mechanisms that underpin demography of ungulates, and ultimately reflects and influences the number of animals that a landscape can support. Body reserves represent the balance of energy intake and expenditure experienced by an animal in its environment (Parker et al. 1999, 2009), and provide an integrated measure of the nutritional status of an individual and the population (Monteith et al. 2013, 2018). Body reserves represent much about the environment in which an animal resides including forage resources, weather, and animal density, but they also relate to future potential for population growth in species that rely partially on stored capital to finance survival and reproduction (Franzmann 1985; Monteith et al. 2014). Vital rates that dictate population change are pregnancy, age of first reproduction, juvenile survival, and adult survival (Gaillard et al. 2000)—all of which are linked to nutrition to varying degrees depending upon the species and the environment. For example, body fat was linked strongly to probability of pregnancy in caribou (Gerhart et al. 1996), moose (Testa and Adams 1998), and to timing of breeding and thus parturition in elk (Cook et al. 2004; Johnson et al. 2019). Tollefson et al. (2010) observed that body fat predicted the probability of twinning in mule deer. Body mass can affect age of first reproduction in bighorn sheep (Jorgenson et al. 1993), mule deer (Monteith et al. 2014), and elk (Cook et al. 2004). Maternal body fat influenced survival and recruitment of young mule deer (Monteith et al. 2014) and survival of juvenile moose (Keech et al. 2000). The collective measure of body reserves of individuals in a population also is hypothesized to relate to population-level growth rates (Parker et al. 2009), and only Monteith et al. (2014) quantified this relationship between body fat and the finite rate of increase in a mule deer population.

Mountain sheep (*Ovis canadensis* and *O. dalli*) inhabit some of the most forage depauperate and climatically harsh landscapes in North America (Krausman and Valdez 1999). Dall's sheep occupy mountainous regions in the arctic (Rachlow and Bowyer 1998), Rocky Mountain bighorn sheep (*O. c. canadensis*) and Sierra Nevada bighorn sheep (*O. c. sierrae*) live in snowy alpine regions in excess of 3,300 m (Goodson and Stevens 1988; Schroeder et al. 2010; Spitz et al. 2018, 2020), and desert bighorn sheep (*O. c. nelsoni*) survive in the hottest and driest mountain ranges in North America (Epps et al. 2004; Abella et al. 2011). Nutritional reserves (body fat and protein stores) may be particularly important to mountain sheep because they occupy habitats that exhibit extreme seasonal variation in forage supply. Accordingly, bighorn sheep are considered capital breeders that rely on stored nutrients to support reproductive performance (Festa-Bianchet et al. 1998), yet body mass has typically been the only metric available to assess their nutritional status (Festa-Bianchet et al. 1997). Body mass is related to survival and reproductive success in mountain sheep (Festa-Bianchet et al. 1997, 1998); however, mass itself is relatively insensitive to fine-scale changes in nutrition, but is instead a product of long-term, and potentially, ontogenetic nutrition (Monteith et al. 2009, 2013).

Our goal was to develop predictive equations to estimate body fat of mountain sheep in vivo, and based on those estimates, begin to link nutritional condition to population performance. Following standardized approaches for other ungulates, we employed ultrasonography and body condition scores based on palpation to assess condition, which we then related to percent body fat as determined through analyses of body composition. We expected nutritional condition to be a valuable metric for assessing acquisition of nutrients on occupied ranges to support population growth in mountain sheep and given previous indications of mountain sheep as capital breeders, we predicted survival, reproduction, and ultimately, population growth to be affected by stored fat reserves. Thus, our approach was to examine the acquisition and storage of energy as the nutrient that can directly determine population performance through energy balance.

Materials and Methods

Body composition evaluation.—We acquired carcasses of the three subspecies (Wehausen and Ramey 2000; Wehausen et al. 2005; Buchalski et al. 2016) of bighorn sheep in North America (Fig. 1) to develop equations to predict body fat during 2002–2010. We used mortalities of adult females from captures for Sierra Nevada bighorn sheep ($n = 5$) in California, United States and desert bighorn sheep ($n = 4$) from the White Mountains and Peninsular Ranges of California. We obtained carcasses of Rocky Mountain bighorn sheep ($n = 15$) from captive animals in Fort Collins, Colorado, United States, and Pullman, Washington, United States.

Bighorn sheep mortalities were sampled incidental to capture efforts (capture mortalities) and captive research (euthanasia). Immediately before or following death, we positioned animals in sternal recumbency and measured rump fat thickness using a Sonosite Micromaxx portable ultrasound device (Fujifilm Sonosite, Inc., Bothell, Washington) with a 5-MHz linear-array transducer. We measured subcutaneous fat thickness (also termed MAXFAT in previous publications—Stephenson et al. 1998; Cook et al. 2007, 2010) at its thickest point cranial to the cranial process of the tuber ischium (pin bone) and 3 cm from the spine; in bighorn sheep the maximum is toward the cranial extent of the rump patch and therefore more cranial than in the cervids (Supplementary Data SD1). We measured maximum thickness of fat with electronic calipers to the nearest 0.01 cm. We also used a body-condition scoring (BCS) system (Supplementary Data SD2; modified from Cook et al. 2007) that involved palpation of the caudal vertebrae (Supplementary Data SD3) and assigning scores between 0.5 and 6. As fat and muscle are catabolized along the caudal vertebrae, the vertebral processes become more prominent and are used to score

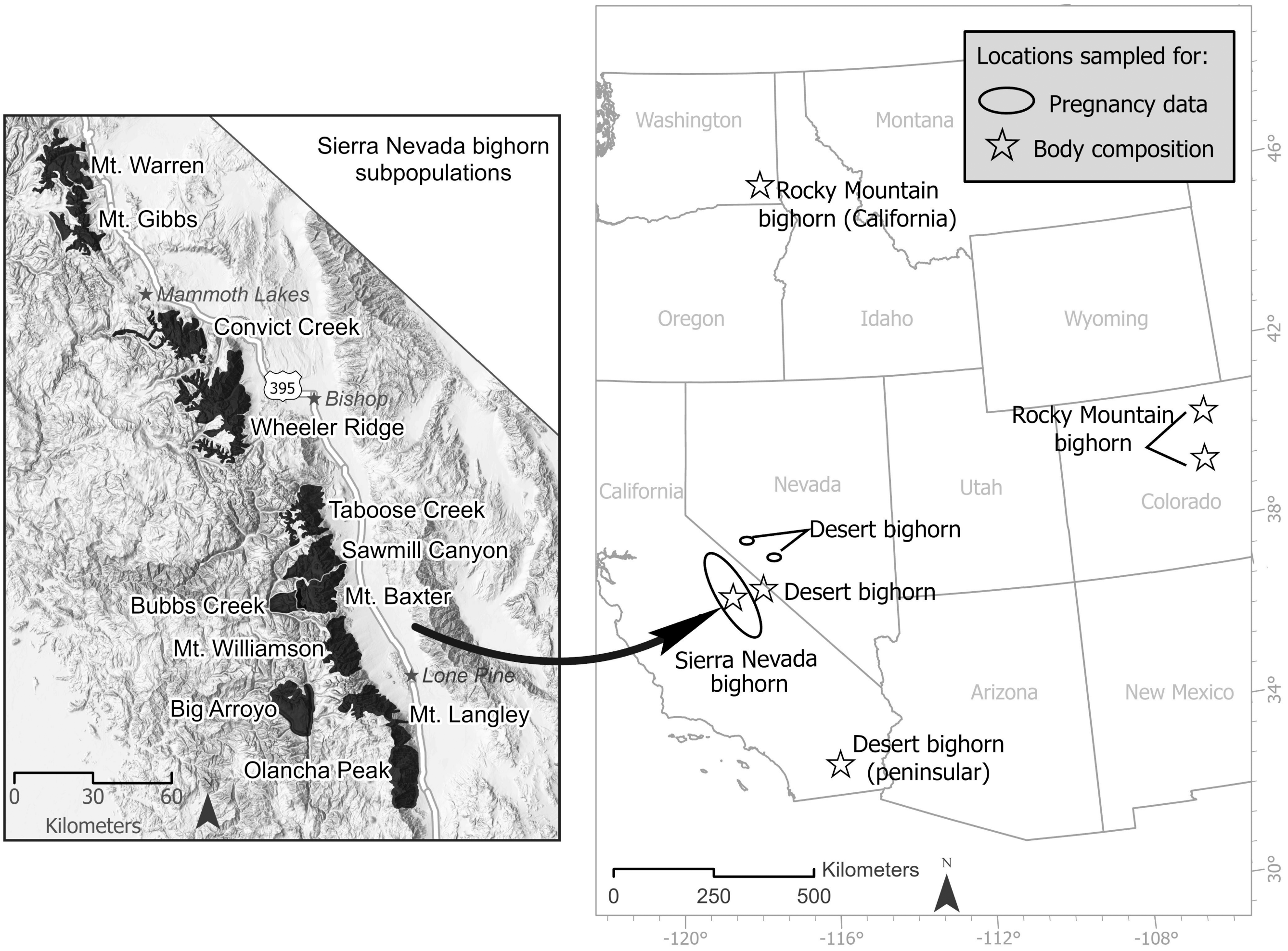

Fig. 1.—Locations of bighorn sheep populations from three subspecies that were used in developing body composition equations (stars), two subspecies used in predicting the probability of pregnancy (ellipses), and Sierra Nevada bighorn sheep monitored to assess survival, growth rate, and relative habitat quality (inset) in relation to ingesta-free body fat of adult female bighorn sheep during 2003–2019 in California, Nevada, Colorado, and Washington, United States.

condition. For application in live animals, we used MAXFAT for animals that had fat measurable by ultrasound, and we used a BCS to predict body fat for individuals lacking measurable fat. Hence, we predicted body fat across the complete physiological range.

We determined body mass of whole animals using an electronic platform scale, and we processed the remains for body composition as described by Stephenson et al. (1998). Briefly, the skinned carcass and viscera (minus ingesta and uterine contents) were frozen and sliced with a commercial band saw at 25-mm intervals; the homogenate at the base of the blade was collected as a subsample for analysis (Huot and Picard 1988). Shaved hide samples (~230 cm^2 each) including the shoulder, loin, and rump were freeze-dried and ground to create a homogenate. We weighed each component part to ascertain the relative proportions of total body mass. We determined fat content of the frozen carcass, viscera, and hide subsamples by ether extraction and expressed fat as a percentage. We calculated percent ingesta-free body fat (IFBFat) by summing the products of the percentage fat of each component and its respective mass, dividing by ingesta-free body mass, and multiplied by 100. We also determined kidney fat mass and calculated the kidney fat index as described by Anderson et al. (1990) and Riney (1955), respectively. We quantified femur marrow fat using ether extraction and expressed it as a percentage (Association of Official Analytical Chemists 1975). Lastly, we visually estimated amount of fat at six indicator sites according to Kistner et al. (1980); however, we did not assign points to body musculature, so our score (Kistner Score) varied between 0 and 90.

Demography study areas.—We studied the survival, population rate of change, and nutritional condition of free-ranging populations of Sierra Nevada bighorn sheep that are endemic to and reside in the southern and central Sierra Nevada (U.S. Fish and Wildlife Service 2007). The Sierra Nevada is a mountain range in eastern California that is 650 km long and 75–125 km wide (Hill 2006); it is the largest single mountain range and has the highest elevation (4,421 m; Mt. Whitney) in the contiguous United States. The western slope is gentle and mesic in contrast to the very steep escarpment of the eastern slope that is much more xeric because of a strong rain shadow (Hill 2006). Annual precipitation was highly variable and occurred mainly during October–May in the form of snow with snowbanks often persisting throughout the summer (California Department of Water Resources 2019). The Sierra Nevada has the potential to receive extreme snowfall (Powell 2000). Snowfall was common at elevations above 1,800 m and the higher elevations received 500–1,500 cm of snow annually (California Department of Water Resources 2019). Winds associated with storms exceeded 288 km/h at times (Bair et al. 2015) and consistently scoured snow off alpine ridges. During 2001–2019, winter severity was measured by average annual snow depth during December–April from multiple snow stations (California Department of Water Resources 2019) and varied between 63.5 and 381 cm; mild and severe winters were < 75% and > 125% of average, respectively.

Sierra Nevada bighorn sheep spend summers in the alpine (elevations > 3,300 m) and winters in the alpine or at lower elevations (1,525–2,500 m); they occupy elevations ranging from 1,525 to > 4,000 m. Low elevations (1,525–2,500 m) were characterized by sagebrush-steppe (*Artemesia tridentata*) vegetation; mid-elevations (2,500–3,300 m) by piñon–juniper (*Pinus monophyla–Juniperus grandis*) woodland, subalpine meadows, and forest; and high elevations (> 3,300 m) by sparse alpine vegetation interspersed with meadows. Average daily low and high temperatures in the alpine were −2°C to 15°C during summer and −14°C to −1°C during winter (California Department of Water Resources 2019). On winter range at low elevation, average daily low and high temperatures during winter were −2°C to 7°C (California Department of Water Resources 2019). Alpine environments can receive snowfall during any month of the year. In contrast, winter range at the lowest elevations began to green-up as early as January during mild winters but could receive snow during November–March. Sierra bighorn sheep were partially migratory with some individuals in almost all populations exhibiting either of two strategies: residents that spent winter and summer in the alpine and migrants that migrated to low elevations during winter (Spitz et al. 2018). Only three native subpopulations of Sierra bighorn sheep remained as of the 1970s and those herds were used to reestablish bighorn sheep throughout much of the range during 1979–1988. Four additional subpopulations were reestablished during 2013–2015 bringing the total number of subpopulations to 14. During 2001–2019, the population of Sierra bighorn sheep increased from just over 100 individuals to 600; sizes of individual subpopulations varied between 9 and 138 animals during the period that we report and densities ranged from 0.1 to 1.0/km^2. The highest sources of adult mortality of Sierra bighorn sheep were winter starvation, avalanche, predation by mountain lions (*Puma concolor*), and unknown, and occurred almost entirely during January–April (Conner et al. 2018).

We examined the relationship between body fat and probability of pregnancy using a combined sample of Sierra Nevada bighorn sheep and Great Basin desert bighorn sheep on Lone Mountain and the Garfield Hills, Nevada. The population on Lone Mountain is endemic, occurs at a similar latitude, and is located adjacent to the Sierra Nevada. The nearby Garfield Hills population was recently established via translocation from populations in Lone Mountain and the adjacent Gabbs Valley, Nevada, during January 2016; no female bighorn sheep were known to occur in this area before translocation events. Vegetation on Lone Mountain is characterized primarily by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), Stansbury's cliffrose (*Purshia stansburiana*), spiny hopsage (*Grayia spinosa*), shadscale saltbush (*Atriplex confertifolia*), and piñon–juniper woodlands. Lone Mountain ranges from ~1,450 to 2,780 m in elevation with abundant precipitous terrain. Average daily low and high temperatures on Lone Mountain were 11°C to 33°C during summer and −7°C to 12°C during winter (National Oceanic and Atmospheric Administration 2019). The Garfield Hills are characterized by Wyoming sagebrush communities, and elevations range from

~1,330 to 2,460 m with minimal precipitous terrain. In the Garfield Hills, average daily low and high temperatures during summer were 14°C to 35°C and −5°C to 14°C during winter months (National Oceanic and Atmospheric Administration 2019). In both mountain ranges, the predominant form of precipitation is snowfall during winter, with Lone Mountain receiving ~53 cm of precipitation and the Garfield Hills receiving ~33 cm annually.

Field sampling of live animals.—We captured bighorn sheep using a handheld net gun fired from a helicopter (Krausman et al. 1985). We estimated age by tooth replacement and wear and by counting horn annuli (Krausman and Valdez 1999). We determined body mass using a spring scale (± 1 kg). We estimated body fat using ultrasonography and a body condition score as developed herein. We determined pregnancy status of female bighorn sheep during 30 December to 2 February using ultrasonography; we positioned a 3-MHz convex transducer to the hairless region of the abdomen in proximity to the udder to facilitate transabdominal scanning (Stephenson et al. 1998). We classified females as pregnant if a fetus or cotyledons (placenta) were observed. If females were not identified as pregnant during the period of early gestation (late December and early January) using ultrasonography, we also assayed serum for the presence of pregnancy-specific protein B to confirm absence of pregnancy (Sasser and Ruder 1987; Huang et al. 2000). Our primary captures to quantify autumn nutritional condition occurred during October–December and we also assessed lactation status based on the presence of an udder with milk that could be expressed. We also recaptured a limited number of adult females in March following their original capture in October. We deployed VHF and GPS collars on bighorn sheep to determine survival; we recorded whether individuals lived or died during the first 6 months postcapture (we excluded mortalities potentially associated with capture from the analysis) to assess overwinter survival. To estimate population sizes and recruitment, we conducted repeated annual ground counts using experienced observers equipped with binoculars and spotting scopes, who systematically hiked and scanned each herd area. Upon locating bighorn sheep, observers classified each animal by sex and stage class (lambs, yearlings, and adults—Johnson et al. 2010b). All methods of animal capture and handling were in accordance with University of Montana Institutional Animal Care and Use Committee (IACUC) protocols 024-07MHWB-071807 and 012-16MMMCWRU-022916, federal Fish and Wildlife Service permit numbers TE050122-4, -5, and -6, University of Nevada, Reno IACUC Protocol 00651, and procedures approved by the American Society of Mammalogists (Sikes et al. 2016).

Energetics and statistical analysis.—We used linear regression to develop predictive equations for IFBFat based on BCS for animals without measurable fat and maximum thickness of rump fat for animals with measurable subcutaneous fat, and for developing predictive equations of IFBFat from kidney fat index, kidney fat mass, and Kistner Score. Before analysis, we log-transformed kidney fat mass and kidney index because it was curvilinear. We also used a negative reciprocal transformation of IFBFat when using linear regression with femur marrow fat (Cook et al. 2007).

We estimated the potential for fat reserves to meet metabolic demands over winter when movements are restricted by snow and limited forage is available. Our intent was not to develop a complex energetics model but rather to use a simple mathematical approach to illustrate a practical application of the energy reserves associated with stored fat. We calculated the energy content of fat reserves as the product of the quantity of fat reserves (kg) in adult female bighorn sheep and energy content of fat (39.5 kJ/g—Robbins 1993). We determined energy balance associated with fat reserves as the quotient of the energy content of fat reserves and the energy costs of lying (resting [nonfasting] metabolic rate—Chappel and Hudson 1979). We used a resting metabolic rate of 291 kJ/kg$^{0.75}$/day (69.54 kcal/kg$^{0.75}$/day—Chappel and Hudson 1979) and calculated the number of days that stored energy would enable an animal to survive if they relied solely on energy provided by catabolizing fat. We calculated change in body fat for individuals who were captured during autumn and the following spring to assess changes in energy reserves associated with winter.

We examined the shape of the influence of nutritional condition on individual vital rates. Specifically, we used logistic regression to quantify the relationship between probability of pregnancy and percent IFBFat as measured during 30 December to 2 February; pregnancies could reliably be detected after about 20 days postconception. We also used logistic regression to evaluate the relationship between percent IFBFat as measured during October–December (91% of captures occurred during 12–30 October) and survival up to 6 months postcapture (overwinter). We also used linear regression to evaluate the number of days that an animal survived relative to its level of body fat in animals that survived less than 6 months postcapture. We tested for a relationship between age and autumn IFBFat in adult females to evaluate the role of age on fat gain.

To evaluate the response of entire subpopulations to the collective measure of nutritional condition of individuals in a subpopulation, we estimated the annual finite rate of population increase (λ) from vital rates using a stochastic, discrete time, stage-structured demographic matrix model based on four stages: lamb, yearling, adult, and senescent (Johnson et al. 2010a; Cahn et al. 2011); we calculated λ as the dominant (largest) eigenvalue of the matrix (Morris and Doak 2002). We used count data to estimate fecundity (Cahn et al. 2011) and used a Kaplan–Meier known-fate analysis to parameterize adult and yearling survival (White and Garrott 1990). To ensure consistency in the analysis, we only included subpopulations in years with fecundity data collected postbirth pulse (Morris and Doak 2002) and with associated IFBFat from the previous autumn. IFBFat was measured in autumn and λ was calculated using vital rates for the following year. We regressed λ against IFBFat for lactating and nonlactating adult females separately. Because we expected considerable difference in IFBFat between lactating and nonlactating females, we tested for differences among subpopulations using ANOVA separately between these two reproductive categories. Following a significant ANOVA, we used Fisher's Least Significant Difference test to conduct multiple comparisons.

RESULTS

IFBFat exhibited strong linear relationships with in vivo and postmortem indices in bighorn sheep (Table 1). Estimation of IFBFat in vivo across the full range was best accommodated using two separate equations. When rump fat was measurable (7.75% IFBFat), we used ultrasound to predict body fat IFBFat ($R^2 = 0.91$; Supplementary Data SD4); otherwise, we used our body condition score ($R^2 = 0.77$; Supplementary Data SD5) to predict body fat. Of the postmortem indices of nutritional condition that we evaluated, the Kistner Score explained the most variation in IFBFat ($R^2 = 0.87$). Kidney fat exhibited a linear relationship with IFBFat when log-transformed; the relationship was curvilinear without transformation and failed to predict variation in IFBFAT at high levels of kidney fat (Table 1). Femur marrow fat remained high (> 70%) above 6% body fat but by 3% body fat, marrow fat declined below 30%. In contrast to other condition indices, live body mass was a relatively poor predictor of IFBFat (Table 1).

We evaluated the relationship between nutritional condition and demographic parameters from 360 individual captures of 267 female bighorn sheep distributed among 12 of 14 subpopulations in the Sierra Nevada during 2002–2018. Twelve bighorn sheep were captured during consecutive seasons and provided estimates of changes in body fat between seasons. For analyses requiring population growth rates, we used data from six subpopulations that possessed corresponding nutritional data.

Ingesta-free body fat in the Sierra Nevada ranged from 0.5% to 33% for adult (> 1 year old) females, whereas body mass ranged from 40 to 72 kg. Autumn IFBFat of adult females was not related to age ($F = 0.29$, $n = 218$, $P = 0.591$). Females with a high level of fat reserves (~26%) had 533.8 MJ of stored energy from fat to meet metabolic demands of winter (Table 2). Based on resting metabolic rate, a female with a high level of body fat would carry energy reserves sufficient to survive for 83 days on body fat alone. In autumn in the Sierra Nevada, body fat differed ($t = 11.7$, *d.f.* = 221, $P < 0.001$) between lactating (mean = 11.9%, $SE = 0.37$) and nonlactating females (mean = 18.5%, $SE = 0.42$). Females that lactated were an average of 6.6 percentage points leaner than females that did not lactate. Mean estimated fat reserves of adult lactating and nonlactating females during October provided 229.3 and 359.8 MJ of energy, respectively, to support the energetic requirements of bighorn sheep over winter. Consequently, nonlactating females entered winter with 130.5 MJ (56%) more stored energy on average than lactating females. Mean body mass differed ($t = 2.05$, *d.f.* = 223, $P = 0.04$) by 1.5 kg between lactating (mean = 55.9 kg, $SE = 0.51$) and nonlactating females (mean = 57.4 kg, $SE = 0.53$).

Among pregnant adult females that were recaptured in the spring (late March and early April) across a range of winter severities following autumn (late October) captures, fat loss ranged from 0 to 12.5 percentage points. Mean loss was 5.4 ($SE = 1.4$) percentage points of body fat. Females who lost the mean amount of fat catabolized 85.8 MJ of energy from body fat and females who lost the most fat catabolized 240.2 MJ.

Probability of pregnancy was related to IFBFat as measured in early gestation (late December to late January) in adult females ($a = -1.062$, $b = 0.432$, $P = 0.004$, $n = 108$; Fig. 2). In contrast, body mass was not related to probability of pregnancy ($P = 0.098$). Body fat in autumn predicted survival to 6 months postcapture ($a = -0.570$, $b = 0.205$, $n = 203$, $P < 0.001$; Fig. 3), and body mass was also related to survival of individuals ($a = -3.026$, $b = 0.091$, $n = 199$, $P = 0.023$). When considering only adult females that died within 6 months postcapture, body fat was related to the number of days that an animal survived ($R^2 = 0.253$, $n = 29$, $P = 0.005$).

Finite rate of population increase ranged from 0.60 to 1.22, whereas mean IFBFat of lactating females in autumn spanned

Table 1.—Linear regression equations for predicting ingesta-free body fat (IFBFat % and kg) from measurements of bighorn sheep ($n = 24$) in the western United States, 2002–2010. All equations are significant at $P < 0.001$ except body mass where $P = 0.046$.

Y	X	Equation	R^2	SE	Live[a]
IFBFat (%)	Rump fat thickness (cm)	$Y = 13.28X + 7.78$	0.91	1.08	Live
	Body condition score	$Y = 3.92X - 1.48$	0.77	0.51	Live
	Ln kidney fat index	$Y = 4.87X - 7.42$	0.75	0.63	Dead
	Ln kidney fat mass (g)	$Y = 4.74X - 5.08$	0.75	0.62	Dead
	Femur fat (%)[b]	$-1/Y = 0.01X - 1.082$	0.65	0.22	Dead
	Kistner score	$Y = 0.2X + 0.33$	0.87	0.02	Dead
	Body mass (kg)	$Y = 0.23X - 1.54$	0.26	0.10	Either
IFBFat (kg)	Rump fat thickness (cm)	$Y = 6.85X + 3.28$	0.80	0.91	Live
	Body condition score	$Y = 2.11X - 1.46$	0.73	0.30	Live
	Ln kidney fat index	$Y = 2.77X - 5.32$	0.72	0.38	Dead
	Ln kidney fat mass	$Y = 2.76X - 4.2$	0.75	0.36	Dead
	Femur fat (%)	$-1/Y = 0.04X - 3.33$	0.65	0.70	Dead
	Kistner score	$Y = 0.11X - 0.42$	0.78	0.01	Dead
	Body mass (kg)	$Y = 0.16X - 3.95$	0.44	0.05	Either
	IFBFAT (%)	$Y = 0.55X - 0.80$	0.93	0.03	Either

[a] Live, dead, and either refer to whether the methods were developed for use in vivo or postmortem.

[b] Equation for femur marrow only is appropriate for body fat < 6%. Above that level of body fat, femur marrow is not predictive because marrow fat is at maximum levels.

Table 2.—Ingesta-free body fat (% IFBFat) and energy (MJ) available to be metabolized from fat reserves in adult female Sierra Nevada bighorn sheep when sampled during autumn 2002–2018. Hypothetical number of days survived where energy demands are met from fat catabolism are calculated as the quotient of the energy content of fat reserves and the energy costs of lying (resting [nonfasting]) metabolic rate.

Category of fat reserves during autumn sampling	% IFBFat	MJ from fat	Days surviving on fat alone
High	26	533.8	83
Nonlactating average	18	359.8	56
Lactating average	12	229.3	35
Low	8	142.3	22

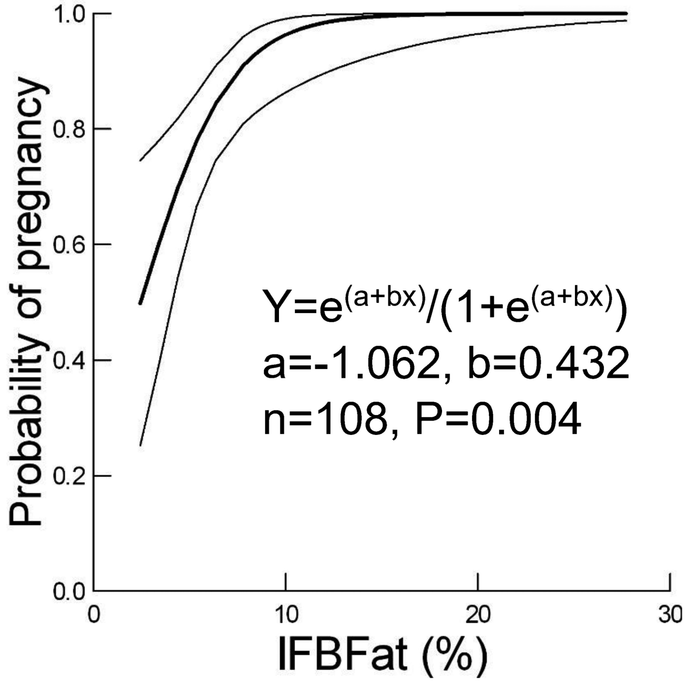

Fig. 2.—Logistic regression (± 95% *CI*) for predicting probability of pregnancy from ingesta-free body fat (IFBFat) in adult female bighorn sheep measured in autumn during 2003–2018 in the Sierra Nevada, California, and Lone Mountain and Garfield Hills, Nevada, United States.

8.32–19.80% during the same years. IFBFat of lactating females in autumn was positively related to population growth rate ($R^2 = 0.44$, $n = 14$, $P = 0.01$; Fig. 4) in subpopulations that wintered in the alpine. Population growth was stable ($\lambda = 1$) at an average of 11.5% IFBFat for lactating females. We did not detect a relationship between body fat of nonlactating females and population growth rate ($P = 0.48$).

Mean IFBFat of lactating adult females in autumn varied among 11 subpopulations in the Sierra Nevada ($F_{10,122} = 2.55$, $P = 0.008$; Fig. 5) and ranged from 8.8% to 15.0%. IFBFat of nonlactating adult females in autumn varied less among subpopulations ($F_{7,82} = 1.86$, $P = 0.086$) and averaged from 16.4% to 20.9%.

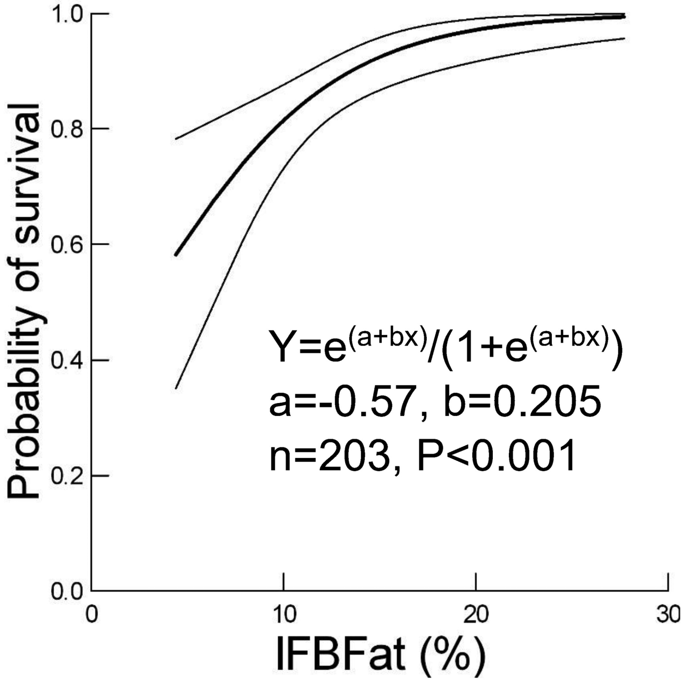

Fig. 3.—Logistic regression (± 95% *CI*) for predicting probability of survival from ingesta-free body fat (IFBFat) in adult female bighorn sheep measured in autumn during 2003–2019 in the Sierra Nevada, California, United States.

Discussion

Adipose tissue provides the primary macronutrient used by many animals to finance reproduction and survival in seasonal environments, because it is an efficient and labile source of energy. Energy stored as fat may be accumulated during periods of positive energy balance and subsequently, catabolized during periods of negative energy balance when deficiencies in forage supply fail to meet metabolic requirements. Thus, body reserves can dictate the likelihood of successful pregnancy, young rearing, and the length of time that ungulates will survive during periods of food shortage as somatic reserves become the primary source of energy (Torbit et al. 1985). To further our ability to understand the influence of this labile source of energy on the ecology of a long-lived, iteroparous mammal, we validated in vivo methods to estimate IFBFat. By using thickness of subcutaneous rump fat measured with ultrasonography and a body condition score via manual palpation, we predicted IFBFat of female bighorn sheep across what we suspect is the physiological range for the species (0.55–33% IFBFat). The animal at 0.55% IFBFat died of malnutrition, and the individual at 33% IFBFat experienced an optimal nutritional state by living at low density in alpine summer range without the costs of lactation. Therefore, we expect our equations to be robust to estimating body fat in mountain sheep across a wide range of conditions. Interestingly, our models also demonstrated the same in vivo procedures used for ungulates can be applied to a bovid—all other previous body condition validations for ungulates have

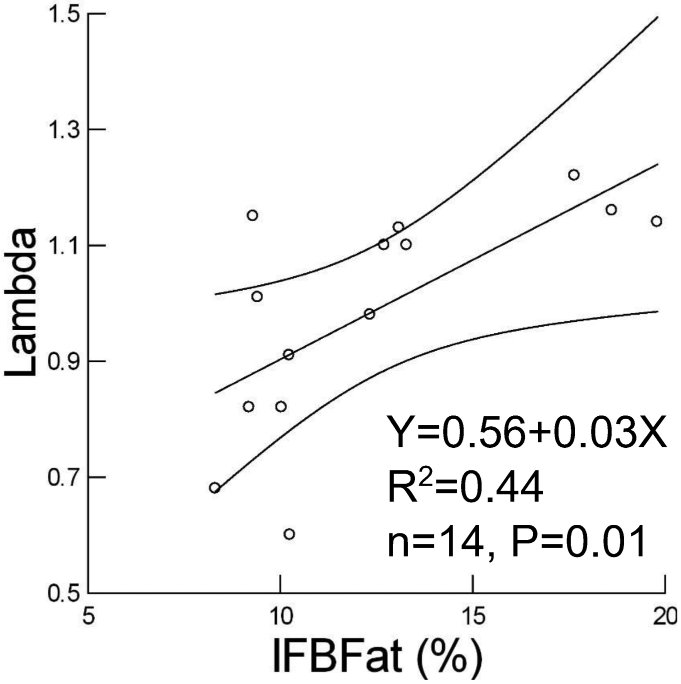

Fig. 4.—Linear regression (± 95% *CI*) for predicting finite rate of population increase for bighorn sheep from autumn ingesta-free body fat (IFBFat) of lactating adult females during 2007–2018 in the Sierra Nevada, California, United States.

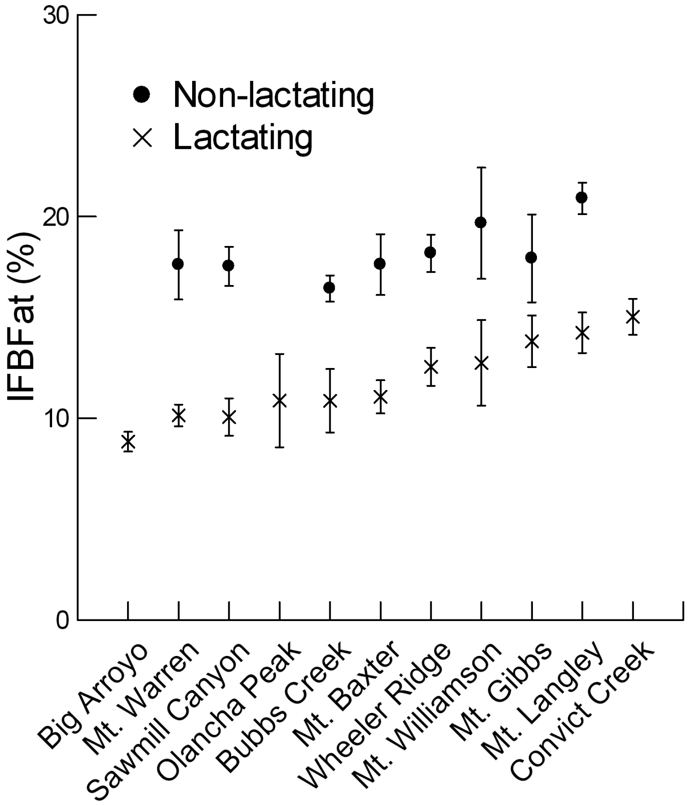

Fig. 5.—Percent ingesta-free body fat (IFBFat ± *SE*) of lactating (*n* = 133) and nonlactating (*n* = 94) adult (≥ 2 years old) female Sierra Nevada bighorn sheep measured during autumn across 11 subpopulations, 2002–2018, Sierra Nevada, California, United States. Data for the Big Arroyo subpopulation only represent individuals that summered at lower elevations in canyons well below alpine.

been developed for cervids (Stephenson et al. 1998, 2002; Cook et al. 2010). We observed that subcutaneous rump fat was depleted at a higher level of body fat in bighorn sheep than in the cervids, as indicated by the *y*-intercept in the equation. In addition, these models for estimating IFBFat in bighorn sheep were highly accurate and predictive, and we demonstrated that in vivo estimates of IFBFat were related to probability of pregnancy, overwinter survival, and lambda, across subpopulations of bighorn sheep.

Bighorn sheep are considered capital breeders who rely on somatic reserves to meet the energetic demands of reproduction (Festa-Bianchet et al. 1998). Nevertheless, previous work has focused on relationships with body mass as an indicator of condition; however, body mass itself is a poor indicator of body fat (Table 1; Gerhart et al. 1996; Cook et al. 2001, 2007; Stephenson et al. 2002; Monteith et al. 2013, 2018). Body mass includes, and is sensitive to, ingesta, water consumption, products of conception, hair, bones, antlers/horns, etc., making its predictive value for nutritional condition, or in relation to performance, less accurate than measures of lean muscle or fat. Indeed, a large animal may have few fat reserves, whereas a small animal may have abundant fat reserves, but body mass as a nutritional indicator would imply an opposite relationship. Body fat solely represents a labile source of energy and is a product of energy balance (Franzmann 1985; Stephenson et al. 1998).

We demonstrated that fat reserves characterize resource limitation and represent dietary intake needed to meet the necessary energetic costs associated with the phases of reproduction in bighorn sheep. During the second trimester, IFBFat > 7.7% corresponded with a probability of pregnancy > 90%, whereas IFBFat < 4% corresponded with a probability of pregnancy < 50% providing an indication that a relatively low level of nutrition is required by bighorn sheep to ovulate and conceive. During the years that we sampled pregnancy in January in our study areas, November and December snow did not substantially limit forage availability and IFBFat was likely comparable in November at conception. Gestation requires energy and protein (Robbins 1993); body mass (and its association with lean body tissue) and body fat therefore both are related to the nutritional requirements of successful reproduction (Monteith et al. 2013). Nevertheless, the energetic costs of gestation are < 10% of basal metabolic rate (BMR) during the first and second trimester of gestation but increase to 44% BMR just prior to parturition (Robbins 1993) when foraging conditions are more likely to improve in the spring. Thereafter, energetic demands associated with lactation far exceed those associated with basal metabolism or gestation (Moen 1973; Cook 2002), and accordingly, can come at the cost of fat accretion or even catabolism over summer (Cook et al. 2004, 2013; Monteith et al. 2013, 2014). At the population level, Sierra bighorn sheep tended to have the greatest fat reserves in autumn; however, females that successfully reared young over summer were on average 6.1 percentage points of IFBFat leaner than those that were not lactating. Therefore, successful reproduction came at the cost of accumulating 130.5 MJ of stored energy in fat, or > 20 days of resting metabolic demands to allocate toward survival over winter.

Finite rate of population increase (λ) is most sensitive to changes in adult survival (Gaillard et al. 2000). Yet in most populations of abundant large herbivores, recruitment of juveniles typically drives population change (Gaillard et al. 1998), because adult survival is typically high and invariable, whereas juvenile survival varies markedly. Nevertheless, in small, isolated populations, such as those of many bighorn sheep populations, adult survival can vary more than expected and thereby underpin population change (Johnson et al. 2010a). Although survival rate of adult females in the Sierra Nevada was high and typically exceeded 90% in most years (Conner et al. 2018), we did experience severe winters and stochastic predation events that reduced survival. Females with greater fat reserves had a higher probability of overwinter survival (Fig. 3). Adult females sampled in both autumn and the following spring catabolized a mean of 85.8 MJ during conditions of mild winter severity; consequently, they appeared to have a considerable buffer to ensure their survival and to allocate toward energetic costs of late gestation and early lactation. However, recaptured females that experienced severe winter conditions in alpine landscapes catabolized 240.2 MJ; this exceeds the average fat reserves of lactating females that we observed in the Sierra Nevada.

The contribution of nutrition during various seasons should be viewed as an integrated equation, whereby energy demands of the individual are met through a combination of energy intake and catabolism of reserves; this relationship is particularly important for capital breeders and capital survivors. Females that entered the season of senescent forage (e.g., winter in alpine climates) with a high level of body fat of 26% had 553.8 MJ of stored energy and thus carried energy reserves sufficient to meet the requirements of resting metabolism for an estimated 83 days on body fat catabolism. Accordingly, body fat in autumn was related strongly to overwinter survival (Fig. 3), and explained 25% of the variation in time an animal survived through winter for those that died. Contributions from the summer range functionally carry over and are available during winter through body fat. Although individuals can metabolize muscle as an energy store, energetic yield is less than half that of body fat, and catabolism of body fat is prioritized over that of protein reserves (Parker et al. 1993; Monteith et al. 2013). Assessing the role of muscle catabolism for energy also is complicated because pregnant females may mobilize protein to meet the nitrogen demands of a rapidly growing fetus in late gestation (Adamczewski et al. 1997). Moreover, in alpine-dwelling ungulates, resting is an important behavior to minimize energy expenditure and conserves body reserves (Kohli et al. 2014), which also can be facilitated by a reduction in metabolically active tissue (Burrin et al. 1990). Bighorn sheep in particular may reduce metabolic rate as an adaptation to cold winter, and further conserve limited energy reserves (Chappel and Hudson 1978, 1979). Breeds of domestic sheep that store abundant fat may fast for as long as 70 days without detrimental effect and recover condition following refeeding (Chilliard et al. 1998). In harsh winter environments with limited forage availability, fat reserves accumulated during the previous season provide a labile energy reserve to supplement nutritional demands during winter. Desforges et al. (2010) modeled that the "average" muskoxen in northern Canada can survive 44 days on its own reserves during winter; we estimated 56 and 33 days for the average nonlactating and lactating bighorn females, respectively. Alternatively, landscapes that may be unable to provide adequate nutrients during one season may be adequate if they are accompanied by migration to a range that yields sufficient fat gain or maintenance during other seasons (Schmelzer and Otto 2003). We hypothesize that bighorn sheep that live in landscapes with extreme scarcity in seasonal forage are obliged to store and mobilize fat reserves—relationships that we can now explore given our efforts to validate in vivo techniques to estimate IFBFat in bighorn sheep.

The ultimate measure of the response of a population to its environment is its finite rate of population increase (λ), which can be influenced by a suite of top-down and bottom-up factors (Hunter and Price 1992; Power 1992; Pierce et al. 2012; Bowyer et al. 2014), and in bighorn sheep the presence of respiratory disease (Cassirer and Sinclair 2007). Nevertheless, capacity for population increase ultimately is contingent upon sufficient nutritional resources—the basic driver of populations. If resources are inadequate or density-dependent feedbacks reduce energetic capabilities of individuals, populations inevitably will fail to grow regardless of other top-down influences. Understanding potential capacity of ranges to sustain and support growing populations therefore depends not on top-down influences, but understanding bottom-up inputs and herbivore density relative to food supply. Decades ago, Caughley (1970) suggested that body fat probably was the most useful correlate with rate of increase; thereafter, Monteith et al. (2014) linked body fat with λ in a single population of mule deer living in a highly seasonal and variable environment. Likewise, we observed a similar relationship between λ and IFBFat across multiple populations of bighorn sheep using a diversity of landscapes. Mean IFBFat of adult females that were lactating in autumn was related positively to λ over the following year, with 1 percentage point increase in IFBFat being associated with a predicted increase in population growth rate of 3% (Fig. 4). Our analyses and that of Monteith et al. (2014) demonstrate the link between body fat and population growth under different circumstances, yet both characterize the importance of stored energy reserves in depicting the nutritional resources of a landscape and linking it to population performance. IFBFat of mule deer in the Sierra Nevada mostly was a product of interactions between annual production of food and animal density, which dictated the potential for population growth on an annual basis (Monteith et al. 2014). With monitoring multiple subpopulations of bighorn sheep over time, we suspect that variation in resource availability and quality among populations likely drove variation in nutritional status, because populations in the Sierra Nevada (densities ranged from 0.1 to 1.0 km^2) were well below the size at which we expected diet quality to be limited by density-dependent competition for forage (Conner et al. 2018). Intrinsic habitat quality (McLoughlin et al. 2007) therefore was a primary factor, along with annual weather (e.g., deep snow), in determining the nutritional status of individuals within our populations.

Mean body fat of lactating females among subpopulations in the Sierra Nevada spanned 8.8–15.0% and extended to 20.9% when nonlactating females were included. We demonstrated the range of variability across subpopulations within a large and diverse mountain range (the Sierra Nevada) that was associated with lactation status, nutritional quality of habitats (Greene et al. 2012), and variation in the strategy and tactics of migrants (Spitz et al. 2018). Because intrinsic habitat quality varies among different Sierra Nevada environments, the number of animals that an area can support will differ, as will maximum densities for any given population (sensu Hempson et al. 2015). Similarly, we observed a nutritional condition—growth rate connection whereby a population that falls below zero growth is nutritionally constrained if factors such as disease and predation are not limiting a population. We observed population growth rates between 0.60 and 1.22 in subpopulations of Sierra bighorn sheep that wintered in the alpine zone. During autumn, most individuals had mean body fat well above the physiological minimum required for overwinter survival and pregnancy. Yet lactating females were less likely to survive than nonlactating females based on fat reserves. In bighorn sheep that wintered in an alpine environment, population growth was stable ($\lambda = 1$); thus, an animal-indicated nutritional threshold occurred at 13% IFBFat in autumn of lactating females; 95% confidence intervals illustrate variation around that value, which is undoubtedly tied to a range of factors (e.g., forage availability, winter severity, and predation) that differed among our subpopulations. We observed multiple subpopulations that were at low densities (i.e., presumably they did not exhibit strong density-dependent competition for forage), yet adult females in those subpopulations differed greatly in autumn body fat and mass as an apparent result of realized habitat quality. When density is so low that it is not a factor, either the intrinsic habitat quality (McLoughlin et al. 2007) differed, the ability to acquire nutrients (e.g., allee effects, risk averse behavior, or recent transplants to unfamiliar environments) was constrained, or some combination of the two, determined the level of autumn body condition. Nevertheless, nutritional effects on population growth remained evident in lactating females, regardless of the underlying cause of lower than expected nutritional condition (Fig. 4). Nonlactating females appear to reach a maximum set point of fatness under a greater range of forage conditions, so their fat reserves did not predict population growth of populations. Body fat represented variation in the acquisition of nutrients across populations and integrated the landscape in a manner that would be difficult to duplicate by measuring habitat variables.

Mautz (1978) emphasized that northern herbivorous homeotherms accumulate fat during summer and autumn, when forage is readily available to meet energetic demands during winter, when forage is of much lower quantity and quality. As such, species that are well adapted to harsh environments intentionally catabolize fat stores during periods of nutrient scarcity (King and Murphy 1985). Muskoxen live in a sparsely vegetated, snow-packed environment, with long winters, where they reduce activity and rely heavily on stored energy reserves of up to 29% IFBFat (Adamczewski et al. 1997). Simmons (1982) noted periods of inactivity during extreme winter weather in Dall's sheep when they relied on stored body reserves. Mountain sheep have evolved a strong propensity to store fat as a source of energy to supplement subsequent periods when highly digestible forage is limited. Those stores buffer them against severe winter conditions, enable them to reside in the alpine zone during winter (Spitz et al. 2018), and promote high rates of survival among adult females (Jorgensen et al. 1997; Conner et al. 2018).

The importance of nutrition in any one season cannot be fully understood without examining it with respect to the nutrition provided during all other seasons (Monteith et al. 2013). Indeed, the marked nutritional carryover that we observed among alpine-living bighorn sheep demonstrates not only the potential for an inadequate seasonal range to be livable if coupled with a robust seasonal range, but that bighorn sheep are adapted to experience and persist through seasons of severe resource limitation. As expected for a species that so strongly relies on capital, survival, pregnancy, and population growth were underpinned by body fat. Establishing the link between habitat and demography is the foundation for conserving populations, whether they are endangered and undergoing recovery, or healthy and available for harvest. Indeed, nutritional condition yields the context for understanding if other extrinsic factors (e.g., predation, disease) could be responsible for failed population growth, and consequently, can help identify intervening actions that could yield positive population response. Large stores of body fat are an adaptation to highly seasonal, harsh environments. Consequently, quantifying fat dynamics is critical for identifying habitat requirements and the prospects for populations to persist or be restored.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Diagram of anatomical location for measuring rump fat.

Supplementary Data SD2.—Diagram of anatomical locations for body condition score.

Supplementary Data SD3.—Body condition score for bighorn sheep.

Supplementary Data SD4.—Relationship between rump fat thickness and ingesta-free body fat.

Supplementary Data SD5.—Relationship between body condition score and ingesta-free body fat.

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