Survival of the fattest: How body fat and migration influence survival in highly seasonal environments

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Abstract

1. Energy stores and migration are important adaptations for animals in seasonal environments, but their roles may vary relative to an animal’s endogenous and exogenous environment. In partially migratory populations, migrants and residents experience different seasonal environments; thus, the influence of energy stores on survival may differ relative to migratory tactic, with potential consequences to survival and fitness.

2. Using data from Sierra Nevada bighorn sheep (Ovis canadensis sierrae; hereafter, Sierra bighorn), we tested the hypothesis that body fat (energy stores) buffers animals against their environment, but that buffering capacity differs across environments experienced by high-elevation residents (using a single range year-round), traditional migrants (making 1 round-trip movement between high- and low-elevation ranges during winter) and vacillating migrants (making ≥2 round trips between high- and low-elevation ranges during winter). We predicted that: for animals with high levels of body fat, survival would be high regardless of migratory tactic; residents would require larger stores of body fat to survive than migrants; energy stores would be least influential to survival for vacillating migrants.

3. High levels of body fat in autumn (≥14% for females and ≥19% for males) largely buffered animals against harsh environments (survival >0.90) regardless of migratory tactic. At lower levels of body fat, traditional migrants had higher survival than residents. Vacillating migrants exhibited nearly 100% survival with no detectable effect of body fat on survival.

4. Collectively, these results support the hypothesis that body fat buffers animals against harsh environments but that the buffering capacity differed relative to the environment and highly flexible behaviours (i.e. vacillating migration) can allow animals to decouple survival from body fat.

5. Our work reveals that synergies between physiological and behavioural adaptations of animals in highly seasonal environments carry potential fitness consequences for individuals and demographic consequences for populations.
Seasonal environments pose unique challenges to life and exert tremendous selective pressures by forcing life-history trade-offs related to differential investment in growth, reproduction and survival (Varpe et al., 2009). To balance trade-offs associated with life in seasonal environments, animals rely on adaptations (Tyler et al., 2020; Varpe, 2017) including accumulation of energy stores. Tactics for accumulating energy stores differ among species (e.g. food caching, hyperphagia, and fat accumulation), but the bioenergetic functions are similar: energy stores provide a buffer against seasonally limited energy supplies (Parker et al., 2009). Accumulation of energy stores, however, is not a ubiquitous life-history strategy and even within a single population, seasonal body fat stores can vary substantially (Cook et al., 2013; Stephenson et al., 2020). Thus, the function of body fat in the life-histories of many species may be diverse and variable relative to other aspects of life history (e.g. capital versus income breeders; Drent & Daan, 2002) and environment.

The extent to which animals can accumulate energy stores is underpinned by elements of the endogenous and exogenous nutritional environment of the animal. Endogenously, the amount of fat an animal accretes is influenced by nutritional state (i.e. level of body fat stores) and nutritional requirements (e.g. lactation, growth). Generally, skinner animals accrete more fat over summer than fatter animals (Cook et al., 2013; Monteith et al., 2013; Smiley et al., 2022) and lactating females with elevated requirements for milk production often are less able to meet nutritional requirements, including those for fat accretion, than non-lactating animals (Cook et al., 2013; Denryter et al., 2020; Stephenson et al., 2020).

The exogenous nutritional environment also exerts important constraints on fat accretion regardless of the endogenous environment of the animal. For example, quantity, quality and other aspects (e.g. plant architecture and effects on bite mass) of available food supplies determine maximum rates of energy intake (Cook et al., 2016; Denryter et al., 2020), which can be further constrained by population density, competitive interactions and predation risk (Ceaceero et al., 2012; Festa-Bianchet & Jorgenson, 1998; McNamara & Houston, 1990). In environments where body fat is required seasonally for reproduction or survival, limits to acquiring energy may be catastrophic for individuals or populations, with the potential to result in substantial costs to fitness (e.g. delayed age of primiparity, reduced fertility; Cameron et al., 1993; Créte & Huot, 1993; Gerhart et al., 1996; Reimers, 1983). Thus, for populations to persist, the environment must either support levels of energy acquisition needed to satisfy nutritional requirements or animals must modify their exposure to that environment to alleviate the energy deficit.

Migration is a behavioural adaptation to seasonal environments that functions, in part, to allow animals to modify their nutritional environment. Migration allows animals to access seasonal pulses of nutrients and increase rates of energy acquisition or reduce energy expenditures by escaping deep snow (Aikens et al., 2017; Fryxell & Sinclair, 1988; Monteith et al., 2011). Migrants often face elevated risk of predation (Hobblewhite & Merrill, 2011; T. Stephenson, unpublished data), thus in partially migratory populations (i.e. wherein not all individuals migrate; Chapman et al., 2011) the decision of whether to migrate may be a function of an individual’s risk tolerance for starvation versus predation. Animals with large body fat stores are well buffered against seasonal energy limitations and can choose to be risk-averse to predation. Animals with low to moderate stores of body fat face a challenging dilemma: if winter is mild, they may have enough fat to buffer against the nadir in energy intake in winter, but if winter is severe fat stores may be an insufficient buffer against undernutrition. Intermediate migratory tactics, such as vacillating migration or commuting between ranges (Cagnacci et al., 2011; Denryter, Stephenson, et al., 2021; van de Kerk et al., 2021), may alleviate this dilemma and provide a greater breadth of options to maximize survival relative to the buffer provided by fat reserves. Indeed, fat stores should be accreted and used somewhat anticipatorily to looming conditions dictated by an animal’s environment (Bårdsen et al., 2011), but the requisite level of fat needed to survive may differ depending on how animals behaviorally ameliorate their environment.

Sierra Nevada bighorn sheep (Ovis canadensis sierra) are exemplary for the study of interactions between energy reserves and migration. Body fat of Sierra bighorn can vary 3-fold in autumn, ranging from 8 to 26% (Stephenson et al., 2020), and Sierra bighorn have diverse migratory portfolios comprising traditional migrants, residents and vacillating migrants (Denryter, Stephenson, et al., 2021). Among Sierra bighorn, traditional migrants winter at low elevations (typically 1,500–2,700 m) where they experience little to no snow, early green up and higher risk of predation by mountain lions (Puma concolor; Conner et al., 2018; Gammons et al., 2021; Johnson et al., 2013). Residents remain on high-elevation (2700–3500 m) ranges year-round, including during winter, and can experience substantial amounts of snow (500–1,500 cm annually; California Department of Water Resources, 2019), late green up and historically have had low risk of predation (Greene et al., 2012; Spitz et al., 2020). Vacillating migrants make multiple round trips between high and low-elevation ranges during winter, thus experiencing the
full range of environmental conditions available to traditional migrants and residents, with respect to forage, snow and predation risk (Dennryter, Stephenson, et al., 2021; Greene et al., 2012; Spitz et al., 2020). Differences in environmental conditions across elevational gradients thus may underpin differences in the requisite amount of body fat required for overwinter survival.

We investigated potential synergies between physiology (i.e. body fat stores) and behaviour (i.e. migratory tactics) that may contribute to fitness in seasonal environments. Using data from Sierra bighorn, we tested a set of competing hypotheses (Table 1) that aimed to explain how body fat and migratory tactic interact to affect survival in highly seasonal and variable environments. We hypothesized that body fat buffers animals against the environment, but that the buffering capacity differs relative to the environment (as dictated by migratory tactic). Regardless of migratory tactic, we predicted that large fat stores would lead to high survival because they provide a large energetic buffer. We predicted that larger stores of body fat would be required to survive as a high-elevation resident, given the harsh environmental conditions, than would be required to persist as a traditional migrant that winters at low elevation where conditions are milder and food is more predictable. Finally, we expected that survival would be highest and fat stores least influential to survival for vacillating migrants because they possess the greatest potential to mitigate their exposure to risk factors associated with predation and starvation.

2 | MATERIALS AND METHODS

The Sierra Nevada mountains lie between California’s Central Valley and Great Basin (Figure 1). Vegetation communities vary across elevational gradients comprising Great Basin sagebrush-bitterbrush scrub (1,500–2,500m); pinyon-juniper woodlands, subalpine meadows and forests (2,500–3,300m) and sparsely vegetated areas and alpine meadows (>3300m; Johnson et al., 2010). Low-elevation plants include a variety of grasses (e.g. *Achnatherum* spp., *Poa* spp.), forbs (e.g. *Phacelia* spp., *Eriogonum* spp.) and shrubs (e.g. *Artemisia* spp., *Ceanothus* spp., *Chrysothamnus* spp.), whereas other grasses (e.g. *Agrostis* spp., *Elymus elymoides*), forbs (e.g. *Hulsea algida*, *Polemonium eximium*, *Solidago multiradiata*) and shrubs (e.g. *Salix* spp., *Ribes cereum*) predominate at high elevations (Greene et al., 2012).

We studied Sierra Nevada bighorn sheep that were >1-year old and captured using a handheld net gun fired from a helicopter during autumn 2006–2018. Animal capture and handling protocols were approved in accordance with California Department of Fish and Wildlife Animal Welfare Policy (Protocol Number: Sierra Nevada Bighorn Sheep Capture Plan 2006-10-2018-10) and United States Fish and Wildlife Service Permit TE050122-6. We aged bighorn based on tooth eruption and replacement (animals <4-years old) or horn annuli (animals >4 years old; Festa-Bianchet et al., 2004). We determined body mass of Sierra bighorn with a tripod weighing system and determined percent ingesta-free body fat (IFBFat) scaled to body mass using standardized methodologies for ultrasonography and manual palpation validated for bighorn sheep (Stephenson et al., 2020). Ingesta-free body fat (y) is a linear function of rump fat thickness (x) when rump fat is >0 cm (IFBFat >7.75%) according to the equation $y = 13.28x + 7.78$ ($R^2 = 0.91$; Stephenson et al., 2020). When rump fat thickness is <0 cm (IFBFat <7.75%), ingesta-free body fat (y) is a linear function of body condition score (x) according to the equation $y = 3.92x - 1.48$ ($R^2 = 0.77$; Stephenson et al., 2020). We fitted animals with GPS collars with mortality sensors (various models by Lotek, Newmarket, Canada; Telonics, Mesa, USA; Tellus, Lindesberg, Sweden; Vectronic Aerospace, Berlin, Germany; North Star, Oakton, USA; ATS, Isanti, MN) and investigated mortality signals to confirm mortality after receiving a signal. Information on reproductive histories of individual females was largely lacking and what information was available was too limited for use in our analyses (i.e. would have reduced our sample size significantly).

To classify migratory tactics of Sierra bighorn we used migrateR (Spitz et al., 2017), which extends net-squared displacement models for long-distance migrants (Bunnefeld et al., 2011) to elevational migration. We fit models using default parameter estimates and visually inspected plots of daily elevation against ordinal day to assess goodness of fit and overlap (or lack thereof) of seasonal ranges.

<table>
<thead>
<tr>
<th>Hypothesis number</th>
<th>Hypothesis</th>
<th>Model</th>
</tr>
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<tbody>
<tr>
<td>H1</td>
<td>Neither body fat nor migratory tactic influence survival</td>
<td>$S$–base model&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>H2</td>
<td>Body fat alone influences survival</td>
<td>$S$–base model + sex $\times$ body fat</td>
</tr>
<tr>
<td>H3</td>
<td>Migratory tactic alone influences survival</td>
<td>$S$–base model + sex $\times$ migration</td>
</tr>
<tr>
<td>H4</td>
<td>Body fat and migratory tactic influence survival</td>
<td>$S$–base model + sex $\times$ body fat + sex $\times$ migration + body fat $\times$ migration</td>
</tr>
<tr>
<td>H5</td>
<td>Body fat moderates the influence of snow on survival</td>
<td>$S$–base model + sex $\times$ body fat + snow $\times$ body fat</td>
</tr>
<tr>
<td>H6</td>
<td>Migratory tactic moderates the influence of snow on survival</td>
<td>$S$–base model + sex $\times$ migration + snow $\times$ migration</td>
</tr>
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<sup>a</sup>Base model ($S(sex + age)$) was determined from a set of competing models including variables for sex, age, a binary variable for whether snow accumulation was above-average that winter (bigsnowyear), capture year and metapopulation unit.
(Mysterud et al., 2011) and adjusted starting parameter estimates as needed (Spitz et al., 2017). We expanded the classification of migratory tactic from traditional migrant and resident to include vacillating migrant (Denryter, Stephenson, et al., 2021). Residents remained at approximately the same elevation year-round, traditional migrants made a single round-trip migration between seasonal ranges from December to May, and vacillating migrants are a diverse group that made ≥2 round-trip migrations between lower and higher-elevation ranges during winter (Spitz et al., 2018; Denryter, Stephenson, et al., 2021). Sample elevational profiles of each tactic are shown in Supporting Information S1.

We estimated survival for the autumn-spring (approximately 15 October to 1 June) post-capture because we expected survival during this period to be related to body fat as measured during autumn captures and because we wanted the study period to include the duration of the winter migratory period. We estimated survival using the known-fate model in Program MARK (White & Burnham, 1999) – an extension of Kaplan–Meier model (Kaplan & Meier, 1958) that accommodates staggered entry and exit (by censoring) of marked individuals (Pollock et al., 1989).

Model construction focused on determining interactions between body fat and migratory tactic on survival. To reduce the total number of models considered and avoid potentially spurious effects, we developed two phases of models in a sequential process (Burnham & Anderson, 2002; Nichols et al., 1997) – an approach used in highly scrutinized analyses of spotted owl demographic data (Franklin et al., 2004; Zabel et al., 2003). We chose variables for the first phase of modelling based on previous survival analyses of Sierra bighorn (Conner et al., 2018; Johnson et al., 2010). All base models included sex and age as well as spatial (herd or metapopulation unit) and temporal effects (capture year and a binary variable for whether snow accumulation was above the 20-year average in the capture year; that is, 2010–2011 [although no animals were captured this year], 2016–2017,
2018–2019) because previous analyses showed a strong relationship between survival and age and that survival differed between females and males (Conner et al., 2018). We defined herds by existing herd boundaries (Figure 1). Because sample sizes were small by herd, we combined herds into two sets of metapopulations. The first metapopulation units were southern (Mt. Langley, Sawmill Canyon, Mt. Baxter, Bubbs, Taboose Creek, Mt. Williamson), central (Wheeler Ridge and Convict Creek) and northern (Cathedral Range, Mt. Gibbs and Mt. Warren) recovery units. The second set of metapopulation units had the same southern and central combinations, but Cathedral Range, Mt. Gibbs and Mt. Warren were separated, based on previous analyses (Conner et al., 2018) and the prediction that Cathedral Range herd would be different due to it being recently (2015) reintroduced (California Department of Fish and Wildlife, 2016). Sierra bighorn from other herds were not included in this analysis owing to a lack of autumn body fat measurements from animals in those herds. We used Akaike’s Information Criterion adjusted for small sample sizes (AICc) and normalized AICc weights ($w_i$) to rank models (Burnham & Anderson, 2002) and carried through the structure of the top model(s) from the first phase of modelling as the base model for all subsequent analyses.

We constructed the second phase of models as testable hypotheses associated with survival resulting from interactions between body fat and migratory tactic (Table 1). Our base model, which was the top model from the first phase of modelling, was the null model (H1, Table 1) and did not include body fat or migratory tactic. Our other models included a model to evaluate whether: body fat alone influenced survival (H2); migratory tactic alone influenced survival (H3) and an interaction between body fat and migratory tactic (representing synergistic effects) influenced survival (H4). Finally, we included two additional models with an interaction between years of above-average snowfall and body fat or migratory tactic (H5–6). For these two models we expected years with high snowfall may unequally favour greater fat reserves compared with moderate or low snowfall years.

### 3 RESULTS

From 2006 to 2018, we collected known-fate, GPS locations and ingesta-free body fat, on 215 females and 67 males in autumn. The proportion of Sierra bighorn displaying each migratory tactic was approximately 0.33 for females ($n = 70$ traditional migration, $n = 73$ vacillating migration and $n = 72$ residency) and varied from 0.27 to 0.39 for males ($n = 25, 25, 17$), but varied by herd (Supporting Information S2: Figure S2.1). Males ranged in age from 1 to 11 years and females ranged in age from 1 to 15 years (Figure S2.2). Autumn ingesta-free body fat (IFBFat) of Sierra bighorn ranged from 8.3 to 28.3% for males and 4.4 to 26.5% for females and overall mean IFBFat of males (16.5%) was greater than in females (14.1%; Figure 2a). Mean autumn IFBFat did not differ among residents, vacillating migrants and traditional migrants for either sex (Figure 2b).

The top base models (models within 2 ΔAICc units of the top model) for survival included sex and age (Supporting Information S3: Table S3.1). Survival was lower for males than females and decreased with age, but there was no detectable difference in survival by metapopulation unit, years with above-average snowfall or year for the overwinter period. Although the top model was $S(\text{age} \times \text{sex})$, the beta coefficient for the interaction was not significant ($0.33, 95\% \text{CI} = -0.10–0.76, p = 0.26$), and it was $<0.6$ ΔAICc units from the simpler $S(\text{age} + \text{sex})$ model. We chose to use the less parameterized additive structure to have more power for IFBFat and migration covariates. Based on this first phase of modelling, we used $S(\text{sex} + \text{age})$ as the base model, to which we added IFBFat and migratory tactic to evaluate our hypotheses (Table 1).

In our second (final) phase of modelling, the top model indicated that sex, IFBFat and migratory tactic were important to survival, with significant interactions between sex and IFBFat, sex and migratory tactic and IFBFat and migratory tactic (Table 2). Survival was related positively to IFBFat, but the relationship to survival varied by migratory tactic (Figure 3; Table S3.2). Survival
was highest for vacillating migrants for both sexes, regardless of body fat (Figure 3). At low levels of body fat, survival was lower for high-elevation residents than migrants of both sexes (Figure 3). Of n = 104 vacillating migrants, all but one survived the overwinter period, even though 25% of vacillating migrants had <7% (females) and <13% (males) IFBFat; in comparison, probability of survival for residents with those levels of IFBFat were ~0.80 for females and 0.75 for males. Females with above average body fat (>14.4%) had high survival (≥0.90), regardless of migratory tactic. Migrant males, traditional and vacillating, had high survival (>0.95), but resident male sheep had high survival only at the highest body fat (i.e. >22%; only 5% of males had body fat in this range; Figure 3); although sample sizes were small, resulting in wide confidence intervals.

### DISCUSSION

Energy stores are important to an array of life-history attributes for animals in seasonal environments, and larger energy stores are associated with higher survival and reproductive rates, with implications to fitness (Cook et al., 2013; Monteith et al., 2013; Stephenson et al., 2020; this study). Above a threshold of ~14% body fat for females and ~19% for male survival was high (>0.90) regardless of...
migratory tactic, suggesting body fat provided a buffer across environmental conditions. Nevertheless, at a given level of body fat, survival differed among individuals using different migratory tactics, thereby supporting our hypothesis that the buffering capacity of energy stores depended on the animal’s environment. As expected, the requisite amount of fat needed to survive was greater for animals in harsher environments (high-elevation residents) than in milder environments (traditional migrants). In contrast, vacillating migrants effectively decoupled survival from a requisite amount of body fat and exhibited nearly 100% survival during the study period; however, higher survival of vacillators than traditional migrants or residents may not necessarily equate to higher fitness, which also is contingent upon lifetime reproductive success and whether migratory tactics are fixed or conditional (Lundberg, 1988; Spitz et al., 2018).

Although large fat stores almost guaranteed survival regardless of migratory tactic, the amount of fat needed for Sierra bighorn to predictably survive winter varied relative to their environment. High-elevation residents required more fat to achieve high survival than traditional or vacillating migrants and experienced significantly lower survival at low levels of body fat than their migratory counterparts—an effect that was more pronounced in females. High-elevation residents face limited access to forage and elevated costs for locomotion in high-snowfall years (Dailey & Hobbs, 1989; Fancy & White, 1987; Parker et al., 1984), and we would expect that residents have increased probability of death as winter progresses and they catabolize the last of their reserves. In contrast, traditional migrants largely avoid snow and can track green forages across large elevational gradients (2500 m or more) for 8 months annually (T. Stephenson, unpublished data), likely reducing their need to accrete large stores of body fat and allowing their reserves to last longer into the winter season. That survival was lower for high-elevation residents than migrants, even at the same level of body fat, reinforces how the environment in which an animal lives alters the buffering capacity of its energy reserves. Based on a limited number of re-captured animals, resident Sierra bighorn are estimated to catabolize three times as much body fat during winter as their migratory counterparts at low-elevations (Stephenson et al., 2020). Although the nominal value of body fat is equal (1 kg of fat = 39.5 MJ; Robbins, 1993) regardless of migratory tactic, an equal amount of fat will provide a relatively greater buffer in the milder environment where energy requirements are lower than in the harsher environment. The different buffering capacity of fat relative to environment likely explains why at low levels of body fat, survival of traditional migrants was up to 40% greater than for residents with the same level of body fat. Thus, differences in requisite levels of body fat for survival relative to an animal’s environment may create selective pressure on fat accretion and use.

The relationship between autumn body fat and overwinter survival reflects the important role of summer range in the life-history of ungulates in seasonal environments (Mautz, 1978). Northern ungulates spend summer replenishing body reserves needed for overwinter survival, but quantity and quality of available forages, nutritional state (e.g., lactating or not), population density, etc. (Adamczewski et al., 1993; Cook et al., 2013; Denryter, German, et al., 2021; Piper & Wiley, 1990; Stephenson et al., 2020) can limit nutrient intakes and may explain why not all individuals accreted large fat stores. Failure to accrete large stores of body fat may reflect nutritional limitations of summer ranges, which are increasingly reported for northern ungulates (Cook et al., 2013; Cook et al., 2021; Denryter, Cook, et al., 2022; Monteith et al., 2014; Stephenson et al., 2020). Sierra bighorn may have some capacity to ameliorate nutritional limitations on summer ranges by migrating to low-elevation winter ranges where they can survive winter with less reliance on fat. Thus, in partially migratory populations, migration may function to increase survival when animals are not well buffered against their current environment. For animals less apt to switch their migratory tactic, selective pressures should affect how energy is allocated (i.e. reproduction versus fat stores) over summer and thus, what fat levels are attained leading into winter (Bårdsen et al., 2008; Monteith et al., 2013; Smiley et al., 2022).

Unlike residents and female traditional migrants, vacillating migrants decoupled survival from body fat stores, while also largely avoiding predation. Thus, the utility of this migratory tactic may be that in possessing high potential to respond to changing environmental conditions, they can mitigate their exposure to risk factors associated with starvation and predation. Animals that match their behaviour to their endogenous state and environmental conditions should be best positioned to maximize fitness relative to the constraints they face, which is key to the hypothesized benefits of migration (Chapman et al., 2011). Choice of migratory tactic, however, typically is preemptive with migrants and residents selecting their tactic based on anticipated future conditions (Dingle & Drake, 2007) and risk tolerance (Monteith et al., 2011). Unlike residents and traditional migrants, vacillating migrants could directly assess and compare alternative seasonal ranges, and thus potentially tailor their behaviour to proximate temporal changes in available forage, winter severity, predation risk or some combination thereof, and in doing so achieved higher survival. High overwinter survival of vacillating migrants, regardless of the quantity of body fat reserves or sex, suggests vacillating migration allowed Sierra bighorn to minimize mortality risk, thus begging the question why are not all Sierra bighorn vacillators?

Vacillating migration has been reported only recently (Denryter, Stephenson, et al., 2021), but movement patterns consistent with vacillating migration have been observed in many ungulates (mule deer Odocoileus hemionus van de Kerck et al., 2021; black-tailed deer O. h. hemionus D. Spitz, Victoria University of Wellington, pers. comm.; elk Cervus canadensis K. Hersey, Utah Division of Wildlife, pers. comm.; bighorn sheep A. Holland, M. Miller, Colorado Parks and Wildlife, pers. comm.; pronghorn Antilocapra americana T. Stephenson, unpublished data). Therefore, studies aiming to understand the adaptive significance of vacillating migration are in their infancy. Nevertheless, studies of migration generally may provide fundamental insights into the evolution and ecology of vacillating migration. For example, knowledge of migration is culturally transmitted and re-establishing diverse migratory portfolios takes
decades (Jesmer et al., 2018; Lowrey et al., 2019). Only 3/14 extant populations of Sierra bighorn have continuously occupied their range for >40 years and herds established in the last 5–30 years generally had smaller proportions of vacillating migrants than the oldest, continuously occupied herds (Figure S2.1). Ecologically, factors such as snow, forage availability, predation risk and even habitat type may determine propensity for vacillation as they do for traditional migration (Spitz et al., 2020). Avalanches can be an important stochastic source of mortality for ungulates (Conner et al., 2018; Hebblewhite et al., 2010) and may be a potential barrier to any type of migration. For Sierra bighorn, visual assessment of conditions on alternate ranges also may play a role in decisions to embark on migration (Berger et al., 2022). Thus, even when a herd has been established long enough to have cultural knowledge for diverse migratory tactics, vacillation may be limited to areas where the potential costs of moving between ranges in winter are negligible or where they can assess conditions of alternate ranges in real time. Furthermore, it is still unclear whether vacillating migration represents a true migratory tactic or patch choice behaviour. Nonetheless, vacillating migration is distinct from other migratory tactics in this system and carries different demographic consequences.

Survival estimates for vacillating migrants were high and may be biased if we misclassified migratory tactics of individuals, especially those that died before they had the opportunity to vacillate. Because animals that die early in winter, typically before they may choose to migrate or vacillate, could have vacillated had they survived longer, we can speculate that survival of vacillators may be lower than what we documented. Few animals classified as residents (n = 5) died before the time that most migrations typically occur, thus any bias associated with this type of misclassification likely is small. Additionally, we only had one measurement of body fat for each individual and did not have recruitment data, which prevented us from conducting longitudinal analyses with body fat and recruitment that undoubtedly would provide greater insights into life-history strategies and trade-offs (Monteith et al., 2013, 2014; Smiley et al., 2022). Nonetheless, vacillating migration appears to be a highly successful tactic where it can be employed and may allow individuals to experience the best of both migrant and resident environments.

Sierra bighorn combined body fat stores and migratory tactic to produce synergistic effects on overwinter survival, thereby exemplifying the crucial yet varied role of physiological and behavioural adaptations to seasonal environments in delimiting the fitness of individuals and populations (Williams et al., 2017). The buffering capacity of body fat stores differed across environments, as dictated by migratory tactic, but large fat stores consistently provided a generous buffer, regardless of migratory tactic. While residency was inviable without large body fat stores, except perhaps during mild winters with low snowfall, vacillating migration allowed animals to decouple overwinter survival from body fat. Our findings suggest that selective pressures should affect how body fat is accreted and used across seasons (Bårdsen et al., 2014; Smiley et al., 2022), especially for species with a greater propensity to have fixed and faithful migratory tactics (Morrison et al., 2021; Sawyer et al., 2019). Collectively, our results reveal that synergies between physiology and behaviour of animals in highly seasonal environments carry potential fitness consequences for individuals and demographic consequences for populations and may help explain why diverse migratory portfolios contribute to greater resilience and population persistence (Fryxell & Sinclair, 1988; Lowrey et al., 2020; Sawyer et al., 2016): animals that have a diverse set of migratory tactics to choose from can select the option that affords the greatest odds of survival relative to their current nutritional state and available environments. Our findings further highlight that interactions among physiological and behavioural adaptations are key to understanding nutritional prerequisites for persistence in variable environments.

AUTHORS’ CONTRIBUTIONS
Kristin Denryter, Mary M. Conner, Thomas R. Stephenson, and Kevin L. Monteith conceived and designed the study; Thomas R. Stephenson, David W. German, Mary M. Conner and Kristin Denryter collected data; Mary M. Conner led data analysis and all other authors contributed to interpretation of results; Kristin Denryter led writing of the manuscript with contributions from all authors. All authors contributed critically to the drafts and approved the final version of the manuscript.

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CONFLICT OF INTEREST
The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT
Data are archived for public use in the Sierra Nevada Bighorn Sheep Database of the California Department of Fish and Wildlife, but not elsewhere owing to the sensitive nature of biological data for endangered species in this study (Sierra Nevada bighorn sheep). Data requests can be submitted to asksnbs@wildlife.ca.gov reference number FE-2022-00464 (Denryter, Conner, et al., 2022).

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REFERENCES


**SUPPORTING INFORMATION**

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

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