Pursuit and escape drive fine-scale movement variation during migration in a temperate alpine ungulate

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Abstract

Climate change reduces snowpack, advances snowmelt phenology, drives summer warming, alters growing season precipitation regimes, and consequently modifies vegetation phenology in mountain systems. Altitudinal migrants cope with seasonal variation in such conditions by moving between seasonal ranges at different elevations, but vertical movements may be complex and are often not unidirectional during the spring migratory season. We uncover drivers of vertical movement variation in an endangered alpine specialist, Sierra Nevada bighorn sheep. We used integrated step-selection analysis to determine factors that promote vertical movements, and factors that drive selection of destinations after vertical movements. Our results reveal that high temperatures consistently drive uphill movements, and provide some evidence for the contribution of precipitation events to downhill movements. Furthermore, bighorn select destinations that have a high relative index of forage growth and maximize delay since snowmelt. These results indicate that although Sierra bighorn seek out foraging opportunities related to landscape phenology, they compensate for short-term environmental stressors by undertaking brief vertical movements. Migrants may therefore be impacted by future warming and increased storm frequency or intensity, both in terms of their fine-scale vertical movements, and in terms of tradeoffs between forage access and predation risk.

Keywords

Altitudinal migration, bighorn sheep, endangered species, green wave hypothesis, migration phenology, step selection functions

Introduction

Recent and ongoing climate change disrupt the spatiotemporal pattern of spring plant growth in temperate regions through modified precipitation and temperature regimes [1–3]. Because ungulates commonly track plant phenology during their spring migration [4–6], climate change may affect spatiotemporal patterns of herbivore movement and migration [7]. Forage tracking is a useful tactic for ungulates in landscapes with gradients in plant phenology, because access to highly digestible plant material is maintained or maximized through time [8,9].

Many migratory ungulates track forage phenology across elevational gradients in a form of seasonal vertical migration [10–12]. Although vertical migration in ungulates may emerge in a traditional, “undistracted” form of movement from one range to another, the geographical proximity of seasonal ranges separated by elevation allows migrants to use a broader portfolio of redistribution tactics that span a range of directedness [13]. Migrants may undergo several movements during a foraging season to maximize resource access across multiple sub-seasonal ranges [14,15].

However, fine-scale movements during the migratory season could be additionally influenced by factors other than foraging opportunities. Because landscapes of relief generate multiple axes of ecoclimatic variation, vertical movements enable herbivores to realize change in multiple environmental conditions [16]. Vertical movements may allow migrants to alleviate or intensify realized environmental conditions through both static landscape variation (ecological variability across space but not time) and dynamic landscape variation (variability across both space and time). Whereas seasonal variation in snow cover and forage availability may ultimately underlie seasonal redistribution of migrants, variation in exposure to high temperatures or severe storms can be mitigated by moving across elevation at daily or hourly scales [17,18]. Because temperatures tend to decrease at higher elevations, upward movements can lead to a reduction in experienced heat; conversely, dangers associated with precipitation and storms on alpine plateaus can be relieved by moving downslope into comparatively protected canyons [19].

The objective of this study was to evaluate the extent to which static and dynamic variation in environmental conditions leads to complex use of elevation in an herbivorous altitudinal migrant, Sierra Nevada bighorn sheep ("Sierra bighorn", *Ovis canadensis sierrae*). Sierra bighorn are a federally endangered subspecies of bighorn sheep endemic to the Sierra Nevada mountains of California (USA) that migrate between the Owens Valley and High Sierra each spring, but with substantial variation in day-to-day elevation use[13] (Figure 1). We expected that spring migration timing and habitat selection would broadly correspond with landscape phenology, but that fine-scale variation in elevation use during the migratory season would arise in response to fine-scale stressors such as high temperature and potentially dangerous precipitation events. To test these expectations, we used a three-part approach to explore Sierra bighorn movement responses to dynamic landscape variation: First, we determined whether upslope migration timing was related to snowmelt and green-up timing. Second, we tested the extent to which variation in environmental stressors and resources promoted adjustments in elevation use. And third, we evaluated how step selection differed by sex, migratory status, and migratory strategy.

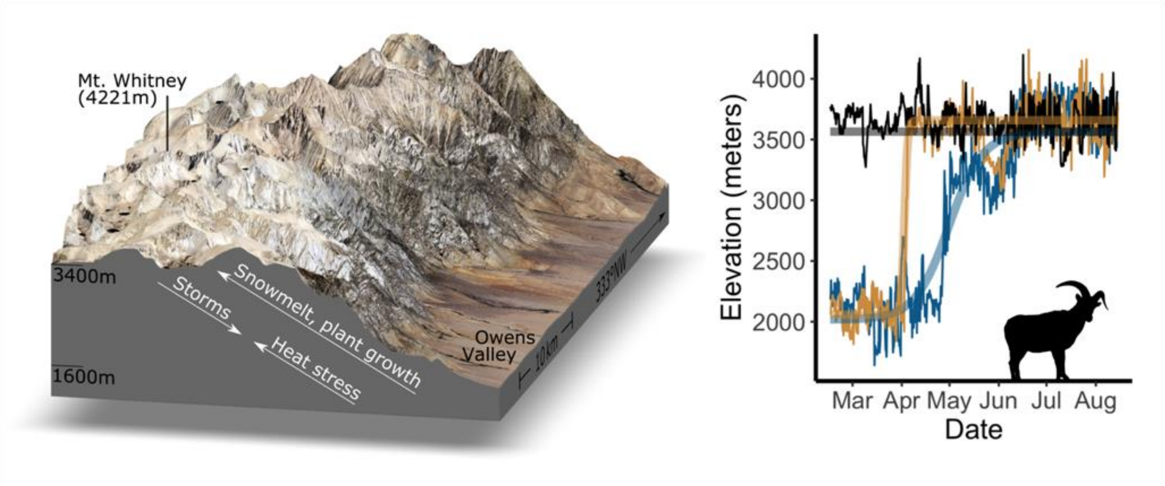

Figure 1. Sierra Nevada bighorn sheep confront variation in stressors and resources throughout spring migrations between low-elevation winter range and high-elevation summer range (left). For some individuals, spring migration follows a unidirectional, undistracted path (right, tan), whereas for others multiple up-and-down movements slow down the mean pace of vertical redistribution (blue). For yet other individuals, wintertime residency at high elevations leads to consistent use of a narrower range of elevational strata throughout the spring (black).

Methods

Study system

Sierra Nevada bighorn sheep are alpine specialists and partial, facultative, altitudinal migrants in the Sierra Nevada mountains of California (Spitz et al. 2020, Berger et al. 2022; Figure 1). The gradient from the base of the Sierra's escarpment to its highest peaks often exceeds 2km elevation and features a predictable elevational delay in plant phenology [21]. Individuals that undergo uphill spring displacement typically follow one of two migratory patterns [13]: In undistracted migrations, individuals undertake a single, uphill trip, departing from low-elevation winter range and settling on high-elevation summer range. In vacillating migrations, individuals undertake multiple up-and-down movements over a period of days or weeks before settling on high-elevation summer range. Sierra bighorn occupy 14 "herd units", a spatial delineation used for conservation metrics and management strategies, and which approximately represent discrete bighorn populations [22].

Movement data

Bighorn were fit with GPS collars (various models from Advanced Telemetry Systems, North Star Science and Tech LLC, LOTEK Engineering Ltd., Televilt, VECTRONIC Aerospace GmbH, Followit, and Sirtrack LTD; described in [23]) during spring and fall capture seasons (March and October) between 2002-2022. Animal handling was done under veterinarian supervision and approved under the California Department of Fish and Wildlife Animal Welfare Policy (2017-02). In total, 311 unique individuals were tracked for a total of 702 animal-years, with an average of 35.1 animals per year. Collars were deployed in all 14 herd units, spanning the full latitudinal, longitudinal, and elevational range occupied by the species. Collars were programmed to collect GPS locations at a minimum frequency of 1 fix per 12 hours.

Habitat covariates

USGS 3DEP 10m National Map elevation data were acquired via Google Earth Engine [24,25]. Slope and aspect were calculated using the 4-neighbor rule. Bighorn sheep strongly rely on being on or near escape terrain (rugged terrain where they are relatively safe from predators); as is typically done, escape terrain was classified using a 30° slope threshold (sensu [26]). Distance from escape terrain was calculated using the fasterraster v.0.6.0 R plugin for QGIS v.3.22 [27,28].

Seasonal and spatial variability in vegetation production were summarized using MOD13Q1 NDVI at 250m resolution[29] following [30,31]. For each pixel, NDVI was rescaled by transforming the bottom 2.5 percentile and top 97.5 percentile to 0 and 1, respectively. Negative values were raised to 0. The rescaled time series was smoothed using a moving median window (width = 3; see [31]). The smoothed time series was fit to a double logistic function following the form:

$$NDVI = \frac{1}{1+\exp\left(\frac{xmidS-x}{scalS}\right)} - \frac{1}{1+\exp\left(\frac{xmidA-x}{scalA}\right)} \qquad [1]$$

where x is the ordinal day of year, xmidS and xmidA are the ordinal days of green-up and senescence inflection points respectively, and scalS and scalA are scaling parameters describing the rate of green-up and senescence, respectively [30]. The pixel-specific parameterization of Equation 1 was used to index seasonal variability in forage production (“relative NDVI”). Relative NDVI has values close to 1 when a pixel is at its peak level of biomass production for the year, and values close to 0 when a pixel is at its lowest levels of production. Forage production (“absolute NDVI”) was indexed by un-scaling the parameterized predictions of Equation 1 using the 2.5 and 97.5 percentile scaling parameters from the original raw NDVI transformation. In this way, areas with dense vegetation have values closer to 1 and areas with sparse vegetation have values closer to 0. Green-up timing was measured using the pixel-specific xmidS parameter, which is the date during which relative NDVI increases at the fastest rate, and time from peak green-up was calculated as the difference between a given date and the date of green-up timing.

A modeled daily snow dataset was used to index fractional snow cover (FSC) and snowmelt timing [32]. This dataset was generated using a data fusion and machine learning approach that combines Landsat 5, Landsat 7, and spatially and temporally complete (STC) MODIS satellite imagery[33] to generate daily FSC estimates at 30m resolution. Both the MODIS STC algorithm and the Landsat 5 and 7 FSC rely on spectral mixture analysis [34] to estimate FSC which is considered more accurate than index-based methods for estimating snow cover [35–38]. The 30m FSC modeled dataset was developed using 5% of inputs as training and 95% as validation, and showed a 97% accuracy with 1% bias. To increase confidence in the accuracy of FSC, the product was additionally validated using snow cover data from an independent *in situ* sensor network [21,39]. The validation reveals strong concurrence among the modeled FSC dataset and point estimates of snow cover throughout the range of Sierra bighorn (Supplementary materials S1). To summarize seasonal snow cover variability, FSC was fit to Equation 1 above. Snow cover fraction (with a range of 0-100%) was used in place of NDVI and the curve was accordingly fit on a [0,100] interval. Year was offset to start on August 15 and end on August 14 so that each FSC time series began at a summertime baseline (0% snow cover), accumulated to a wintertime maximum, and then deteriorated during the melt season back to 0. Snowmelt timing was measured using the pixel-specific xmidA parameter, which is the date at which the fitted FSC decreases at the fastest rate, and time from peak snowmelt was calculated as the difference between a given date and the date of snowmelt timing.

Daily temperatures and precipitation were extracted from the DAYMET V4 dataset at 1km resolution [40]. Heat can be physiologically taxing for alpine ungulates that are adapted for cold temperatures, and may drive uphill movements that mitigate heat stress experienced at lower elevations at the cost of foraging opportunities [18,41]. We used daily maximum temperature to index potential thermal stress across the eastern Sierra. Precipitation is infrequent in the Sierra outside winter, but is often associated with high winds and lightning, and causes terrain in the alpine zone to become wet and particularly unstable [42]. Rock slides have been attributed to mortality in several alpine caprine species, including ibex [43] and Dall sheep [44], and mountain sheep have been observed to react quickly to warning signs of rockfall [45]. We used water-equivalent total daily precipitation (mm) to index rainfall variability in the region.

Migration classification

Seasonal elevation use was determined by extracting elevation from the 3DEP National Map using bighorn GPS location data. Migrants were classified using the migrateR package [46]. MigrateR uses an elevational analogue for measuring net squared displacement, and classifies individuals as “resident”, “disperser”, or “migrant” based on a model comparison approach between a consistent position through time, a single upward movement across time, or an up-and-down redistribution through time. We used minimum thresholds of 500m between elevational ranges and 21 days spent on each seasonal range when classifying individuals as residents, dispersers, and migrants based on previous work in this system [46,47]. Because the focus of this study was on uphill spring migration, any uphill dispersers were combined into the migrant class. Migration timing was quantified using the theta parameter from the elevational net squared displacement curves, which indexes the midpoint of the individual’s departure movement. Migration rate was quantified using the phi parameter; migrants were classified as “fast migrants” if the migration lasted one day or less and “slow migrants” if the migration lasted as least one week.

Step selection modeling

Habitat selection was examined using integrated step-selection analysis (iSSA, [48]). We conducted a single (population-level) iSSA (rather than multiple individual iSSAs) because minimal endpoint variance in predictor variables constrained our ability to resolve movement processes for animals that used short step lengths relative to coarse-resolution remote sensing data. A population-level model allowed inclusion of a greater number of individuals and testing of a greater number of candidate movement drivers simultaneously. To maintain sampling consistency across individuals, the 21 days centered on each migrant’s migratory window was used for the analysis. For residents, the three weeks centered on the mean migration timing of that individual’s herd unit in that year was used. If no migrants were detected in a resident’s herd unit in a given year, the resident was excluded from the analysis. Our model included equal numbers of GPS observations from each individual in order to avoid bias in the model design.

In cases where the GPS fix rate was more frequent than 12 hours, relocation data were temporally rarified to a 12-hour frequency. Each resampled fix was treated as a startpoint, with the following fix treated as a used endpoint. Thirty random destinations were used as available endpoints. Endpoints were drawn from gamma and von Mises distributions fitted to the population’s step length and turning angle history, respectively [48–50].

Environmental covariates were extracted at all start- and endpoints. Terrain features were treated as fixed across time. Snowmelt timing and green-up timing were fixed across time within years, while FSC, distance from snow, relative NDVI, absolute NDVI, maximum temperature, and total precipitation all varied daily. Elevation, terrain slope, and temperature were scaled using z-scores across the full extracted dataset to aid in model fitting. Aspect was cosine-transformed such that north-facing slopes were 1 and south-facing slopes were -1. Precipitation, distance from escape terrain, and distance from snow were transformed using log(value + 1) to accommodate 0’s and because we were interested in variability at fine scales.

Hot days were identified as temperatures exceeding the 75th percentile of daily temperatures at the level of the individual bighorn-year.

Drivers of habitat selection during migration movements were evaluated by fitting an integrated step-selection function to the data using conditional logistic regression [51,52] with case (observed endpoint = 1; randomly sampled endpoint = 0) as the response variable, habitat covariates as candidate predictor variables, and step ID as the stratification variable. Two model families were built: First, a complete movement model included fixed endpoint conditions to identify drivers of habitat selection (i.e., a movement outcome). Endpoints included terrain parameters (elevation, slope, aspect, and distance to escape terrain), daily weather parameters (high temperatures and cumulative precipitation), snow parameters (FSC, distance to snow, and time from peak snowmelt), and forage parameters (absolute NDVI, relative NDVI, and time from peak green-up). Interactions were included between endpoint elevation and the binary statuses of "hot day" and "raining" at the beginning of movement. The model was cross-validated using a 5-fold partition with 100 repetitions (Supplementary materials S2, [53,54]). In the second family of models, we sought to explore patterns of variation in movement behaviors between sex and migratory strategy in order to test two hypotheses: Step selection during the migratory season will differ between male and female bighorn sheep if competing life history demands outweigh potential benefits of alternative movement options. And, step selection will differ according to migratory strategy if responsiveness to environmental variability underlies migratory decision-making. We took subsets of the full movement dataset representing females and males; migrants and residents; and fast migrants and slow migrants. All of the same predictor variables were used as in the overall population-level iSSA.

All statistical analyses were done using R version 4.1.2 [55].

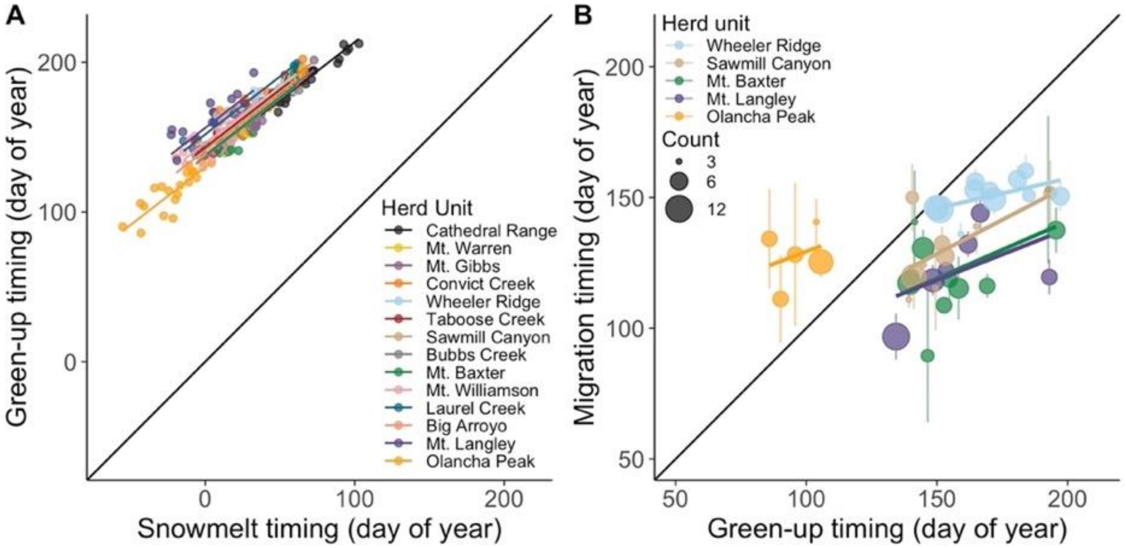

Figure 2. Range-wide mean green-up timing vs. snowmelt timing by herd unit, 2003-2022 (A). Mean migration timing vs. green-up timing for herd units with at least 3 individuals tracked in at least 5 years (B; migration timing points scaled by number of individuals tracked and bars are 1 standard error).

Results

Across the study system, green-up timing (as measured at the herd unit level) was consistently later in years when snowmelt timing (as measured at the herd unit level) was later (Figure 2A). In a mixed-effects model with green-up timing as the response variable, snowmelt timing as the predictor variable, and year as a random intercept, green-up was 7.7±0.15 days later per 10-day delay in snowmelt ($p < 0.001$; conditional $R^2 = 0.92$). Thus, years with especially early snowmelt were characterized by a greater lag between the snowmelt timing and green-up timing. The mean difference in timing between peak snowmelt and peak green-up was 136.7±0.86 days.

Uphill migration timing covaried with green-up timing, and in years with later green-up timing, migration timing was delayed as well (Figure 2B). Mean migration timing occurred before mean green-up timing at the herd unit level in 75.2% of cases; however, anomalously late migrations were observed in several cases when bighorn undertook out-of-season vertical movements. The earliest migration (relative to green-up timing) occurred 124 days prior to mean green-up timing (at the herd unit level), while the latest was 79 days after mean green-up timing. A linear mixed-effects model with migration timing as the response variable, green-up timing and sex as predictors, and herd unit identity and year as random intercepts, revealed that the midpoint of migration was 4.1±1.1 days later per 10-day delay in green-up timing ($p = 0.001$; conditional $R^2 = 0.46$). Migration was 5.9±3.5 days earlier for females than males, but this difference was not significant ($p = 0.09$).

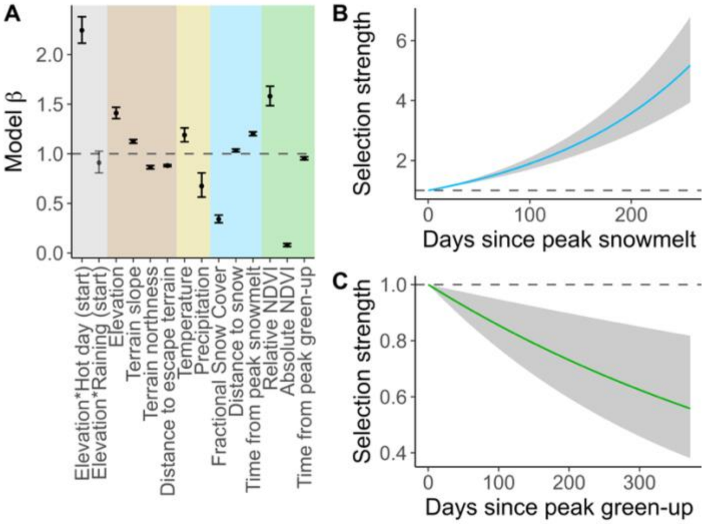

Figure 3. Coefficients from population-level integrated step-selection analysis of Sierra bighorn movement (A). Terrain parameters shown in brown, weather parameters in beige, snow parameters in blue, and forage parameters in green. Interactions between startpoint conditions (the binary statuses of hot day and raining) and endpoint elevation shown in grey. Selection strength increased for destinations with increasing days since peak snowmelt relative to destinations where snowmelt occurred 0 days ago (B). Conversely, selection strength decreased for destinations with increasing days since peak green-up relative to destinations where green-up peaked 0 days ago (C).

Throughout the spring migratory season, bighorn selected steep, south-facing slopes close to escape terrain (Figure 3A). Bighorn selected warmer areas and avoided precipitation. A strong positive interaction between high temperature at the start of movement and endpoint elevation indicates that bighorn were especially likely to select uphill steps on hot days (*Elevation*Hot day (start)*). They generally avoided snow, selecting habitat with low fractional snow cover, away from dense snowpack, and that had melted out longer ago (Figure 3B). Bighorn avoided moving toward areas with large absolute NDVI (i.e. sites with high overall plant biomass) and instead preferred areas with high relative NDVI (i.e. sites that were near their local greenness maxima for the year), and sites that were at or near their peak rate of green-up (Figure 3C). Comparison by QIC among models fit with all predictors and nested models fit with only terrain, weather, snow, or forage parameters revealed the most support for the overall model (ΔQIC > 500 for all nested models).

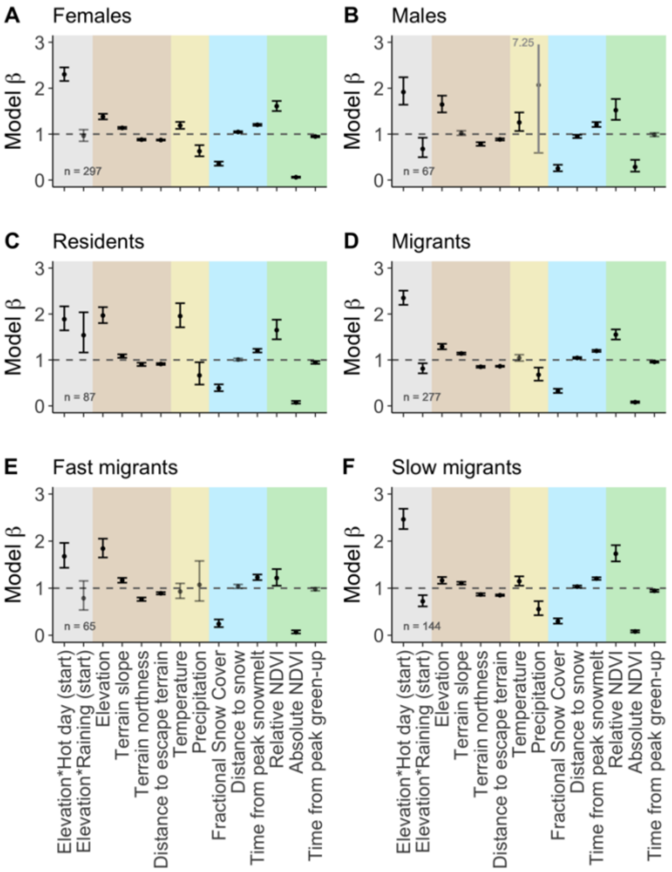

Figure 4. Model coefficients (exponential estimated parameter ± s.e.) from population movement subsets for females (A), males (B), residents (C), migrants (D), fast migrants (E), and slow migrants (F). Inset "n" refers to the number of animal-years represented in the population subset model. Note that in (B), one error bar exceeds axis limits and its terminus is indicated numerically.

Selection for high-elevation, steep, south-facing slopes that were close to escape terrain was consistently evident across population subsets (Figure 4A-F). A positive interaction between high temperature at the start of movement and endpoint elevation (*Elevation*Hot day (start)*) was also detected for all groups. Patterns of selection in response to snow and forage parameters were generally conserved across groups. A negative interaction between rain at the start of movement and endpoint elevation (*Elevation*Raining (start)*) indicated that males, migrants, and in particular slow migrants selected against high elevations on rainy days. The interaction was positive or neutral for females, residents, and fast migrants.

Discussion

Sierra Nevada bighorn sheep undertake a partial, facultative vertical migration during the spring snowmelt and green-up season [20], but their vertical movements are rarely unidirectional and often lead to complex use of elevation [13]. Although seasonal variation in space use leads to a general pattern of redistribution across elevation, our results indicate that fine-scale vertical movements during the migratory season might allow bighorn to realize multiple goals, including pursuing foraging opportunities, avoiding heat stress, and seeking refuge from storms.

Uphill migration timing by Sierra bighorn was broadly associated with green-up timing at the herd unit level, which was in turn associated with snowmelt timing. Coordinating migration timing with resource phenology is common among ungulates, presumably because foraging efficiency increases with access to highly digestible early-stage plant growth [56–58]. The Sierra Nevada mountains feature strong interannual variation in snow cover, snowmelt timing, and green-up timing, with over three months between the earliest and latest green-up records over the course of this study. Although most uphill migrations occurred before mean green-up timing at the herd unit level, some individuals underwent comparatively late uphill movements, possibly related to breeding or reproduction, intraspecific competition, or social avoidance.

Our full step selection model identified strong associations between terrain, weather, snow, and forage factors in driving step selection. Furthermore, the terrain-only model was the best performing nested step selection model. Among the subset models, terrain factors were consistently important regardless of individuals' migratory status or sex. Together, these results reflect the considerable importance of these factors for bighorn sheep movement and habitat selection [45].

High temperatures stand to impact bighorn sheep through heat stress, while precipitation may lead to terrain instability, wetting leading to hypothermia, or exposure to lightning. Uphill forays by bighorn in this study were associated with lower destination temperatures, presumably related to refuge from heat stress. Heat stress in other ungulates drives similar behavioral responses, leading to selection toward higher elevation and modified daily foraging schedules during hot days [18]. In the eastern Sierra Nevada, high spring temperatures accelerate snowmelt, and, where snowmelt is earliest, the lag between snowmelt timing and green-up timing is greatest [21]. Therefore, higher spring temperatures may cause bighorn to spend increased time at high elevations while there is still high-quality forage below.

Conversely, we found a negative effect of precipitation on elevation selection, indicating that storms may drive downhill movements, presumably related to escape from either risk of lightning strike, rockslides, or wind. While downhill movements in response to storms are known in birds [17], our study provides evidence of similar responses to storms by ungulates. Notably, the effect of precipitation on selection for elevation was only significantly negative for males, migrants, and in particular slow migrants, indicating that these groups may be more flexible than females and alpine residents in their response to sudden environmental changes. If the frequency of spring and summer storms increases across the Sierra, bighorn sheep may sacrifice foraging opportunities at high elevations in favor of seeking out protected combes and canyons further down mountainsides.

Vertical movements may also effectuate refuge from predation. Because the migratory season of bighorn sheep generally corresponds with lambing, ewes must balance heightened nutritional requirements with selection of habitat that accommodates safe lamb rearing [59,60], leading to shifts in habitat selection by bighorn ewes after lambing [61]. In the eastern Sierra, mountain lions hunt bighorn sheep with particular success at low elevations [62,63]. Movements toward steep terrain at high elevations may therefore reflect habitat selection for parturition and lamb rearing rather than habitat selection for foraging. In our study, females migrated uphill earlier than males and did not move downslope during storms, possibly reflecting an increased risk of predation at low elevations. Other species of wild sheep also exhibit sex-specific habitat selection, with ewes prioritizing areas that will facilitate lamb growth and survival, and rams prioritizing foraging opportunities at the expense of access to safe terrain [64].

Model comparison revealed that terrain was the most important class of predictors for step selection by bighorn. Following terrain, snowpack factors were more important than forage factors for step selection. Notably, however, we analyzed snowpack using a daily 30m modeled fractional snow cover product [32], whereas we analyzed forage using 16-day 250m MOD13Q1 satellite imagery [29]. We suspect the snow model was selected over the green-up model due to the comparatively fine spatial and temporal resolution of the snow product, coupled with the use of a coarse MODIS based NDVI product representing vegetation growth perhaps not completely predictive of forage in sparsely vegetated high alpine landscapes. Combined, these factors could result in the snow product revealing fine-scale landscape phenological variation that is masked at coarser scales [65]. Because snowmelt and plant growth are so tightly linked in alpine systems (e.g. Winkler et al. 2018, John et al. 2023), we attribute habitat selection for snow properties in this analysis to forage phenology and availability. Indeed, at the coarse level, relative selection was strong for relative NDVI (Figure 3A), suggesting that bighorn selected for areas when NDVI peaked at that site.

The 3000m elevational gradient of the Sierra Nevada generates a broad ecoclimatic window that bighorn sheep can use in response to both short- and long-term abiotic stressors. Future reduced snowpack and higher temperatures at low to mid elevations along the Sierra escarpment [67,68] will likely modify the historic pattern of vegetation green-up, thereby complicating the balance between stress avoidance, forage pursuit, and access to escape terrain. Because the delay between snowmelt and green-up timing is greatest at low elevations where snowmelt is earliest, increasingly early snowmelt at low to mid elevations may lead to a vertical contraction in the range of terrain where plant growth predictably and immediately follows snowmelt. Simultaneously, a higher frequency of hot days may drive bighorn away from areas at a period of peak forage quality. Therefore, if abiotic stress avoidance and forage access are to be maintained, site visitation by bighorn during spring will likely shift toward higher elevations where escape terrain is nearby while maintaining a resource supply that is digestible and nutritious.

To better understand how movement responses to diel and seasonal environmental variation translate into nutritional and energetic outcomes, finer data on bighorn movement and landscape patterns in digestible nutrients are required. Work combining accelerometry and high-resolution remote sensing data could shed light on energy expenditure and intake, particularly if they are paired with measurements of bighorn body condition [69,70] and plant nutrient concentration. Furthermore, factors such as social information [56], perception [19], group cohesion [71], and intraspecific competition [72] all play a role in ungulate migrations and will become increasingly important as the Sierra bighorn recovery effort leads to increasing population sizes. Improving inference about individual survival and reproductive capacity, and ultimately carrying capacity at the level of management units, will facilitate conservation of existing Sierra bighorn populations and potentially inform site selection for future reintroductions.

Whereas long-distance (often latitudinal) migrations allow animals to capitalize on broad-scale variation in resource availability [10,73,74], elevational migrants (or altitudinal migrants) exploit similar resource dynamics [75,76] while potentially maintaining a semi-local proximity that lends flexibility to movements between seasonal ranges [13]. An elevational migrant can visit out-of-season ranges, double back over the migratory corridor, and make fine-scale movement adjustments during the migration season that could not be achieved by a migrant whose seasonal ranges are separated by hundreds of kilometers [77]. Our work indicates that bighorn sheep make movement decisions during the migration season in response to environmental stressors while seeking out preferred fine-scale terrain features and simultaneously maintaining coarser responses to landscape phenology. This suggests that movement decisions may be guided by static landscape variability (terrain) and then further informed by dynamic landscape variability, which can emerge in the form of a resource (forage access) or a stressor (storms or high temperatures). For these elevational migrants, the close geographic proximity of seasonal ranges presents an opportunity to draw out the migration as they respond to dynamic landscape variability that can be mitigated by moving a few hundred meters up- or downhill. Together, these findings highlight the importance of examining nested scales of movement and interrelated landscape dynamics in migratory species faced with multifaceted environmental change.

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Author contributions

Conceptualization: CJ. Methodology: CJ, TA, JS, and TRS. Software: CJ and TA. Formal analysis: CJ. Data curation: CJ, LWS, TRS, and KR. Writing – original draft: CJ. Writing – Review and editing: All authors. Visualization: CJ. Supervision: TRS and EP. Funding acquisition: CJ and EP.

Data availability

Workflow code and input data for iSSF models are available at [***LINK AVAILABLE UPON ACCEPTANCE FOR PUBLICATION]. GPS data are archived in the Sierra Nevada Bighorn Sheep Database of the California Department of Fish and Wildlife. Because of the sensitive nature of biological data for endangered species, data requests are handled on a case-by-case basis and data requests can be submitted to asksnbs@wildlife.ca.gov.

Additional Information (including a Competing Interests Statement)

The authors declare no competing interests. Bighorn sheep collaring activities were approved under University of Montana Institutional Animal Care and Use Committee (024-07MHWB-071807 and 46-11), California Department of Fish and Wildlife Animal Welfare Policy (Sierra Nevada Bighorn Sheep Capture Plan 2006-10-2018-10), and United States Fish and Wildlife Service Recovery Permit (#TE050122-6 to TRS).

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