

Alternative foraging strategies enable a mountain ungulate to persist after migration loss

ALYSON B. COURTEMANCH ^{1,2,†} MATTHEW J. KAUFFMAN,³ STEVE KILPATRICK,⁴ AND SARAH R. DEWEY⁵

¹Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA

²Wyoming Game and Fish Department, P.O. Box 67, Jackson, Wyoming 83001 USA

³U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA

⁴Wyoming Wild Sheep Foundation, P.O. Box 666, Cody, Wyoming 82414 USA

⁵Grand Teton National Park, Science and Resource Management, National Park Service, P.O. Box 170, Moose, Wyoming 83012 USA

Citation: Courtemanch, A. B., M. J. Kauffman, S. Kilpatrick, and S. R. Dewey. 2017. Alternative foraging strategies enable a mountain ungulate to persist after migration loss. *Ecosphere* 8(6):e01855. 10.1002/ecs2.1855

Abstract. The persistence of many migratory ungulate populations worldwide is threatened due to anthropogenic impacts to seasonal ranges and migration routes. While many studies have linked migratory ungulate declines to migration disruption or loss, very few have explored the underlying factors that determine whether a population perishes or persists. In some cases, populations undergo severe declines and extirpation after migration loss; however, others appear able to persist as residents. We predict that to persist, populations must replace the traditional benefits of migration by altering the foraging strategies they employ as residents within one seasonal range. We propose the alternative foraging strategies (AFS) hypothesis as a framework for identifying various behavioral strategies that populations may use to cope with migration loss. We tested the hypothesis using the formerly migratory Teton bighorn sheep population in northwest Wyoming, which ceased migrating over 60 yr ago, but has persisted as a resident population. We used global positioning system data to evaluate winter and summer habitat selection and seasonal elevational movements for 28 adult female bighorn sheep (*Ovis canadensis*) from 2008 to 2010. Resource selection functions revealed that bighorn sheep employ winter foraging strategies to survive as residents by seeking out rugged, high-elevation, windswept ridgelines. Seasonal movement analyses indicated that bighorn sheep undergo a newly documented “abbreviated migration” strategy that is closely synchronized with vegetation green-up patterns within their one range. Bighorn sheep descend 500 m in elevation and travel up to 10 km in spring, gaining access to newly emergent forage approximately 30 d before it appears on their high-elevation winter and summer ranges. Our findings indicate that the Teton bighorn sheep population has persisted due to its habitat selection, AFS, and unique movement patterns, which allow migration loss to be mediated to some extent. The identification of AFS and the habitats that support them can help reveal the underlying benefits of migration and conserve populations in the face of future migration loss.

Key words: abbreviated migration; alpine; alternative foraging strategies; bighorn sheep; Greater Yellowstone Ecosystem; habitat selection; migration; normalized difference vegetation index (NDVI); *Ovis canadensis*; phenology; ungulate; Wyoming.

Received 10 February 2017; **accepted** 15 February 2017. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2017 Courtemanch et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† E-mail: alyson.courtemanch@wyo.gov

INTRODUCTION

Many ungulates migrate to access resources that seasonally change over vast landscapes. Migratory populations generally support higher numbers and demographic rates than resident populations (Fryxell et al. 1988, Albon and Langvatn 1992, Hebblewhite and Merrill 2011). Migratory individuals benefit by seeking out the highest quality forage available throughout the year (Fryxell and Sinclair 1988, Hebblewhite et al. 2008) and in some cases, lower their predation rates (Hebblewhite and Merrill 2007, 2011). Migratory ungulates maximize nutritional benefits and minimize energetic costs by timing their seasonal movements across elevational and latitudinal gradients (Albon and Langvatn 1992, Pettorelli et al. 2007, Sawyer and Kauffman 2011, Bischof et al. 2012). By optimizing their seasonal movements and in turn, energetics, migratory ungulates often achieve higher pregnancy rates (Hebblewhite and Merrill 2011), greater body mass (Albon and Langvatn 1992, Hebblewhite and Merrill 2011), and larger population sizes (Fryxell et al. 1988) than resident conspecifics. Despite these benefits, many migratory ungulates are in decline globally (Bolger et al. 2008, Harris et al. 2009). Migration routes and seasonal ranges are threatened by physical barriers (Ben-Shahar 1993, Ito et al. 2008, Sawyer et al. 2013), habitat loss (Serneels and Lambin 2001, Sawyer et al. 2006), overhunting (Milner-Gulland et al. 2001), and climate change (Post and Forchhammer 2008). As a result, the persistence of many migratory populations is uncertain.

Population declines following migration loss have been well documented (Berger 2004, Bolger et al. 2008, Harris et al. 2009). Commonly, animals become restricted to one seasonal range, as was the case for migratory wildebeest *Connochaetes taurinus* in the Serengeti-Mara ecosystem (Serneels and Lambin 2001), zebra *Equus burchellii* and wildebeest in the Kalahari in Botswana (Williamson and Williamson 1985), and hartebeest *Alcelaphus buselaphus* and giraffe *Giraffa camelopardalis* in Lake Nakuru National Park in Kenya (Mwangi 1998). In other cases, migratory populations may become split between two seasonal ranges with some individuals isolated on each (Ito et al. 2008). Migrations may be truncated by land-use changes (Serneels and Lambin 2001), artificial feeding (Jones et al. 2014), or shifting resource

availability that benefits resident strategies (Post and Forchhammer 2008, Middleton et al. 2013). Such disruptions are typically followed by population declines and sometimes extirpation (Williamson and Williamson 1985, Mwangi 1998). In some cases, however, ungulates appear able to adapt to a resident lifestyle and continue to persist on one seasonal range (Ben-Shahar 1993, Bennitt et al. 2016). Unfortunately, we know little about the mechanisms that underpin the ability of some populations to persist and the associated seasonal range attributes or life-history characteristics that support continued survival. Such information would advance our understanding of the ecology and conservation of migration.

Temperate migrations are typified by altitudinal movements from high-elevation summer range to low-elevation winter range (Festa-Bianchet 1988, Albon and Langvatn 1992, Hebblewhite et al. 2006). On winter range, individuals are exposed to cold temperatures, deep snow, and low forage quality (Parker et al. 2009), causing decline in body condition due to loss of body fat and body mass (Festa-Bianchet et al. 1996, Parker et al. 2009). To mediate winter fat loss, migratory ungulates often establish winter ranges at low elevations with less snow, sufficient thermal cover, milder temperatures, greater forage availability, and decreased energetic demands (Albon and Langvatn 1992).

The emergence of highly nutritious vegetation in spring (i.e., high crude protein and digestibility) marks the end of winter fat loss and the beginning of summer fat gain (Parker et al. 2009). These phenological changes in vegetation occur predictably across the landscape due to elevation and topography (Hebblewhite et al. 2008). Migratory ungulates track plant phenology, following the emergence of highly nutritious forage, thus optimizing their forage quality (Hebblewhite et al. 2008, Sawyer and Kauffman 2011, Bischof et al. 2012). Longer green-up durations have been shown to positively influence pregnancy (Middleton et al. 2013) and juvenile survival (Pettorelli et al. 2007) in temperate ungulates. Thus, seasonal access to high-quality forage is widely viewed as the primary fitness benefit of a migratory foraging strategy.

It is reasonable to expect that migratory ungulates will suffer demographic consequences when they lose access to traditional seasonal

ranges. However, population responses to migration disruption and loss have differed widely (Bolger et al. 2008). For example, fencing around Lake Nakuru National Park in Kenya caused local extinction of hartebeest and giraffe (Mwangi 1998). Yet, fencing around a game reserve in South Africa caused initial declines in migratory wildebeest (66%) and zebra (33%) populations, which then stabilized and persisted at lower numbers (Ben-Shahar 1993). The severity of population decline following migration disruption may be mediated by the availability of alternative habitats and foraging strategies. Indeed, recent research has elucidated the diversity in movement and foraging strategies that exist within single ungulate populations (White et al. 2007, Hebblewhite et al. 2008, Middleton et al. 2013, Bennitt et al. 2016). Ungulate populations are often partially migratory with various segments employing different strategies to survive in the same landscape. It is important to identify the foraging strategies that will prevail after migration loss in order to conserve migratory ungulates into the future.

Here, we describe a formerly migratory bighorn sheep population that ceased migrating over 60 yr ago, but continues to persist on its high-elevation summer range year-round in northwest Wyoming (Fig. 1). Historically, bighorn sheep summered at high elevations (2800–3100 m) in the Teton Range and migrated to lower elevations (1900–2300 m) in the surrounding valleys to winter (Whitfield 1983, Fig. 2). Like many mountain ungulates, the Teton bighorn sheep population was likely partially migratory with a small resident segment remaining on high-elevation range year-round (Whitfield 1983). Whitfield (1983) pieced together historical seasonal ranges and movements of Teton bighorn sheep using over 100 historical sheep observation records from trapper journals and letters in the 1800s, early settler accounts from around the turn of the 20th century, and interviews with long-time residents from the early to mid-1900s. During the early 20th century, the cumulative effects of permanent human settlement of the valleys, construction of roads and fences across migration routes, housing development on winter range, and widespread domestic sheep grazing caused bighorn sheep to abandon their historical migration to low-elevation areas (Whitfield 1983). The specific mechanisms behind

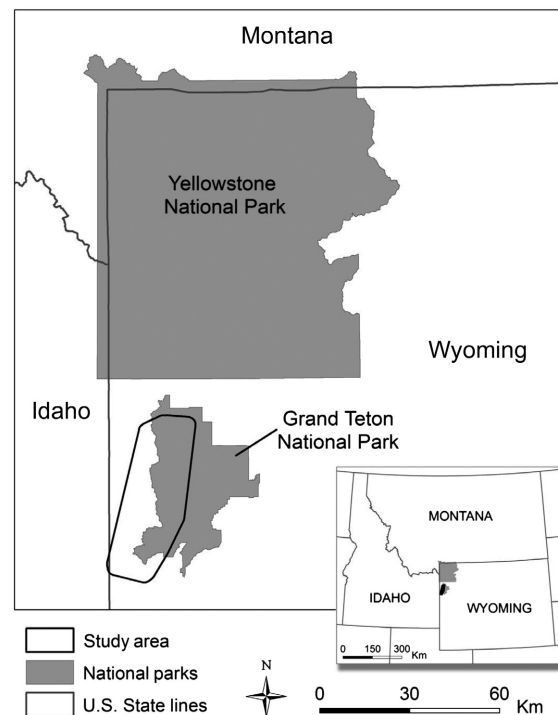


Fig. 1. Study area in the Teton Mountain Range in northwest Wyoming, USA.

this shift are unknown due to lack of rigorous population surveys or research of this herd in the early 1900s (Whitfield 1983). Migratory individuals may have shifted their winter ranges or the migratory segment could have died out over several decades, leaving the entire herd with a resident strategy. Regardless of the mechanism, the population as a whole contracted to its high-elevation summer range (Fig. 2), where it currently persists year-round with approximately 100–125 individuals. There are few examples of populations that have survived after complete migration loss, thus teasing apart why it has persisted is informative for conservation efforts elsewhere.

We hypothesized that the Teton bighorn sheep population has been able to persist after migration loss because of the utilization of alternative foraging strategies (AFS) other than migration from high-elevation summer range to low-elevation winter range. We propose the AFS hypothesis, whereby persistence on one seasonal range after migration loss is possible when individuals either possess or adopt alternative habitat selection or

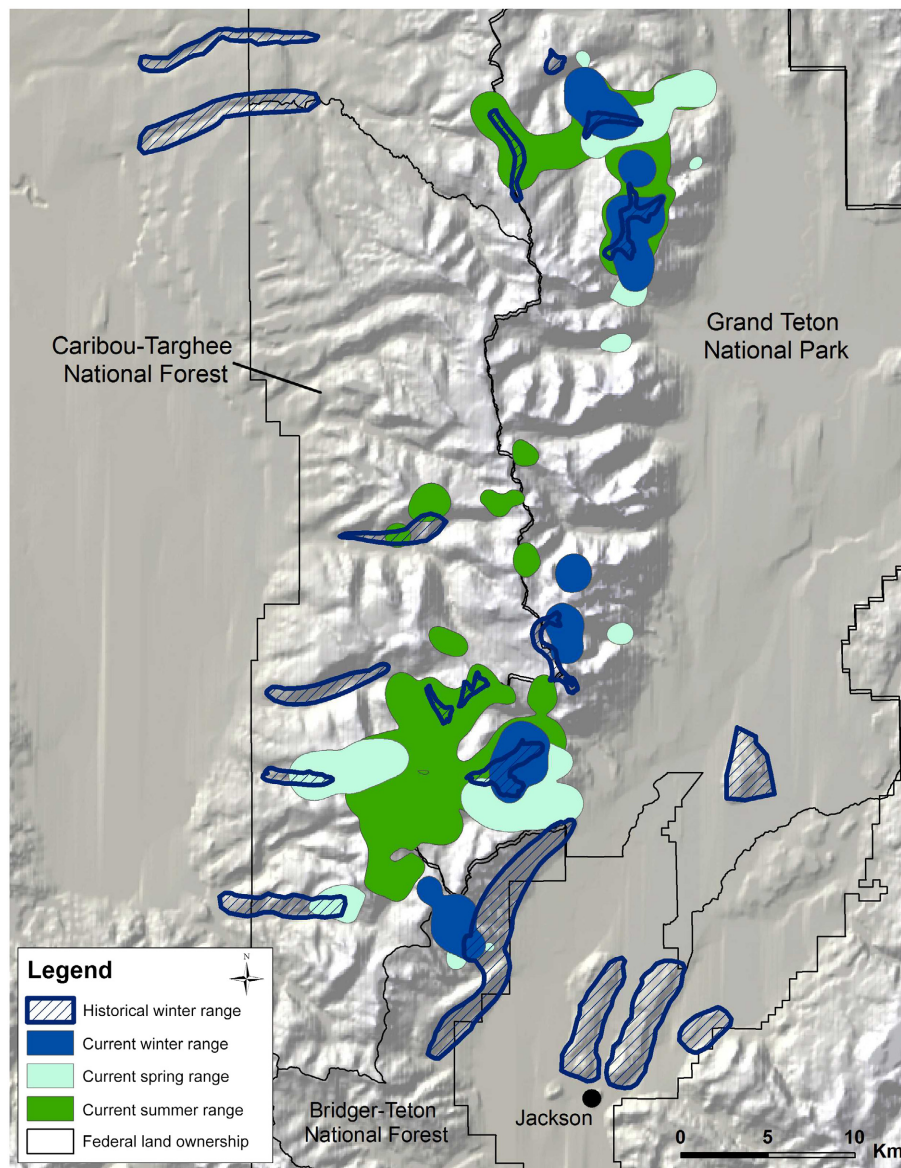


Fig. 2. Historical winter range (pre-1950; hatched blue polygons; adapted from Whitfield 1983) and current (post-1950; solid polygons) winter (blue), summer (dark green), and spring (light green) ranges of the Teton bighorn sheep population.

foraging strategies that allow them to minimize the energetic demands of winter and/or maximize the nutritional gains of summer. To persist, residents must replace the traditional benefits of migration with different foraging strategies to survive within one seasonal range. The AFS Hypothesis is supported if the formerly migratory population (1) exhibits demographic rates consistent with population stability or growth, (2) uses

vegetation phenology in a non-traditional manner so as to exploit spatial and temporal variation in forage quality, (3) selects winter habitat that minimizes energetic demands on a resident winter range, and/or (4) selects summer habitat that maximizes nutritional gain, at the expense of predator avoidance. A better understanding of the seasonal range attributes, life-history characteristics, and types of foraging strategies that

mediate the ability of ungulates to successfully adapt to migration loss will help advance the ecology and conservation of threatened migratory populations.

METHODS

Study area

We studied bighorn sheep habitat selection from February 2008 to July 2010 in the Teton Mountain Range, within the Greater Yellowstone Ecosystem in northwest Wyoming, USA. The study area includes portions of Grand Teton National Park (GTNP), Caribou-Targhee National Forest (CTNF), and Bridger-Teton National Forest (BTNF) (Fig. 1). The town of Jackson, Wyoming, is located 10 km southeast of the study area. The Teton Range is typified by rugged, rocky peaks that rise from foothills at 2000 m to peaks over 4000 m. Higher elevations are comprised of alpine meadows and talus and scree slopes. Mid-elevations are diverse, with mixed conifer forests, mountain shrub communities, and montane grasslands. Lower elevations near the valley floors (historical bighorn sheep winter ranges) are mainly comprised of mixed grassland and sagebrush habitats.

Capture and monitoring

We used helicopter net-gunning to capture 20 female bighorn sheep during February 2008 and eight during March 2009 in the Teton Range. We fitted individuals with store-on-board global positioning system (GPS) collars (model TGW-3500; Telonics, Mesa, Arizona, USA) programmed to acquire a fix every five hours and automatically release after 29 months (for 2008 capture) or 17 months (for 2009 capture). Blood was collected for pregnancy testing, using pregnancy-specific protein B, at the Wyoming State Veterinary Laboratory in Laramie, Wyoming, USA. All animal captures were conducted according to protocols approved by the University of Wyoming's Institutional Animal Care and Use Committee.

We monitored GPS-collared ewes from a fixed-wing aircraft once every month during winter to detect mortality signals. Mortalities were investigated on the ground as soon as possible to determine cause of death. Field teams followed GPS-collared ewes during summers 2008–2010 to monitor summer lamb recruitment.

Seasonal movements

To evaluate how bighorn sheep may exploit vegetation phenology while isolated on one seasonal range, we examined the elevational movements of marked sheep. We extracted the elevation of each GPS-collar location from a 10-m digital elevation model (DEM; U.S. Geological Survey [USGS]). We calculated the average elevation of each sheep by week, and averaged all sheep for each week to develop a year-long elevational movement profile.

We expected that spatial and temporal patterns of vegetation phenology would influence seasonal movements of sheep (Hebblewhite et al. 2008, Sawyer and Kauffman 2011). We calculated the weekly average normalized difference vegetation index (NDVI) within spring (8–31 May)- and winter (15 January–21 February)-use areas from 2008 to 2010 to characterize phenology timing. Use areas were delineated with 97% kernel home ranges from sheep GPS locations (Hawth's Tools version 3.27, Beyer 2004). We downloaded weekly Moderate Resolution Imaging Spectroradiometer (MODIS-TERRA) imagery (National Aeronautics and Space Administration, USA) from 2008 to 2010 and calculated NDVI [(near infrared + red)/(near infrared – red)]. We re-sampled all rasters to 30-m pixels using bilinear interpolation in ESRI ArcGIS 10.0. We clipped rasters to corresponding seasonal-use areas, extracted NDVI values, and calculated weekly NDVI averages.

Seasonal foraging strategies

To evaluate AFS used by bighorn sheep, we evaluated the influence of landscape variables on winter and summer habitat use. We used each GPS-collared sheep in each season as the sampling unit (winter, $n = 23$; summer, $n = 19$) and utilized a discrete choice modeling approach (Manly et al. 2002) to estimate coefficients for each individual. We removed individuals from the analysis that survived for less than one month during either season. Based on observed snow accumulation and melt-out, winter and summer periods were delineated as 15 November–15 April and 15 June–15 September, respectively.

In winter, we evaluated the influence of proximity to rugged escape terrain, proximity to snow-free areas, elevation, solar radiation, tree cover, and slope (Smith et al. 1991, Dicus 2002, DeCesare and Pletscher 2006) on sheep habitat

selection. In summer, we used the same covariates, except we removed proximity to snow-free areas and added proximity to natural mineral licks. We defined winter and summer habitat availability at the home range scale for each sheep using a local convex hull polygon in X Tools Pro 9.0 extension for ArcGIS. Because the majority of collared sheep only utilized either the northern or southern portion of the study area, we chose to evaluate third-order habitat use (Thomas and Taylor 2006) to account for variation in each individual's use and availability.

Habitat covariates and sampling design

Previous work suggests that Teton bighorn sheep seek out snow-free areas (e.g., wind-swept ridges) during winter (S. Cain, Senior Wildlife Biologist, GTNP, *personal communication*). Snow depths at mid- and high elevations in the Teton Range can reach 3.5 m (BTNF, <http://www.jhavalanche.org>), which vastly exceeds the movement capacity of bighorn sheep (Dailey and Hobbs 1989, Smith et al. 1991). Some ridges and slopes, however, are blown free of snow by persistent wind. To spatially delineate these snow-free areas, we developed a new technique utilizing the normalized difference snow index (NDSI) with Landsat satellite imagery from 1993 to 2011 (USGS, <http://glovis.usgs.gov>; see Appendix S1). We analyzed 30 images over this time period and averaged NDSI values across years to develop a map of perennially snow-free areas. These areas only cover 4.2% (55 km²) of the study area, but may represent critical habitat for this population.

Elevation and slope covariates were derived from a 10-m DEM (USGS). Percent tree cover was derived from a 30-m National Land Cover Database for Wyoming (2001). Winter and summer solar radiations were estimated using the Spatial Analyst solar radiation function (ESRI ArcGIS 10; Kumar et al. 1997, Dicus 2002). We combined terrain ruggedness and escape terrain into one variable, defined as "rugged escape terrain" that had slope >30°, terrain ruggedness index >0.001 (Sappington et al. 2007), and patch size ≥1 ha (Dicus 2002, DeCesare and Pletscher 2006). We identified 17 natural mineral lick locations in the study area by observing sheep during summer.

We conducted a Pearson's pairwise correlation analysis before modeling to identify multicollinearities and determine whether any variables should

be excluded from modeling ($|r| > 0.60$). Slope and solar radiation in the summer model had $|r| > 0.66$. We removed the solar radiation variable and retained the slope variable because of its importance to sheep (Shackleton et al. 1999).

We created a sampling grid of 100 × 100 m cells clipped to each sheep's local convex hull polygon for winter and summer. This sampling scale captures biologically important variation in landscape features, while being large enough to model use as a continuous response (Sawyer et al. 2006). We calculated the mean of each covariate for each cell in the sampling grid using the Spatial Analyst zonal statistics tool. We standardized values for each covariate by subtracting the measured value from the mean and dividing by the standard deviation within each sheep's area of availability for each season.

Habitat selection models

The GPS collars produced a relatively low fix success rate during winter (mean 83.4% ± standard error [SE] = 1.3%) and a slightly higher rate during summer (87.5% ± 0.5%), indicating a potential habitat bias in fix locations (Frair et al. 2004, Nielson et al. 2009). To account for this, we used a modified discrete choice resource selection function for GPS fix bias (MDC-RSF) (Nielson et al. 2009). The MDC-RSF simultaneously models resource selection and probability of detection by the GPS collar, given selection (Nielson et al. 2009). We modeled probability of detection as a function of slope and percent tree cover because these landscape features can reduce GPS performance (D'Eon et al. 2002, Frair et al. 2004). We used the MDC-RSF for our winter analysis, but the large home ranges of sheep during summer made the computational time for this analysis untenable. To evaluate the potential bias of not using the MDC-RSF in summer, we compared the MDC-RSF coefficient estimates in winter against a discrete choice RSF (Manly et al. 2002) that did not account for GPS fix bias (Appendix S2). Because we found that coefficient estimates between the two approaches were not different, we proceeded with a discrete choice RSF for our summer analysis. To evaluate significance of habitat coefficients, we calculated mean and 95% confidence intervals for each coefficient using estimates from each sheep (winter, $n = 23$; summer, $n = 19$). Significance of coefficients was

determined based on whether confidence intervals overlapped zero (Marzluff et al. 2004).

To evaluate the spatial distribution of modeled winter and summer habitat, we mapped the predicted probability of bighorn sheep habitat use from each seasonal population-level model over the entire year-round range on a grid of 30 × 30 m cells. The model prediction for each cell was assigned a value of one to seven based on quantiles of the distribution of predictions for each season. We classified these values as highest, high, moderate-high, moderate, low-moderate, low, or lowest probability of sheep use for each season.

Model validation

We validated the winter habitat selection model using bighorn sheep group observations ($n = 137$) from 12 winter aerial surveys of un-collared bighorn sheep from 1991 to 2010 conducted by the Wyoming Game and Fish Department (WGFD) and GTNP, and winter observations ($n = 329$) from 54 aerial surveys of very high frequency (VHF)-instrumented bighorn sheep from 1994 to 2000 conducted by GTNP. We calculated the proportion of survey observations located within each range of predicted probability of use from the winter model. Due to a paucity of summer bighorn sheep observations, we were unable to validate the summer model using these methods.

Foraging activity budgets

We investigated summer foraging activity budgets to determine whether Teton sheep increased their foraging rates at the expense of vigilance compared to published rates for migratory sheep. During June–August 2008–2010, we collected 15-min focal-animal observations on collared and un-collared adult ewes during active foraging bouts (Festa-Bianchet 1988, Frid 1997). We did not initiate observations when animals were bedded. We classified behaviors as feeding, licking (at mineral lick), vigilant, moving, standing, or bedded. Feeding was defined as when a sheep's head was below shoulder level and it was clipping vegetation with its mouth. Vigilant behavior was defined as when a sheep had its head above shoulder level, was standing but not moving, and was surveying its surroundings with its attention fixed on the environment. Foraging bouts included short periods of standing or moving between forage patches.

Recording sessions either ended after 15 min or when an animal stopped foraging behavior for longer than 1 min (i.e., by bedding down or moving out of sight). We also recorded reproductive status of the ewe based on lamb nursing behavior and compared mean proportion of time spent feeding and vigilant for reproductive and non-reproductive ewes using a Student's t test.

RESULTS

Population status

Seventeen (90%) of 19 adult ewes were pregnant at capture in 2008. One ewe was a yearling at time of capture and not included. Eight (100%) of eight adult ewes were pregnant at capture in 2009. Different animals were captured in 2008 and 2009. The average age of bighorn sheep at time of capture was 4.8 yr (range = 1.8–8.8 yr).

Average summer lamb recruitment for GPS-collared ewes was 55%. This did not vary dramatically between years: 56% of adult GPS-collared ewes had lambs that survived through summer 2008 ($n = 18$ ewes), 57% in summer 2009 ($n = 21$ ewes), and 50% in summer 2010 ($n = 14$ ewes).

The proportion of GPS-collared ewes that died was 30% (six of 20 ewes) in study year 1 (February 2008–February 2009) and 9% (two of 22 ewes) in study year 2 (March 2009–March 2010). No sheep died from April 2010 until the GPS collars released in July 2010. Of the eight GPS-collared sheep that died during the study, four died from avalanches, one from mountain lion predation, and three from unknown causes. Notably, half of the mortalities were caused by avalanches and all during study year 1.

Abbreviated migration

Despite being residents, Teton sheep underwent distinct seasonal elevational movements. Sheep spent most of the summer at approximately 3000 m, descended to 2700 m during autumn, ascended to 3000–3200 m for the winter, and then made an abrupt descent to 2600 m in the spring, before slowly moving back up to their summering elevations (Fig. 3). Overall, sheep descend approximately 500 m and 10 km in distance in the spring. We termed this newly described movement strategy “abbreviated migration.” Abbreviated migration appears to be synchronized with

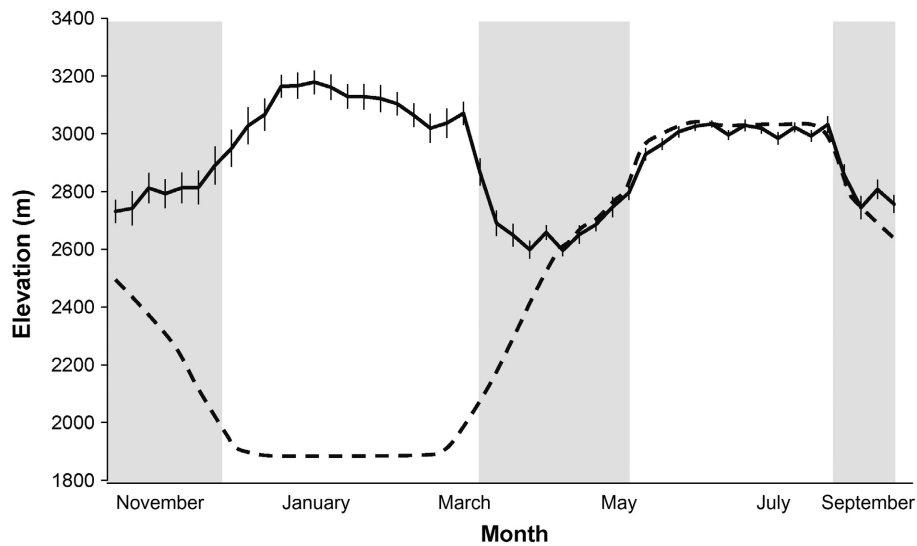


Fig. 3. Average weekly elevation of global positioning system-collared bighorn sheep (mean $\pm$ standard error; solid line; from this study) and approximate historical elevational movements of bighorn sheep (dashed line; adapted from Whitfield 1983). Transparent gray boxes depict historical spring and autumn migration periods.

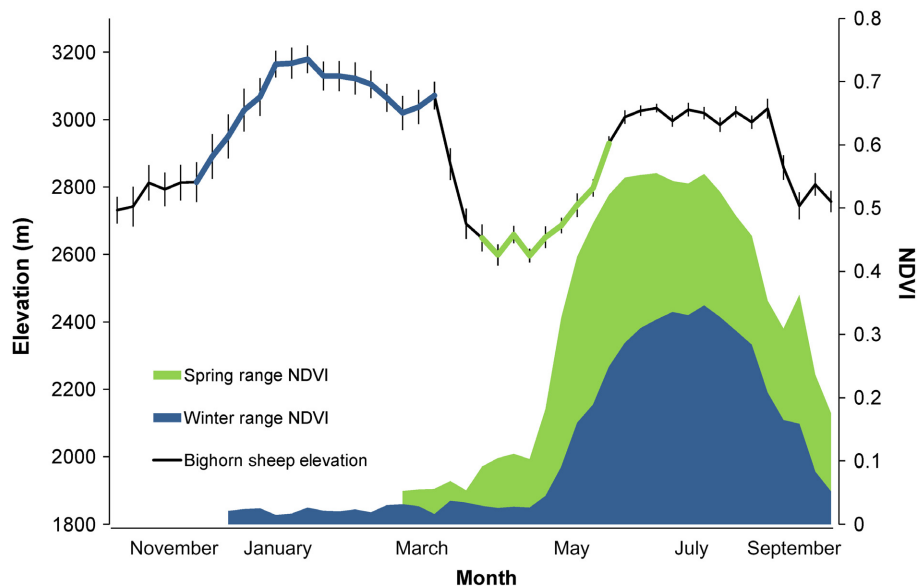


Fig. 4. Average weekly elevation of global positioning system-collared bighorn sheep (mean $\pm$ standard error; line) and weekly average normalized difference vegetation index (NDVI) for spring (green area) and winter (blue area) bighorn sheep ranges. Colored portions of the line correspond to when bighorn sheep are on winter and spring ranges.

vegetation phenological changes (Fig. 4). Vegetation emergence begins in early May on spring ranges at mid-elevations, while emergence does not begin until early June on high-elevation winter and summer ranges, over one month later (Fig. 4).

Abbreviated migration allows sheep to access highly nutritious forage approximately one month before it becomes available in the high peaks (Fig. 4). Sheep also descend (~300 m) to mid-elevations again in autumn before ascending to their

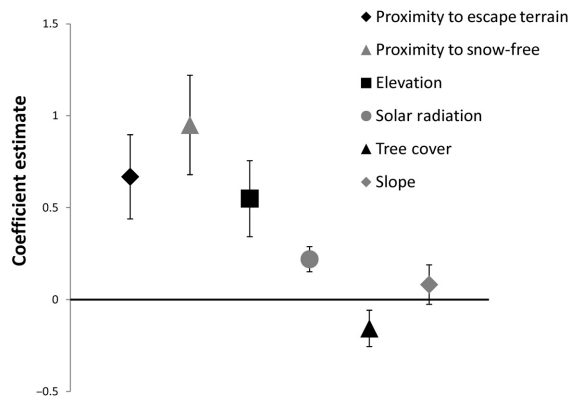


Fig. 5. Averaged coefficients for the winter population-level resource selection function. Bars represent 95% confidence intervals for each coefficient, based on individual model ($n = 23$) estimates. Coefficients with bars that do not overlap zero indicate significant selection (+) or avoidance (-).

high-elevation winter range (Fig. 4), a movement that coincides with the first significant snowfall in the high peaks in early October.

Winter habitat use

Teton sheep showed significant use of areas in close proximity to rugged escape terrain ($\beta = 0.667$; Fig. 5), with high solar radiation ($\beta = 0.220$; Fig. 5) and with minimal to no tree cover ($\beta = -0.157$; Fig. 5) in winter. Teton sheep selected for high elevations ($\beta = 0.549$; Fig. 5) and did not exhibit significant use of steep slopes (Fig. 5). We also found that sheep were tightly associated with consistently snow-free areas ($\beta = 0.949$; Fig. 5). Therefore, winter habitat is typically areas at high elevation on windswept slopes and ridges, near rugged escape terrain, on southerly aspects, with minimal tree cover. The predicted probability map reveals the highest quality winter habitat occurs as fragmented patches on the landscape, surrounded by a matrix of unsuitable areas (Fig. 6). Notably, we also found that sheep wintered at higher elevations than they summered (Fig. 3).

Model validation using past flight locations for un-collared or VHF-collared bighorn sheep showed that 82% of locations ($n = 383$) occurred within areas classified as “very high” predicted probability with our winter MDC-RSF, and an additional 11% ($n = 51$) occurred within “high”

predicted probability. Overall, 93% ($n = 434$) of bighorn sheep groups were observed within the top two probability classifications.

Summer habitat use

Teton sheep showed significant use of steep slopes ($\beta = 0.516$; Fig. 7), areas with minimal to no tree cover ($\beta = -0.451$; Fig. 7), and high-elevation habitats ($\beta = 0.336$; Fig. 7) in summer. Contrary to our prediction, sheep were closely associated with rugged escape terrain ($\beta = 0.95$; Fig. 7), suggesting that ewes do not forego predator avoidance to increase summer foraging. Although some individual ewes exhibited selection for areas in close proximity to mineral licks, this covariate was not significant in the population-level model (Fig. 7). Unlike winter, summer habitat is abundant and well connected throughout the study area (Appendix S3).

Foraging activity budgets

We collected a total of 1125 m of foraging activity observations ($n = 75$) of adult ewes over three

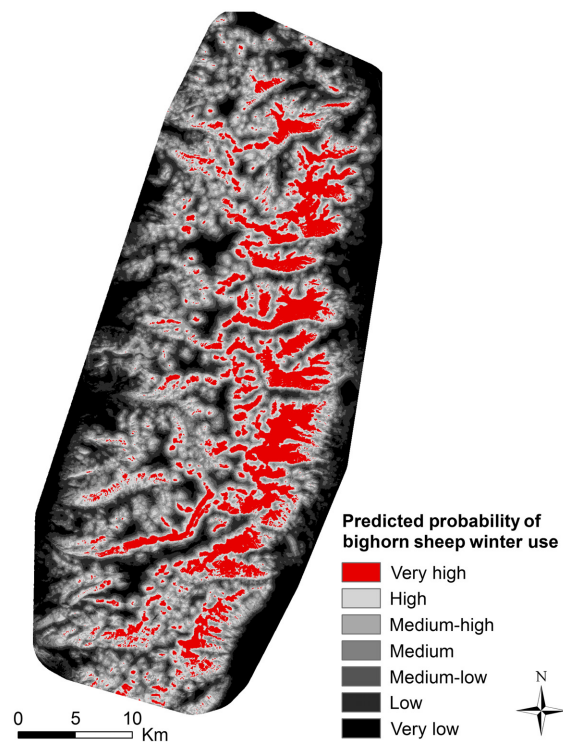


Fig. 6. Predicted probabilities of bighorn sheep use during winter in the Teton Range from very low (dark gray) to very high (red) categories.

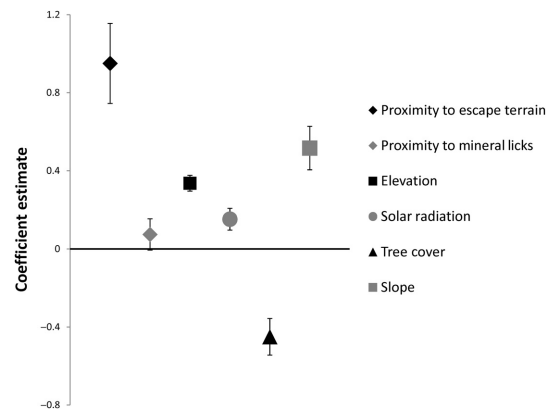


Fig. 7. Averaged coefficients for the summer population-level resource selection function. Bars represent 95% confidence intervals for each coefficient, based on individual model ($n = 19$) estimates. Coefficients with bars that do not overlap zero indicate significant selection (+) or avoidance (-).

summers. Some ewes were observed more than once. We found no difference in average proportion of time spent feeding between reproductive (mean $0.72 \pm \text{SE } 0.03$; $n = 37$) and non-reproductive ewes (0.63 ± 0.05 ; $n = 27$; $P = 0.108$) or time spent vigilant (0.11 ± 0.02 and 0.13 ± 0.02 , respectively; $P = 0.373$); therefore, we pooled all observations for analysis. The average percent of time spent feeding during foraging bouts was 69.9% ($\pm \text{SE } 2.5\%$) and time spent vigilant was 10.9% ($\pm 1.2\%$). Time budgets were similar to those reported for migratory sheep (Festa-Bianchet 1988, Ruckstuhl et al. 2003).

DISCUSSION

Populations typically decline when migration is lost, but we know little about the ability of migratory ungulates to adapt and persist after becoming resident. We proposed the AFS hypothesis as a framework for understanding how ungulate populations may cope with migration loss. We found equivocal evidence for our first prediction that Teton sheep would exhibit demographic rates consistent with persistence. Pregnancy and summer lamb recruitment were adequate for population stability (Shackleton et al. 1999); however, we observed high ewe mortality during some winters. Nevertheless, this herd has survived for over 60 yr following

migration loss, suggesting viable demographic rates over the long term. The second prediction that sheep would make use of vegetation phenological gradients within their resident range was supported. Teton sheep underwent a newly described movement strategy that we termed “abbreviated migration,” whereby they rapidly descended from the high peaks in spring to access newly emergent forage and then tracked its phenology back upslope throughout the growing season (Fig. 4). We found clear support for our third prediction that sheep would utilize winter habitat selection strategies to subsist on non-traditional, high-elevation winter range. Sheep sought out high peaks and ridges that were consistently snow-free, in contrast to the typical pattern of seeking low-elevation habitats during winter (Festa-Bianchet 1988, Fig. 5). Finally, we found no support for our fourth prediction that sheep would alter summer habitat selection strategies to maximize energy intake at the expense of predator avoidance. Summer habitat use (Fig. 7) and foraging time budgets were similar to those reported for migratory sheep (Festa-Bianchet 1988, Ruckstuhl et al. 2003). Our results suggest that Teton sheep have persisted by using AFS to cope with migration loss by selecting high-elevation, windswept ridges in winter and maximizing access to high-quality forage through abbreviated migration.

Population persistence

Demographic rates of the Teton sheep population are largely consistent with a stable, although small population. Annual summer lamb recruitment (50–57%) was within the range reported by previous studies for stable populations (Shackleton et al. 1999). Although we did not monitor lamb survival over winter, WGFD winter aerial surveys indicate lamb recruitment is adequate to sustain a stable population (30 lambs per 100 ewes; WGFD 2010). The proportion of ewes that died during each study year (30% and 9%) was average to high compared to other studies that ranges from 6% to 11% (Hengel et al. 1992, Jorgenson et al. 1997, Singer et al. 2000). In addition, we found that stochastic environmental events (avalanches) contributed to half of recorded mortalities over the course of the study. All avalanche mortalities occurred during one study year when the

snowpack was especially unstable, resulting in a loss of 20% of the GPS-collared ewes at the time (four of 20 ewes). Although our sample size was low, these results highlight the concern that a series of stochastic events could threaten the future viability of this small, isolated population (Berger 1990).

Winter

Having lost their low-elevation winter range, Teton sheep now seek out high-elevation, wind-swept ridgelines and southerly aspects that are relatively snow-free. The patchiness of wintering areas (Fig. 6) causes bighorn sheep to be confined to small home ranges among the high peaks during the winter. The degree to which the use of these snow-free patches offsets the cost of wintering on resident winter range is unknown. Forage quantity and quality are marginal, mostly comprised of lichens and sparse alpine forbs and grasses. It is possible, however, that factors which increase energetic demands and fat loss, such as snow depth, may be more limiting than poor forage quality during winter. Dailey and Hobbs (1989) estimated that the energetic cost to bighorn sheep moving through snow increased exponentially as snow depth increased, doubling at 60% of chest height and quadrupling at 200% chest height. In the Teton Range, where snow depths commonly reach 3.5 m, we suspect the primary benefit of using windswept, high-elevation ridgelines is a reduction in energetic costs and over-winter fat loss (Parker et al. 2009), rather than access to marginal forage.

Summer

We predicted that to compensate for wintering on non-traditional, resident winter range, Teton sheep would maximize summer foraging by foregoing predator avoidance. However, we were unable to detect any differences in summer foraging strategies or habitat selection compared to migratory sheep (Festa-Bianchet 1988, Frid 1997, Ruckstuhl et al. 2003). Vigilance and feeding rates were similar to those reported for migratory bighorn sheep (Festa-Bianchet 1988, Ruckstuhl et al. 2003), Stone sheep (*Ovis dalli stonei*; Walker et al. 2006), and Dall sheep (*Ovis dalli*; Frid 1997).

Summer and autumn accumulation of body fat and protein play a critical role in ungulate demography (Cook et al. 2004, Tollefson et al. 2010, Middleton et al. 2013, Monteith et al. 2013). It is possible that typical bighorn sheep summer foraging strategies are already fully optimized to maximize fat gain, thus constraining the foraging effort of Teton bighorn sheep, at least at the scales we investigated. Ungulates can increase their bite rate, alter diet selection, and lengthen rumination time to enhance nutrient absorption; however, total forage intake is ultimately limited by the rumination process (Hamel and Côté 2008). That Teton sheep achieved pregnancy rates over 90% and average summer lamb recruitment of 55% suggests that energy gain during summer is sufficient to overcome winter deficits and support reproduction. It seems likely that by employing typical sheep foraging strategies during summer, Teton sheep are already fully optimized to maximize fat gain. Thus, ungulates may be constrained in their ability to increase foraging effort to offset the costs of migration loss.

Abbreviated migration

We found that Teton sheep underwent distinct seasonal elevational movements, despite being confined to their resident range, a behavior we termed abbreviated migration. Abbreviated migration is synchronized with mountain vegetation phenology, similar to migratory ungulates that move from low to high elevation in the spring following vegetation emergence (Albon and Langvatn 1992, Sawyer and Kauffman 2011, Bischof et al. 2012; Fig. 4). Teton sheep, however, begin spring in the high peaks and then descend approximately 500 m and 10 km in distance to seek the first vegetation emergence at mid-elevations (Fig. 4). This movement allows them to access highly nutritious forage (Albon and Langvatn 1992, Hamel et al. 2009b) approximately one month before it becomes available in the high peaks (Fig. 4). Spring nutritional quality enhances neonate growth and survival and life-long fitness in temperate ungulates (Pettorelli et al. 2007, Hamel et al. 2009a), indicating these spring movements may be critical to reproduction and the annual foraging budget of Teton sheep. In a sense, abbreviated migration

reconnects Teton sheep with a portion of their historical migration and is likely an important adaptation to migration loss.

Sheep also descend (~300 m) to mid-elevations again in autumn before ascending to their high-elevation winter range (Fig. 4), a movement that coincides with the first significant snowfall in the high peaks in early October and is likely an attempt to prolong their access to summer forage. Once snow begins to accumulate at mid-elevations in the Teton Range, however, sheep ascend to high-elevation, windswept ridges to spend the winter. Snow depths at mid-elevations reached 40 cm by early December in both years of this study (Natural Resources Conservation Service, Snow Telemetry Data, www.wcc.nrcs.usda.gov/snow), which seemed to trigger sheep movement from autumn ranges to higher winter ranges (Appendix S4). The drivers of autumn migration in temperate ungulates have received less attention in the scientific literature than those of spring, especially for ungulates that make non-typical autumn migrations to higher elevations. However, previous studies have demonstrated that autumn migration patterns are dictated by the trade-off of prolonging access to forage while avoiding increasing snow depths (Monteith et al. 2011). In our study area, snow depth appeared to have a major influence on bighorn sheep distribution in autumn (Appendix S4). However, spatial snow depth data were not available for our entire study area, precluding an analysis of autumn elevational movements similar to our spring analysis. Additional research into the drivers behind such movements, particularly in resident mountain ungulate populations, would enhance our understanding of the relevance of autumn habitat.

Our study highlights the importance of evaluating past and future migratory ungulate declines in the context of available alternative foraging and movement strategies. While Teton sheep currently persist as a resident herd living year-round at high elevations, the mechanisms by which this strategy came to dominate the herd are unclear. Historical observation indicates that sheep used to make more traditional migrations to low-elevation winter range (Whitfield 1983). However, a lack of rigorous field observations and research in this herd during the period

of migration loss makes it impossible to know how the shift from migratory to resident occurred. Some sheep may have discovered the resident strategy as migrations became more difficult, a shift that would have required multiple generations of both behavioral and demographic change. The resident strategy likely existed historically as a small fraction of the herd (Whitfield 1983). Indeed, recent research has elucidated the diversity in migration and foraging strategies that exist within single ungulate populations (White et al. 2007, Hebblewhite et al. 2008, Middleton et al. 2013, Bennitt et al. 2016), and populations are often partially migratory. It is possible that sheep from the migratory segment died out in the early 20th century and today's Teton sheep are descendants of an historically resident segment. Additional research and long-term monitoring efforts of imperiled migratory ungulate herds may help shed light on these questions in the future. Regardless of the exact mechanism that led to Teton sheep becoming entirely resident, this work highlights the conservation value of retaining a diversity of migration, movement, and seasonal foraging strategies within populations. Bennitt et al. (2016) found that resident Cape buffalo (*Syncerus caffer caffer*) exploit habitat heterogeneity within their home ranges and animals achieve similar reproductive productivity and body condition to their migratory counterparts. The existence of different strategies to exploit available habitats can facilitate population-level flexibility in adapting to changing conditions.

Relatedly, the severity of population decline following migration loss may depend in part upon the seasonal range where the population becomes isolated (Sutherland 1996, Bolger et al. 2008). Teton sheep were isolated to their more productive summer range. Isolation to a less productive winter range may have yielded a different outcome for the population. For example, Voeten et al. (2010) found that forage quality on dry season ranges would fail to meet the nutritional requirements of lactation if wildebeest were confined to that less productive range year-round. We suggest that the availability of AFS will ultimately determine population performance following migration disruption or loss, regardless of which seasonal range is lost.

Management implications

While many studies have linked ungulate population declines to migration disruption or loss, very few have explored the underlying factors that determine whether a population ultimately perishes or persists. As anthropogenic pressures increase across landscapes, understanding the circumstances under which a migratory population may or may not be able to survive is paramount for planning, managing, and sustaining these populations into the future. Our study suggests that the availability of AFS has allowed the Teton sheep population to persist despite migration loss, albeit at low numbers. Understanding the diverse foraging strategies of migratory ungulates, and attempting to predict potential alternative behaviors and habitats in the event of migration loss, is key to successfully managing populations into the future. Recognizing the importance of conserving multiple population segments that employ diverse strategies may be essential to maintaining resilience in the face of migration loss.

This study provides an example of how a migratory population has continued to endure as resident. In the case of Teton sheep, the population has utilized winter foraging strategies to minimize energy expenditure and an abbreviated migration to lengthen their access to high-quality forage. The impacts of migration loss have been mitigated to some extent by AFS. These findings will help wildlife and land managers focus conservation efforts on the population's limited high-elevation winter habitat and also improve the availability and quality of mid-elevation habitats necessary for abbreviated migration. Sustaining migratory ungulate populations into the future will likely require a deeper understanding of the underlying benefits of migration and the extent to which available AFS may alleviate the consequences of migration loss.

ACKNOWLEDGMENTS

Funding was provided by Wyoming Governor's Big Game License Coalition, Wyoming Wild Sheep Foundation, National Park Service, BTNE, WGFD, Teton Conservation District, GTNP Foundation,

Greater Yellowstone Coordinating Committee, University of Wyoming—National Park Service AMK Research Station, and Eastern Chapter of the Wild Sheep Foundation. Significant in-kind support was provided by staff at GTNP, WGFD, BTNE, and CTNE. We thank the many field assistants who helped with the project. We thank Leading Edge Aviation and Sky Aviation for assistance with sheep captures and telemetry flights. We thank R. Nielson and H. Sawyer for their assistance with developing resource selection models.

LITERATURE CITED

- Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* 65:502–513.
- Bennitt, E., M. C. Bonyongo, and S. Harris. 2016. Effects of divergent migratory strategies on access to resources for Cape buffalo (*Syncerus caffer caffer*). *Journal of Mammalogy* 97:1682–1698.
- Ben-Shahar, R. 1993. Does fencing reduce the carrying capacity for populations of large herbivores? *Journal of Tropical Ecology* 9:249–253.
- Berger, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology* 4:91–98.
- Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. *Conservation Biology* 18:320–331.
- Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. Version 3.27. <http://www.spatialecology.com/htools>
- Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmerman, B. Van Moorter, and A. Myrsterud. 2012. A migratory northern ungulate in the pursuit of spring: Jumping of surfing the green wave? *American Naturalist* 180:407–424.
- Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters* 11:63–77.
- Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs* 155:1–61.
- Dailey, T. V., and N. T. Hobbs. 1989. Travel in alpine terrain: energy expenditures for locomotion by mountain goats and bighorn sheep. *Canadian Journal of Zoology* 67:2368–2375.
- DeCesare, N. J., and D. H. Pletscher. 2006. Movements, connectivity, and resource selection of Rocky Mountain bighorn sheep. *Journal of Mammalogy* 87:531–538.

- D'Eon, R. G., R. Serroya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin* 30:430–439.
- Dicus, G. 2002. GIS-based habitat models for bighorn sheep winter range in Glacier National Park, Montana. Pages 110–127 in G. C. Brundige, editor. *Proceedings of the 13th Biennial Symposium*, Rapid City, South Dakota, April 23–27, 2002. Northern Wild Sheep and Goat Council, Cody, Wyoming, USA.
- Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia* 75:580–586.
- Festa-Bianchet, M., J. T. Jorgenson, W. J. King, K. G. Smith, and W. D. Wishart. 1996. The development of sexual dimorphism: seasonal and lifetime mass changes of bighorn sheep. *Canadian Journal of Zoology* 74:330–342.
- Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* 41:201–212.
- Frid, A. 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. *Animal Behaviour* 53:799–808.
- Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? *American Naturalist* 131:781–798.
- Fryxell, J. M., and A. R. E. Sinclair. 1988. Causes and consequences of migration by large herbivores. *Trends in Ecology and Evolution* 3:237–241.
- Hamel, S., and S. D. Côté. 2008. Trade-offs in activity budget in an alpine ungulate: contrasting lactating and nonlactating females. *Animal Behaviour* 75:217–227.
- Hamel, S., J. Gaillard, M. Festa-Bianchet, and S. D. Côté. 2009a. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology* 90:1981–1995.
- Hamel, S., M. Garel, M. Festa-Bianchet, J. Gaillard, and S. D. Côté. 2009b. Spring normalized difference vegetation index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. *Journal of Applied Ecology* 46:582–589.
- Harris, G., S. Thirgood, J. G. C. Hopcraft, J. P. G. M. Cromsigt, and J. Berger. 2009. Global decline in aggregated migrations of large terrestrial animals. *Endangered Species Research* 7:55–76.
- Hebblewhite, M., and E. H. Merrill. 2007. Multiscale wolf predation risk for elk: Does migration reduce risk? *Oecologia* 152:377–387.
- Hebblewhite, M., and E. H. Merrill. 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage-predation tradeoffs. *Oikos* 120:1860–1870.
- Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs* 78:141–166.
- Hebblewhite, M., E. H. Merrill, L. E. Morgantini, C. A. White, J. R. Allen, E. Bruns, L. Thurston, and T. E. Hurd. 2006. Is the migratory behavior of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. *Wildlife Society Bulletin* 34:1280–1294.
- Hengel, D. A., S. H. Anderson, and W. G. Hepworth. 1992. Population dynamics, seasonal distribution and movement patterns of the Laramie Peak bighorn sheep herd. Pages 83–96 in J. Emmerich and W. G. Hepworth, editors. *Proceedings of the 8th Biennial Symposium*, Cody, Wyoming, April 27–May 1, 1992. Northern Wild Sheep and Goat Council, Cody, Wyoming, USA.
- Ito, T. Y., A. Okada, B. Buuveibaatar, B. Lhagvasuren, S. Takatsuki, and A. Tsunekawa. 2008. One-sided barrier impact of an international railroad on Mongolian gazelles. *Journal of Wildlife Management* 72:940–943.
- Jones, J. D., M. J. Kauffman, K. L. Monteith, B. M. Scurlock, S. E. Albeke, and P. C. Cross. 2014. Supplemental feeding alters migration of a temperate ungulate. *Ecological Applications* 24:1769–1779.
- Jorgenson, J. T., M. Festa-Bianchet, J. Gaillard, and W. D. Wishart. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology* 78:1019–1032.
- Kumar, L., A. K. Skidmore, and E. Knowles. 1997. Modelling topographic variation in solar radiation in a GIS environment. *International Journal of Geographical Information Science* 11:475–497.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource selection by animals: statistical design and analysis for field studies*. Kluwer Academic Publishers, Boston, Massachusetts, USA.
- Marzluff, J. M., J. J. Millsaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. *Ecology* 85:1411–1427.
- Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology* 94:1245–1256.

- Milner-Gulland, E. J., M. V. Kholodova, A. Beke-
nov, O. M. Bukreeva, I. A. Grachev, L. Amgan-
lan, and A. A. Lushchekina. 2001. Dramatic
declines in saiga antelope populations. *Oryx* 35:
340–345.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M.
Pierce, M. M. Conner, R. W. Klaver, and
R. T. Bowyer. 2011. Timing of seasonal migration
in mule deer: effects of climate, plant phenol-
ogy, and life-history characteristics. *Ecosphere* 2:
art 47.
- Monteith, K. L., T. R. Stephenson, V. C. Bleich, M. M.
Conner, B. M. Pierce, and R. T. Bowyer. 2013. Risk-
sensitive allocation in seasonal dynamics of fat and
protein reserves in a long-lived mammal. *Journal*
of Animal Ecology 82:377–388.
- Mwangi, E. M. 1998. Large herbivore dynamics in the
face of the insularization of Lake Nakuru National
Park, Kenya. *African Journal of Ecology* 36:276–
279.
- Nielson, R. M., B. F. J. Manly, L. L. McDonald, H. Saw-
yer, and T. L. McDonald. 2009. Estimating habitat
selection when GPS fix success is less than 100%.
Ecology 90:2956–2962.
- Parker, K. L., P. S. Barboza, and M. P. Gillingham.
2009. Nutrition integrates environmental responses
of ungulates. *Functional Ecology* 23:57–69.
- Pettorelli, N., F. Pelletier, A. von Hardenberg,
M. Festa-Bianchet, and S. D. Côté. 2007. Early onset
of vegetation growth vs. rapid green-up: impacts
on juvenile mountain ungulates. *Ecology* 88:
381–390.
- Post, E., and M. C. Forchhammer. 2008. Climate
change reduces reproductive success of an Arctic
herbivore through trophic mismatch. *Philosophical*
Transactions of the Royal Society of London B:
Biological Sciences 363:2369–2375.
- Ruckstuhl, K. E., M. Festa-Bianchet, and J. T. Jorgen-
son. 2003. Bite rates in Rocky Mountain bighorn
sheep (*Ovis canadensis*): effects of season, age, sex
reproductive status. *Behavioral Ecology and Socio-*
biology 54:167–173.
- Sappington, J. M., K. M. Longshore, and D. B. Thomp-
son. 2007. Quantifying landscape ruggedness for
animal habitat analysis: a case study using bighorn
sheep in the Mojave Desert. *Journal of Wildlife*
Management 71:1419–1426.
- Sawyer, H., and M. J. Kauffman. 2011. Stopover ecol-
ogy of a migratory ungulate. *Journal of Animal*
Ecology 80:1078–1087.
- Sawyer, H., M. J. Kauffman, A. D. Middleton, T. A.
Morrison, R. M. Nielson, and T. B. Wyckoff. 2013.
A framework for understanding semi-permeable
barrier effects on migratory ungulates. *Journal of*
Applied Ecology 50:68–78.
- Sawyer, H., R. M. Nielson, F. Lindzey, and L. L.
McDonald. 2006. Winter habitat selection of mule
deer before and during development of a natural
gas field. *Journal of Wildlife Management* 70:
396–403.
- Serneels, S., and E. R. Lambin. 2001. Impact of land-
use changes on wildebeest migration in the north-
ern part of the Serengeti–Mara ecosystem. *Journal*
of Biogeography 28:391–407.
- Shackleton, D. M., C. C. Shank, and B. M. Wikeem.
1999. Natural history of Rocky Mountain and
California bighorn sheep. Pages 78–138 in
R. Valdez and P. R. Krausman, editors. *Mountain*
sheep of North America. The University of Arizona
Press, Tucson, Arizona, USA.
- Singer, F. J., E. Williams, M. W. Miller, and L. C.
Zeigenfuss. 2000. Population growth, fecundity,
and survivorship in recovering populations of big-
horn sheep. *Restoration Ecology* 8:75–84.
- Smith, T. S., J. T. Flinders, and D. S. Winn. 1991. A
habitat evaluation procedure for Rocky Mountain
bighorn sheep in the Intermountain West. *Great*
Basin Naturalist 51:205–225.
- Sutherland, W. J. 1996. Predicting the consequences of
habitat loss for migratory populations. *Proceedings*
of the Royal Society of London B: Biological
Sciences 263:1325–1327.
- Thomas, D. L., and E. J. Taylor. 2006. Study designs
and tests for comparing resource use and
availability II. *Journal of Wildlife Management*
70:324–336.
- Tollefson, T. N., L. A. Shipley, W. L. Myers, D. H. Keis-
ler, and N. Dasgupta. 2010. Influence of summer
and autumn nutrition on body condition and
reproduction in lactating mule deer. *Journal of*
Wildlife Management 74:974–986.
- Voeten, M. M., C. A. D. M. van de Vijver, H. Olff, and
F. van Landgevelde. 2010. Possible causes of
decreasing migratory ungulate populations in an
East African savannah after restrictions in their
seasonal movements. *African Journal of Ecology*
48:169–179.
- Walker, A. B. D., K. L. Parker, and M. P. Gillingham.
2006. Behaviour, habitat associations, and intrasex-
ual differences of female Stone's sheep. *Canadian*
Journal of Zoology 84:1187–1201.
- WGFD [Wyoming Game and Fish Department]. 2010.
Job completion report for the Targhee bighorn
sheep herd. Pages 187–198 in *Jackson Region:*

- Annual Big Game Herd Unit Reports 2010. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.
- White, P. J., T. L. Davis, K. K. Barnowe-Meyer, R. L. Crabtree, and R. A. Garrott. 2007. Partial migration and philopatry of Yellowstone pronghorn. *Biological Conservation* 135:502–510.
- Whitfield, M. B. 1983. Bighorn sheep history, distributions and habitat relationships in the Teton Mountain Range, Wyoming. Thesis. Idaho State University, Pocatello, Idaho, USA.
- Williamson, D., and J. Williamson. 1985. Botswana's fences and the depletion of Kalahari wildlife. *Parks* 10:5–7.

DATA ACCESSIBILITY

Bighorn sheep GPS-collar data are available for request through the Wyoming Migration Initiative website: <http://migrationinitiative.org>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1855/full>