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The persistence of many migratory ungulate populations worldwide is threatened due to anthropogenic impacts to seasonal ranges and migration routes. Very little is known about the ability of migratory ungulates to adapt to migration disruption or loss. We proposed the Alternative Foraging Strategies Hypothesis (AFSH) as a framework for identifying various seasonal behavioral strategies that ungulates may use to cope with migration loss. We tested the AFSH using the formerly migratory Teton bighorn sheep population in northwest Wyoming, which ceased migrating over 60 years ago, but has persisted as resident. We used global positioning system (GPS) data to evaluate winter and summer habitat selection and seasonal elevational movements for 28 adult female bighorn sheep (*Ovis canadensis*) from 2008-2010. Resource selection functions revealed that Teton bighorn sheep have altered their 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. We also investigated the long-term behavioral responses of bighorn sheep to backcountry skiing and snowboarding, which pose an additional challenge to surviving in their new high elevation habitats. We found that bighorn sheep avoided areas of backcountry recreation, even if those areas were otherwise relatively high quality habitat. Avoidance behavior resulted in up to a 30% reduction in available high quality habitat for some individuals. Bighorn sheep avoided areas with both low and high recreation use. Individual bighorn sheep

exposed to high levels of recreation exhibited increased daily movement rates and home range sizes compared to sheep exposed to low or no recreation. These results reveal that bighorn sheep appear to be sensitive to forms of recreation which people largely perceive as having minimal impact to wildlife, such as backcountry skiing. The identification of alternative foraging strategies, the habitats that support them and the additional challenges to ungulates after migration loss, such as human recreation, can help reveal the underlying benefits of migration and help conserve ungulate populations after migration loss.

SEASONAL HABITAT SELECTION AND IMPACTS OF BACKCOUNTRY RECREATION ON A FORMERLY MIGRATORY BIGHORN SHEEP POPULATION IN NORTHWEST WYOMING, USA

by
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CHAPTER I: ALTERNATIVE FORAGING STRATEGIES ENABLE A BIGHORN SHEEP POPULATION TO PERSIST AFTER MIGRATION LOSS

ABSTRACT

The persistence of many migratory ungulate populations worldwide is threatened due to anthropogenic impacts to seasonal ranges and migration routes. Very little is known about the ability of migratory ungulates to adapt to migration disruption or loss. In many cases, ungulate populations undergo severe declines and extirpation after migration loss, however, others appear able to persist as residents. We predicted that to persist, residents must replace the traditional benefits of migration by altering the foraging strategies they employ within their year-round seasonal range. We proposed the Alternative Foraging Strategies Hypothesis (AFSH) as a framework for identifying various seasonal behavioral strategies that ungulate may use to cope with migration loss. We tested the AFSH using the formerly migratory Teton bighorn sheep population in northwest Wyoming, which ceased migrating over 60 years ago, but has persisted as resident. We used global positioning system (GPS) data to evaluate winter and summer habitat selection and seasonal elevational movements for 28 adult female bighorn sheep (*Ovis canadensis*) from 2008-2010. Resource selection functions revealed that Teton bighorn sheep have altered their 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 and up to 10 km in spring, gaining access to newly emergent forage approximately 30 days before it appears on their high elevation winter and summer ranges. Our findings indicate that Teton bighorn sheep exhibit plasticity in their habitat selection, foraging strategies, and movement patterns, which allows migration loss to be mediated to some extent by alternative foraging strategies. The identification of alternative foraging strategies 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: migration loss, bighorn sheep, *Ovis canadensis*, phenology, alternative foraging strategies hypothesis, abbreviated migration, Teton Range, Wyoming, habitat selection

INTRODUCTION

Many ungulates migrate to access resources that change seasonally over vast landscapes. In general, migratory populations can support greater numbers of individuals and higher demographic rates than resident populations (Fryxell et al. 1988, Albon & Langvatn 1992, Hebblewhite & Merrill 2011). Migratory individuals benefit by seeking out the highest quality forage available throughout the year (Fryxell & Sinclair 1988, Hebblewhite et al. 2008) and in some cases, lowering their predation rates (Fryxell et al. 1988, Hebblewhite & Merrill 2007, Hebblewhite & Merrill 2011). Despite these benefits, many migratory ungulate populations are currently in decline across the globe (Berger 2004, Bolger et al. 2008, Harris et al. 2009). Migration routes and seasonal ranges are threatened by anthropogenic influences, such as physical barriers to migration routes (Williamson & Williamson 1985, Whyte & Joubert 1988, Spinage 1992, Ben-Shahar 1993, Lemke & Jury 2000, Ito et al. 2008, Sawyer et al. 2013), habitat loss (Serneels & Lambin 2001, Ottichilo et al. 2001, Sawyer et al. 2006), overhunting (Milner-Gulland et al. 2001), and climate change (Post & Forchhammer 2008, Middleton et al. 2013). As a result, the persistence of many migratory populations is uncertain.

Although population declines following migration disruption have been well documented (Berger 2004, Bolger et al. 2008, Harris et al. 2009), we know much less about the ability of migratory ungulates to adapt after migration disruption or migration loss. The most common result is for animals to become restricted to one seasonal range. This has been the case for migratory wildebeest (*Connochaetes taurinus*) in the Kenyan part of the Serengeti-Mara ecosystem (Serneels & Lambin 2001), zebra (*Equus burchellii*) and wildebeest in a portion of the Kalahari in Botswana (Williamson & Williamson 1985), hartebeest (*Alcelaphus buselaphus*) and giraffe (*Giraffa camelopardalis*) in Lake Nakuru National Park in Kenya (Mwangi 1998). In other cases, migratory populations become split between two seasonal ranges and isolated on each (Ito et al. 2008), migrations are truncated by land use changes or artificial feeding (Smith 2001, Jones 2013), or shifting resource availability and reduced predation pressure benefit resident strategies (Post & Forchhammer 2008, Hebblewhite & Merrill 2011, Middleton et al. 2013). Typically, such disruptions are followed by population declines and sometimes extirpation (Williamson & Williamson 1985, Whyte & Joubert 1988, Mwangi 1998, Lemke & Jury 2000). In some cases, however, ungulates appear able to adapt to a resident lifestyle and continue to persist on one seasonal range (Ben-Shahar 1993). Unfortunately, we know little about the seasonal range attributes or life-history characteristics that may underpin the ability of ungulates to persist when their migrations have been lost. Such information would advance our understanding of both the ecology and conservation of migratory ungulates.

Migration enables individuals to survive in regions where temperature and precipitation fluctuate dramatically throughout the year, driving temporal and spatial changes in forage production and quality. Migratory ungulates maximize their nutritional benefits and minimize energetic costs by timing their seasonal movements with changes in vegetation phenology and forage quality across elevational and latitudinal gradients (Albon & Langvatn 1992, Pettorelli et al. 2007, Hebblewhite et al. 2008, Sawyer and Kauffman 2011, Bischof et al. 2012). By optimizing their seasonal movements and in turn, nutritional benefit, migratory ungulates often achieve higher pregnancy rates (Hebblewhite & Merrill 2011), greater body mass (Albon & Langvatn 1992, Hebblewhite & Merrill 2011), and larger population sizes (Fryxell et al. 1988) than resident conspecifics. Thus, seasonal access to high quality forage is widely viewed as the primary fitness benefit of a migratory foraging strategy.

Most ungulate migrations in temperate climates are typified by altitudinal movements from high-elevation summer range, where animals distribute widely, to low-elevation winter range where animals congregate at higher densities (Festa-Bianchet 1988, Albon & Langvatn 1992, Sawyer et al. 2005, Hebblewhite et al. 2006). Winter range conditions are relatively harsh for most temperate ungulates and individuals are exposed to cold temperatures, deep snow, and low forage quality (Parker et al. 2009). In general, ungulates decline in body condition throughout the winter due to a net loss in body fat and body mass (Parker et al. 2009). This pattern has been well documented in multiple species (Festa-Bianchet et al. 1996, Allaye Chan-McLeod et al. 1999, Cook et al. 2004, Monteith et al. 2013). Severe, prolonged winters can reduce maternal condition and result in intrauterine losses (Testa & Adams 1998, Parker et al. 2009), lower birth weight of offspring (Adams 2005, Forchhammer et al. 2001), and lasting cohort effects (Forchhammer et al. 2001, Pettorelli et al. 2007, Monteith et al. 2009). To mediate winter severity, migratory ungulates often establish winter ranges at low elevations with shallower snow depths, sufficient thermal cover, milder temperatures, and greater forage availability (Albon & Langvatn 1992).

The initiation of spring green-up and emergence of highly nutritious vegetation (i.e., high crude protein and high digestibility) marks the end of winter fat loss for ungulates and the beginning of summer fat gain (Parker et al. 2009). These phenological changes in vegetation occur predictably across the landscape. For example, Hebblewhite et al. (2008) found that the growing season started 50 days later for every 1000-m increase in elevation, and 8 days earlier on southern aspects. Migratory ungulates track changes in plant phenology throughout the spring and summer seasons, following the emergence of highly nutritious forage across elevational gradients and topographical features, thus optimizing forage quality (Hebblewhite et al. 2008, Sawyer & Kauffman 2011, Bischof et al. 2012). Longer green-up durations have been shown to positively influence pregnancy in elk (Middleton et al. 2013) and juvenile survival in bighorn sheep, alpine ibex (*Capra ibex*), and mountain goats (*Oreamnos americanus*) (Pettorelli et al. 2007).

Due to their strongly seasonal life history, it is reasonable to expect that migratory ungulates would suffer demographic consequences when they lose access to traditional seasonal ranges. However, our understanding of how these consequences manifest at the population-level and affect population persistence is still lacking. Population declines and local extinctions associated with migration disruption or habitat loss have been documented for numerous migratory ungulates (Berger 2004, Bolger et al. 2008, Harris et al. 2009), however, population responses have differed widely (Bolger et al. 2008). Indeed, when facing migration disruption, some populations undergo severe declines and extirpation, while others decline initially and then continue to persist. For example, agricultural expansion outside of the Masai Mara National Reserve in Kenya led to an 81% decline in the migratory wildebeest population within 20 years (Ottichilo et al. 2001, Serneels & Lambin 2001), fencing around Lake Nakuru National Park in

Kenya caused local extinction of hartebeest and giraffe (Mwangi 1998), and land conversion around Lake Manyara National Park in Tanzania caused local extinction of hartebeest (Newmark 1996). Yet, fencing around the Sabi-Sand Wildtuin Game Reserve in South Africa caused initial declines in migratory wildebeest (66%) and zebra (33%) populations, which then stabilized and have persisted at lower numbers (Ben-Shahar 1993). The primary factor determining the severity of population declines following migration disruption may be the benefit of migration itself, and the availability of alternative habitats and foraging strategies. There is often more than one way for animals to utilize the landscape to achieve sufficient body condition to survive and reproduce (Parker et al. 2009). The availability of these alternative habitats and foraging strategies is rarely known, and thus our ability to understand how ungulates might adapt to migration loss is limited.

Here, we describe a formerly migratory bighorn sheep population that ceased migrating over 50 years ago, but continues to persist on its high elevation summer range year-round. Historically, bighorn sheep summered at high elevations (2800 - 3100 m) in the Teton Range in northwest Wyoming and migrated to lower elevations (1900 - 2300 m) in the surrounding valleys to winter (Whitfield 1983). However, during the early 20th century, the cumulative effects of permanent human settlement of the valleys, including construction of roads and fences across migration routes, residential development on winter range, fire suppression, and widespread domestic sheep grazing, caused bighorn sheep to abandon their historical migration to low elevation winter range (Whitfield 1983). Instead, the population retreated to its high elevation summer range (2600 to 3200 m), where it currently persists year-round.

We generated the hypothesis that the Teton Range bighorn sheep population has been able to persist after migration loss because individuals have altered their habitat selection strategies compared to typical migratory sheep. We propose the Alternative Foraging Strategies (AFS) hypothesis, whereby persistence on one seasonal range after migration loss is possible when individuals adopt alternative habitat selection or foraging strategies that allow them to either minimize the energetic demands of winter and/or maximize the nutritional benefits of summer. To persist, residents must replace the traditional benefits of migration by altering their foraging strategies to meet their nutritional requirements within one seasonal range. The AFS hypothesis would be supported if the formerly migratory population: (1) exhibits demographic rates consistent with population persistence, (2) uses phenological gradients within its remaining seasonal range in a nontraditional manner so as to exploit spatial and temporal variation in forage quality, and (3) alters winter habitat selection to subsist on a non-traditional winter range, and/or (4) alters summer habitat selection to maximize nutritional intake, at the expense of predator avoidance. We used the AFS hypothesis framework to disentangle the various seasonal behavioral strategies that Teton bighorn sheep have used to successfully cope with migration loss. A better understanding of the seasonal range attributes and life history characteristics 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 – July 2010 in the Teton Range, located within the Greater Yellowstone Ecosystem (GYE) in northwest Wyoming, USA. The study area includes portions of Grand Teton National Park (GTNP), the Caribou-Targhee National Forest (CTNF), and Bridger-Teton National Forest (BTNF) (Fig. 1). The town of

Jackson, Wyoming is located approximately 10 km southeast of the study area. The Teton Range stretches north to south for approximately 60 km, with elevations ranging from 2,000 m in the foothills to 4,197 m at the summit of the Grand Teton. The Teton Range is typified by rugged, rocky peaks and steep canyons that cut east-west throughout the range. Vegetation varies considerably over elevational and topographical gradients. Surrounding valleys are mostly comprised of mesic sagebrush steppe habitat. Aspen (*Populus tremuloides*) stands are intermixed with conifer forests in the foothills, containing Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and Douglas fir (*Pseudotsuga menziesii*), often with dense shrub understories. South-facing slopes are more open and support complex mountain shrub or forb/grassland communities containing snowberry (*Symphoricarpus* spp.), serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus* spp.), geranium (*Geranium* spp.), columbine (*Aquilegia* spp.), and brome (*Bromus* spp.) with scattered Douglas fir stands. Higher elevations are characterized by dry and wet alpine meadows and talus slopes, with a diversity of forbs and grasses such as milk-vetch (*Astragalus* spp.), sweet-vetch (*Hedysarum* spp.), buttercups (*Ranunculus* spp.), cinquefoil (*Potentilla* spp.), groundsel (*Senecio* spp.) and bluegrass (*Poa* spp.). Other ungulates in the study area include elk, mule deer, and moose (*Alces alces*). The study area supports a suite of predators, including mountain lion (*Puma concolor*), coyote (*Canis latrans*), golden eagle (*Aquila chrysaetos*), wolverine (*Gulo gulo*), black bear (*Ursus americanus*), grizzly bear (*Ursus arctos*), and wolf (*Canis lupus*).

The Teton Range bighorn sheep population is a small, native bighorn sheep herd that numbers approximately 100-150 individuals and resides in the Teton Range year-round. Historically, this population migrated seasonally between high elevation summer range in the Teton Range and low elevation winter range in the surrounding valleys and canyons (Fig. 2)

(Whitfield 1983). However, permanent human settlement in the area, which began in the late 19th century, had a rapid and lasting impact on the population's migration. The cumulative effects of road and fence construction, residential development, widespread domestic sheep grazing, and wildfire suppression on low elevation winter ranges caused the population to abandon its migration by around 1950 (Whitifeld 1983). Consequently, the population now survives year-round on its traditional, high elevation summer range.

Capture and monitoring

We used helicopter net-gunning to capture 20 female bighorn sheep during 14-15 February 2008 and 8 female bighorn sheep during 12-13 March 2009 in the Teton Range, Wyoming, USA. The population is segregated into a northern group and southern group, separated by approximately 15 km. We captured 10 bighorn sheep in the northern group and 18 bighorn sheep in the southern group. We fitted individuals with store-on-board global positioning system (GPS) collars (model TGW-3500, Telonics, Inc., Mesa, Arizona, USA), programmed to acquire a fix every 5 hours and automatically release after 29 months (for 2008 capture) or 17 months (for 2009 capture). Bighorn sheep were aged based on tooth eruption pattern and annual horn rings. Blood was collected for pregnancy and disease testing, and nasal, tonsil, and ear swabs for disease testing. Pregnancy and disease testing were conducted at the Wyoming State Veterinary Laboratory in Laramie, Wyoming, USA. Pregnancy was determined using pregnancy-specific protein B. 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 bighorn sheep from a fixed-wing aircraft once every month during winter and once every 2 weeks during summer to track general movements and detect mortality events. In addition, we tracked GPS-collared ewes on the ground from 2008-2010 to monitor lamb survival for GPS-collared ewes. In 2008, we knew the pregnancy status of all 20 GPS-collared ewes, and we assumed that all pregnant ewes gave birth (Shackleton et al. 1999). Since the majority of lamb mortality occurs within the first few weeks after birth (Shackleton et al. 1999), if we never observed a lamb with a formerly pregnant ewe, we assumed that the lamb died shortly after birth. In 2009, we knew the pregnancy status of 8 GPS-collared ewes and assumed a pregnancy rate of 90-100% for the unknown GPS-collared ewes (Shackleton et al. 1999). In 2010, the pregnancy status of all GPS-collared ewes was unknown, so we assumed a rate of 90-100% for all ewes. We observed each GPS-collared ewe at least once every 2 weeks from June-August each summer to track lamb survival (Shackleton et al. 1999).

Analysis of seasonal movements

To evaluate how bighorn sheep exploit spatial and temporal phenological changes while isolated on one seasonal range, we examined the elevational movements of marked bighorn sheep. We extracted the elevation of each GPS-collar location from a 10-m digital elevation model (DEM), obtained from the U.S. Geological Survey. We calculated the average elevation of each bighorn sheep by week, and then averaged each week across all bighorn sheep to develop an elevational movement profile for all marked sheep.

We expected that spatial and temporal patterns of phenology would influence seasonal movement patterns (Albon & Langvatn 1992, Pettorelli et al. 2007, Hebblewhite et al. 2008, Sawyer and Kauffman 2011). To estimate greenness, we calculated the weekly average Normalized Difference Vegetation Index (NDVI) within sheep spring and winter ranges from 2008-2010. Seasons were defined as spring (8 May – 31 May) and winter (15 January –

February 21) based on major sheep elevational movements. Seasonal ranges were delineated using a 97% kernel home range from bighorn sheep GPS locations during each season (Hawth's Tools version 3.27; Beyer 2004). We downloaded weekly Moderate Resolution Imaging Spectroradiometer (MODIS-TERRA) imagery from 2008-2010 and calculated NDVI [(near infrared + red)/(near infrared - red)]. We re-sampled all rasters to 30-meter pixels using a bilinear interpolation in ArcGIS 10.0. We clipped rasters to corresponding seasonal polygons, extracted NDVI values, and calculated weekly NDVI averages for each seasonal range.

Evaluating seasonal foraging strategies

To evaluate the existence of alternative foraging strategies used by sheep to persist while isolated on one seasonal range, we evaluated the influence of landscape variables on winter and summer habitat use. We used each collared bighorn 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 snow accumulation and melt-out, winter and summer periods were delineated as November 15 – April 15 and June 15 – September 15, respectively.

In winter, we evaluated the influence of proximity to escape terrain, proximity to snow-free areas, elevation, solar radiation, tree cover, and slope (Smith et al. 1991, Dicus 2002, DeCesare & 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 mineral licks. We defined winter and summer habitat availability at the home range level for each bighorn sheep with a local convex hull polygon using X Tools Pro 9.0 extension for ArcGIS.

Because the majority of collared bighorn sheep only utilized either the northern or southern portion of the study area, we chose to analyze third-order habitat use (Thomas & Taylor 2006) to account for variation in each individual's use and availability.

Habitat covariates

Previous work suggests that Teton Range bighorn sheep seek out snow-free areas (e.g., wind-swept ridges) during winter to forage and conserve energy (Steve Cain, *pers. comm.*). Maximum snow depths at mid and high elevations in the Teton Range can reach 3.5 m (Bridger-Teton National Forest, http://www.jhavalanche.org), which vastly exceeds the foraging and movement capabilities of bighorn sheep (Smith et al. 1991). Some ridges and slopes, however, receive significant wind action, blowing them free of snow. To spatially delineate these snow-free areas, we developed a new technique utilizing the normalized difference snow index (NDSI) on Landsat satellite imagery from 1993 – 2011 (U.S. Geological Survey, http://glovis.usgs.gov) (Appendix I). We analyzed 30 cloud-free 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 km^2) of the study area during winter, but may represent critical habitat for bighorn sheep.

Elevation and slope covariates were derived from a 10-m digital elevation model (DEM) (U.S. Geological Survey). Percent tree cover was derived from a 30-m National Land Cover Database for Wyoming (2001). Winter and summer solar radiation were estimated using the Spatial Analyst solar radiation function (ESRI ArcGIS 10) (Kumar et al. 1997, Dicus 2002, DeCesare & Pletscher 2006). We combined terrain ruggedness and escape terrain into one variable, defined as "rugged escape terrain" that had a slope > 30º, terrain ruggedness index >

0.001 (Sappington et al. 2007), and patch-size >= 1 hectare (Dicus 2002, DeCesare & Pletscher 2006). We identified 17 natural mineral lick locations in the study area by observing bighorn sheep during summer. We created proximity to rugged escape terrain, proximity to snow-free areas, and proximity to mineral licks rasters using the Spatial Analyst distance function (ESRI ArcGIS 10).

We conducted a Pearson's pairwise correlation analysis before modeling to identify multicolinearities and determine whether any variables should be excluded from modeling ($|r| > 0.60$). Two variables in the summer model had $|r| > 0.60$, slope and summer solar radiation ($|r| = 0.66$). We retained the slope variable because of its importance to bighorn sheep (Smith et al. 1991, Shackleton et al. 1999).

GIS sampling design

We created a sampling grid of 100 x 100 m cells that was clipped to each sheep's local convex hull polygon for winter and summer. We chose this sampling scale to capture 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% ± 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, Hebblewhite et al. 2007). To account for this potential bias, 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 previous studies have shown these habitats can reduce GPS performance (D'Eon et al. 2002, Heard et al. 2008). 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 II). Because coefficient estimates between the two approaches were not different, we proceeded with a discrete choice RSF for our summer analysis.

We estimated habitat use coefficients for each animal using the modified (winter) and standard (summer) discrete choice models. To evaluate significance, we calculated mean and 95% confidence intervals for each coefficient using estimates from each individual (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 winter and summer habitat, we mapped the predicted probability of bighorn sheep habitat use from each seasonal population-level model over the one, year-round range. To ensure that model predictions were mapped with the same scale used for model estimation, we standardized the raster for each covariate by subtracting the cell value from the mean and dividing by the standard deviation for the study area. We applied the model estimates using Raster Calculator (ESRI ArcGIS 10) on a grid of 30 x 30 m cells. The model prediction for each cell was assigned a value of 1 to 7 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 bighorn sheep use for each season separately.

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 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.

Summer diet selection

We evaluated summer diet selection by comparing bighorn sheep fecal samples to forage availability. We collected 116 fecal samples and combined them into composite samples for June (n=11), July (n=66), and August (n=39). Plant genera in the composite samples were identified by Washington State University Wildlife Habitat and Nutrition Laboratory, Pullman, Washington, USA (Appendix VI). We collected information on summer forage availability by conducting vegetation transects in 30 identified bighorn sheep foraging areas. In each foraging area, we placed 3 parallel 10-m transects, separated by 2 m. Quadrats (20 x 50 cm) were placed every 2 meters along each transect line (*n* = 15 quadrats per foraging area). Within each quadrat, we estimated percent cover for each plant genus present (Appendix VII) and percent cover by type (bare ground or rock, vegetation, and litter). We evaluated forage selection, by calculating a selection ratio, *S*, which is the percent of a given genus in the diet divided by the percent cover of the genus from vegetation plots. We calculated an average selection ratio for each genus that exceeded 5% of the diet (*Bromus*, *Poa*, *Carex*, *Astragalus*, and *Geranium*) during June, July, and August sampling periods. A selection ratio > 1 indicated that use exceeded availability.

Foraging activity budgets

We investigated summer foraging activity budgets to determine if bighorn sheep increased their foraging rates at the expense of vigilance compared to published rates for migratory sheep. We sought to compare tradeoffs between time spent foraging and time spent vigilant, so we collected behavioral observations during foraging bouts (Festa-Bianchet 1988, Frid 1997). We collected 15-minute focal-animal observations on adult ewes. Observations were collected from June - August 2008, 2009, and 2010. We classified behaviors as feeding, licking (at mineral lick), vigilant, moving, standing, or bedded. Foraging bouts included short periods of standing or moving between forage patches. Recording sessions either ended after 15 minutes or when an animal stopped foraging behavior for longer than 1 minute (i.e. by bedding down or moving away). We also recorded reproductive status of the ewe, proximity to escape terrain, group size, and group composition. We calculated the mean and standard error for proportions of time spent feeding and vigilant during foraging bouts. We compared proportions of time spent feeding and vigilant for reproductive and non-reproductive ewes using a Student's *t* test.

RESULTS

Population status

Seventeen of 19 adult ewes (90%) were pregnant at capture in February, 2008. One of the captured ewes was a yearling and not pregnant, which is typical (Shackleton et al. 1999), and therefore, was not included in the total. Eight of 8 adult ewes (100%) were pregnant at capture in March, 2009. The average age of bighorn sheep ewes at time of capture was 4.8 years (range = 1.8 to 8.8 years). Lamb survival for GPS-collared ewes through summer 2008 was 50%, summer 2009 was 60%, and summer 2010 was 56%.

All 28 bighorn sheep tested negative or exhibited very low titers for 10 diseases and 1 parasite in 2008 and 2009, indicating no or extremely infrequent exposure to these pathogens. *Mannheimia glucosida* was cultured from a tonsil swab from one bighorn sheep in 2009, but that bacterial species is not considered pneumonic (Appendix III).

Eight GPS-collared bighorn sheep died during the study (29%), 4 from avalanches, 1 from mountain lion predation, and 3 from unknown causes. Annual mortality rates for GPS-collared ewes were 15%, 22%, and 4% for the biological years during the study. These mortality rates for the reproductive segment of a small population appears high, compared to reported ewe mortality rates of 10.8% (Hengel et al. 1992), 11% (Singer et al. 2000), and 6% for prime aged individuals (2-7 years) (Jorgenson et al. 1997). Notably, half of the mortalities in our study were caused by avalanches, which do not occur on this population's traditional low elevation winter range. Although sample sizes were relatively low, the observed pregnancy and summer lamb survival rates are typical for bighorn sheep populations (Shackleton et al. 1999) and therefore, support the AFS hypothesis. However, the higher adult mortality rate during certain years may call the first condition of the hypothesis into question.

Abbreviated migration

Despite being residents, bighorn sheep underwent distinct seasonal elevational movements on their year-round range. Bighorn sheep spent most of the summer at approximately 3000 m, then descended to approximately 2700 m during the fall, ascended to 3000-3200 m for the winter, and then make an abrupt descent to approximately 2600 m in the spring, before slowly moving back to their summering elevations (Fig. 3). We termed this newly described behavior "abbreviated migration". Notably, we found that bighorn sheep wintered at higher elevations than they summered (Fig. 3). Also, by descending to low elevations during spring, bighorn sheep are positioned to reconnect with their historical migration trajectory during spring, summer, and fall.

This abbreviated migration appears to be synchronized with vegetation phenological changes (Fig. 4), which are closely related to vegetation nutritional quality (Hamel et al. 2009a). 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 1 month later (Fig. 4). By descending to mid-elevations in spring, bighorn sheep are able to capitalize on highly nutritious forage during one of the most energetically demanding times of the year (the last month of gestation) (Shackleton et al. 1999). Green-up occurred approximately 30 days earlier on spring ranges than on higher elevation winter ranges (Fig. 4).

Winter

Similar to migratory populations (Oldemeyer et al. 1971, Tilton & Willard 1982, Hurley 1985, Festa-Bianchet 1988, Dicus 2002), Teton resident bighorn sheep showed significant use of areas in close proximity to rugged escape terrain ($\beta = 0.667$; Table 1, Fig. 5), with high solar radiation ($\beta = 0.220$; Table 1, Fig. 5), and with minimal to no tree cover ($\beta = -0.157$; Table 1, Fig. 5).

However, unlike migratory bighorn sheep, this population selected for high elevations (β = 0.549; Table 1, Fig. 5) and did not exhibit significant use of steep slopes (Table 1, Fig. 5). We also found that bighorn sheep were tightly associated with consistently snow-free areas (β = 0.949; Table 1, Fig. 5), mostly located on windswept ridges. The predicted probability map reveals that the highest quality winter habitat is fragmented and patchy on the landscape, surrounded by a matrix of unsuitable habitat (Fig. 6). The existence of high elevation, windswept ridges and south-facing slopes that remain relatively snow-free throughout the winter appears to form the critical component for this population's alternative winter foraging strategy. These findings support our prediction that Teton bighorn sheep have altered their winter foraging strategy to survive on one seasonal range year-round.

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

Although we predicted that Teton Range bighorn sheep would exhibit habitat selection strategies different from migratory sheep to maximize nutritional intake during summer, we found no evidence to support this. Similar to migratory bighorn sheep (Hurley 1985, Festa-Bianchet 1988), this resident population shows significant use of steep slopes (β = 0.516; Table 1, Fig. 7), areas with minimal to no tree cover (β = -0.451; Table 1, Fig. 7), and at high elevations (β = 0.336; Table1, Fig. 7). Contrary to our predictions, bighorn sheep were closely associated with rugged escape terrain (β = 0.95; Table 1, Fig. 7), suggesting that ewes do not forego predator avoidance to increase forage availability and nutritional intake. Although some individual GPS-collared ewes exhibited selection for areas in close proximity to mineral licks, this covariate was not significant in the population-level model (Table 1, Fig. 7). The predicted probability map shows that summer habitat is abundant and well-connected throughout the study area (Fig. 8).

Bighorn sheep diets were comprised of shrubs, grasses, and sedges during the spring and early summer, and shifted to forbs and grasses later in the summer (Fig. 9). Forbs comprised nearly 60% of the August diet. Summer diets were diverse, including 40 plant genera identified from fecal samples (Appendix VI). However, only 5 genera were present above 5% in the diet: *Bromus* (8%), *Poa* (22%), *Carex* (20%), *Astragalus* (8%), and *Geranium* (6%). Bighorn sheep exhibited significant selection for *Bromus*, *Poa*, *Carex*, and *Astragalus* throughout the summer (Fig. 10).

Foraging activity budgets

We collected a total of 18.75 hours of foraging activity observations on adult ewes (*n* = 75) over 3 summers. We found no difference in average proportion of time spent feeding between reproductive (mean 0.72 ± 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. We were unable to determine reproductive status of ewes for 11 observations. The average percent of time spent feeding during foraging bouts was 69.9% (± SE 2.5%) and time spent vigilant was 10.9% (± 1.2%). On average, ewes were vigilant 0.57 times per minute and the average duration of each vigilance event was 11.4 seconds.

DISCUSSION

When animals are no longer able to migrate, population declines often follow, although the factors that may mediate such declines are largely unknown. We proposed the Alternative Foraging Strategies Hypothesis (AFSH) as a framework for understanding how ungulates cope with migration loss. We found equivocal evidence for our first prediction, that Teton sheep would exhibit demographic rates consistent with population persistence. Nevertheless, over 60 years of persistence by this herd despite migration loss suggests viable demographic rates. The second prediction, that sheep would make use of phenological gradients in vegetation within their remaining range, was supported. Teton sheep undertook a newly described movement strategy, “abbreviated” migration, by rapidly descending from the high peaks in early spring to access newly emergent forage and then track its phenology while moving back to higher elevation throughout spring and summer (Fig. 4). We found clear support for our third prediction, that sheep would alter their winter habitat selection strategies to subsist on 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 habitat during winter (Festa-Bianchet 1988) (Table 1, Fig. 5). Finally, we found no support for our fourth prediction, that sheep would alter summer habitat selection strategies to maximize energy intake. Summer habitat use (Table 1, Fig. 7), foraging time budgets, and diet selection were similar to those reported for migratory sheep herds (Johnson & Smith 1980, Festa-Bianchet 1988, Ruckstuhl et al. 2003). Overall, our results suggest that Teton sheep have adopted alternative foraging strategies to cope with migration loss by modifying their winter habitat selection and maximizing access to high quality forage through abbreviated migration.

Population persistence

The Teton bighorn sheep population has persisted for over 60 years since migration loss, and for the most part, demographic rates appear to be consistent with a stable, although small, population. Summer lamb survival was 55% (± SE 5%); winter aerial surveys indicate that recruitment declines to 29 to 33 lambs per 100 ewes by late winter (Wyoming Game and Fish Department 2008, 2010). Although low, these lamb survival rates are within the range reported by previous studies (Shackleton et al. 1999). Ewe demography may be more of a concern than lamb mortality for the population; annual mortality of Teton ewes was 13.6% (± SE 8.8%) compared to other studies ranging 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 a meaningful proportion of mortalities. Avalanches killed 50% (n=4) of GPS-collared ewes, which represents a novel source of mortality because they occur less frequently on traditional, low elevation winter range (Appendix V). Although our sample size was low, these results raise concerns that a series of stochastic events could threaten the future viability of this small and genetically isolated population (Appendix III, Appendix IV) (Berger 1990, Morris and Doak 2002).

Winter

Having lost their low-elevation winter range, Teton sheep now seek out high elevation, windswept ridgelines and south-facing slopes (Plate 1). While mid-elevations are commonly buried in up to 3.0 m of snow, some high elevation ridgelines in the Teton Range are consistently snow-free, which appear to provide a winter refuge. Interestingly, these snow-free patches lie at significantly higher elevations than occupied summer range, representing some of the highest and most rugged areas in the Teton Range (Fig. 3). The patchiness of wintering areas (Fig. 6) causes bighorn sheep to be confined to small home ranges during the winter. The degree to which the use of these snow-free patches offsets the cost of wintering on non-traditional range is unclear. Forage quality is marginal, mostly comprised of lichens and sparse alpine forbs and grasses – poorer than on traditional winter ranges. However, it is arguable that winter forage quality is universally marginal for both migratory and resident temperate ungulates, forcing individuals to make trade-offs between foraging activity and energy conservation (Parker et al. 2009). Even migratory bighorns sheep typically lose 20-35% of their body mass over winter (Festa-Bianchet et al. 1996). Thus, factors that increase energetic demands and speed body condition decline, such as snow depth, may be more limiting than poor forage quality during winter. Daily & 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 (about 31 cm for males, 26 cm for females), and quadrupling at two times chest height. In the Teton Range, where snow depths commonly reach 3.0 m, we suspect the primary benefit of using windswept, high elevation ridgelines is a reduction in energetic costs, which may minimize over-winter fat loss (Parker et al. 2009).

Summer

We predicted that to compensate for wintering on non-traditional, marginal range, Teton bighorn sheep would enhance their summer foraging efforts by foregoing predator avoidance and/or altering diet selection to maximize nutritional intake. However, we were unable to detect any differences in summer foraging strategies compared to migratory sheep (Festa-Bianchet 1988, Frid 1997, Shackleton et al. 1999, Ruckstuhl et al. 2003, Walker et al. 2006). Teton bighorn sheep selected areas in close proximity to escape terrain, steep slopes, and avoided tree cover. 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). In terms of diet, Teton sheep selected mostly forbs and grasses during July and August, and avoided shrubs, similar to other populations (Cooperrider et al. 1980, Johnson & Smith 1980, Brown & Yde 1988). However, the percent of the diet comprised of forbs was among the highest reported for bighorn sheep (Shackleton et al. 1999), suggesting highly nutritious summer range.

Increasingly, research has demonstrated the critical role that summer and fall accumulation of body fat and protein plays 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 & Côté 2008). That Teton ewes achieved pregnancy rates over 90% and summer lamb survival around 50% suggests that energy gain during summer using typical foraging strategies is sufficient to overcome winter deficits and support reproduction. The existence of high quality summer range and altered winter foraging strategies may enable Teton sheep to approach summer nutritional levels similar to migratory sheep.

Abbreviated migration

We found that Teton bighorn sheep underwent distinct seasonal elevational movements, despite being confined to one range year-round, a behavior that we termed abbreviated migration. Similar to the intact migrations of mule deer (Sawyer and Kauffman 2011), abbreviated migrations by Teton sheep appear to be synchronized with phenological changes within their one seasonal range (Fig. 4). Migratory ungulates typically move from low to high elevation in the spring in concert with vegetation emergence (Albon & Langvatn 1992, Pettorelli et al. 2007, Hebblewhite et al. 2008, Sawyer & Kauffman 2011, Bischof et al. 2012). Unlike these typical migration patterns, however, Teton sheep begin spring in the high peaks and then descend approximately 500 m and up to 10 km to seek the first vegetation emergence at mid-elevations (Fig. 4). The cues that bighorn sheep use to time their descent to coincide with green-up at mid-elevations are unknown. Nevertheless, this movement allows them to access highly nutritious forage (Albon & Langvatn 1992) approximately 30 days before it becomes available on their high elevation summering and wintering areas (Fig. 4). Several studies have demonstrated the critical role of spring nutritional quality for neonate growth and survival and life-long fitness in temperate ungulates (Pettorelli et al. 2007, Hamel et al. 2009b), indicating these spring movements may be critical to the annual foraging budget of Teton sheep.

Interestingly, Teton sheep also descend approximately 300 m to mid-elevations again in autumn before ascending to their high elevation winter range (Fig. 3). This movement appears to coincide with the first snow storms in the high peaks and is likely an attempt to prolong their access to summer forage. Once snow begins to accumulate at mid-elevations, however, sheep ascend to high elevation, windswept ridges to winter. In a sense, abbreviated migration in the spring and autumn reconnects Teton sheep with a portion of their historical migration. This is likely critical to maximizing their access to high quality forage and their ability to gain fat over the growing season.

The abbreviated migration of Teton sheep illustrates the importance of protecting remaining habitats for ungulate populations that have lost their traditional migrations. Although these sheep have become restricted to high elevation ranges during the winter, access to mid-elevation habitats appears to be critical, especially during the short growing season. Many of these areas are former domestic sheep grazing allotments on U.S. Forest Service land that were retired between 2001 and 2004 with financial incentives provided to permittees by a Wyoming wild sheep organization (K. Hurley, *pers. comm.*). Bighorn sheep can contract pneumonia-causing bacteria from domestic sheep (Lawrence et al. 2010), which have been implicated in numerous bighorn sheep population die-offs (Bunch et al. 1999, George et al. 2008). Our study affirms the importance of these conservation measures to Teton bighorn sheep – a previous study of this population (Whitfield, 1983) did not document any bighorn sheep use throughout most of the then active domestic sheep allotments. Now, bighorn sheep routinely use them during their abbreviated migration. These conservation efforts have likely buffered Teton bighorn sheep against contracting many common diseases (Appendix III).

Our study highlights the importance of evaluating past and future migratory ungulate declines in the context of available alternative foraging strategies. Our findings indicate that Teton sheep exhibit plasticity in their habitat selection, foraging strategies, and movement patterns, which allows migration loss to be mediated to some extent by alternative foraging strategies. Relatedly, other authors have suggested that severity of population decline following migration loss may in part depend upon which seasonal range the population becomes isolated (Sutherland 1996, Bolger et al. 2008). In the case of Teton sheep, the population was isolated on its more productive, summer range. In an opposite situation, a bighorn sheep population declined by 40-50% within 3 years of being isolated to its winter range (Lemke & Jury 2000). Voeten et al. (2010) found that forage quality on dry season ranges would not meet the nutritional requirements of lactation if wildebeest were confined there year-round. Unfortunately, there are few studies that directly address this question of which seasonal range is more critical to protect over the other. There are examples of steep ungulate population declines after isolation on less productive, winter/dry season ranges (Williamson & Williamson 1985, Whyte & Joubert 1988, Spinage 1992, Ben-Shahar 1993, Ito et al. 2008) and more productive, summer/wet season range (Serneels & Lambin 2001, Ottichilo et al. 2001, Lemke & Jury 2000). We suggest that the availability of alternative foraging strategies is ultimately what determines how successful a population is after migration disruption or loss, regardless of which seasonal range is lost. As ungulate populations continue to lose their traditional migrations, it will be critical to identify and protect habitats needed to support potential alternative foraging strategies.

Conclusions

While many studies have linked migratory ungulate declines to migration disruption or loss, very few have explored the underlying factors that contribute to the severity of these declines or in some cases, continued persistence. We demonstrated that the availability of alternative foraging strategies have likely allowed the Teton bighorn sheep population to persist despite migration loss. Teton sheep have altered their winter foraging strategies in a manner that minimizes energy expenditure and also undertake an abbreviated migration to lengthen their access to high quality forage during the year. Although these strategies have allowed the population to persist thus far, its future remains precarious due to its small size. It will be imperative for managers to protect the population's limited high elevation winter habitat and also improve the availability and quality of mid-elevation spring, summer, and autumn habitats. Efforts are increasing worldwide to protect migratory ungulate populations, and identification of alternative foraging strategies and the habitats that support them can help us to understand the underlying benefits of migration and manage for persistence in the face of migration loss.

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

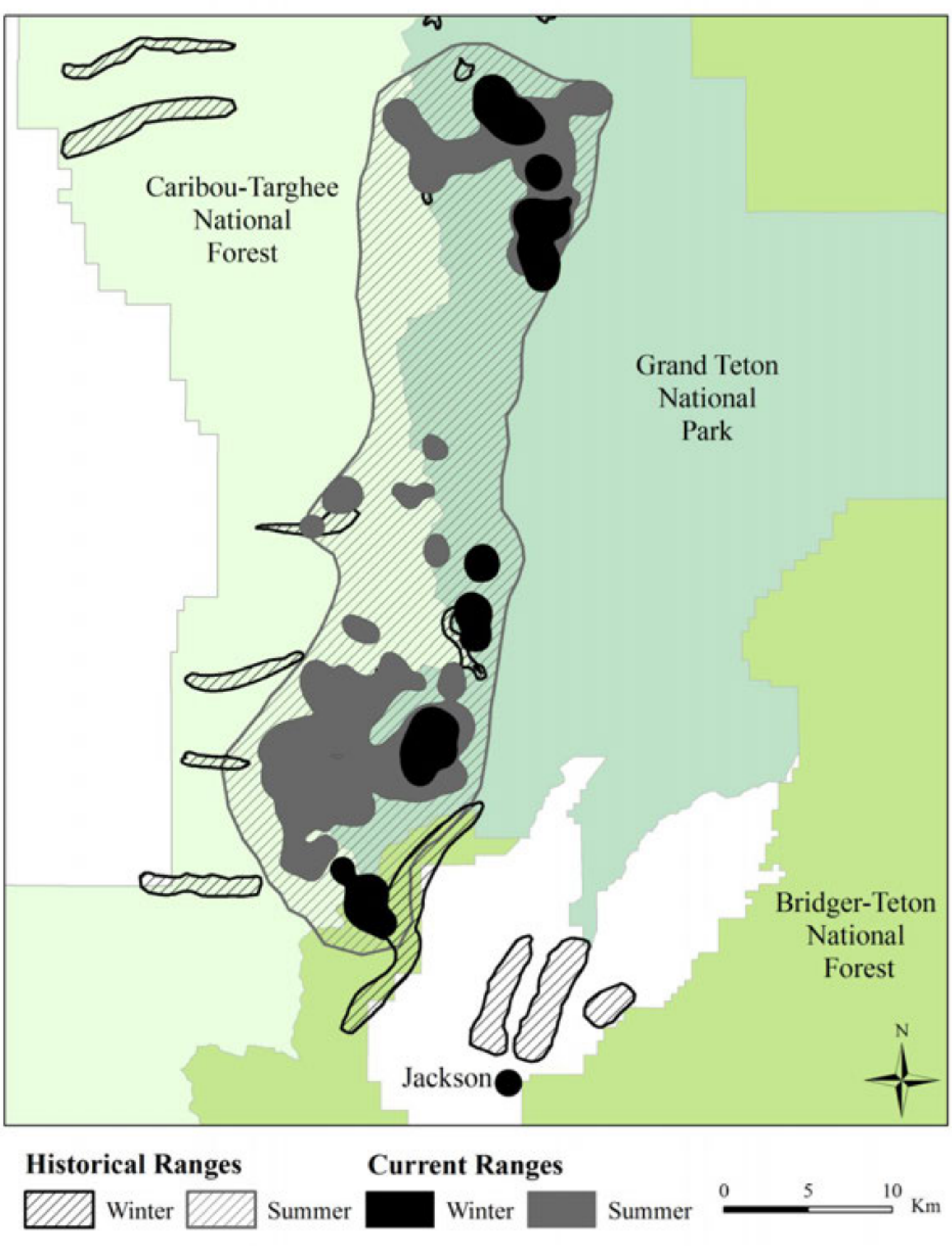


Figure 2. Historical (pre-1950) (lined polygons) and current (post-1950) (solid polygons) winter (black) and summer (grey) ranges of the Teton bighorn sheep population.

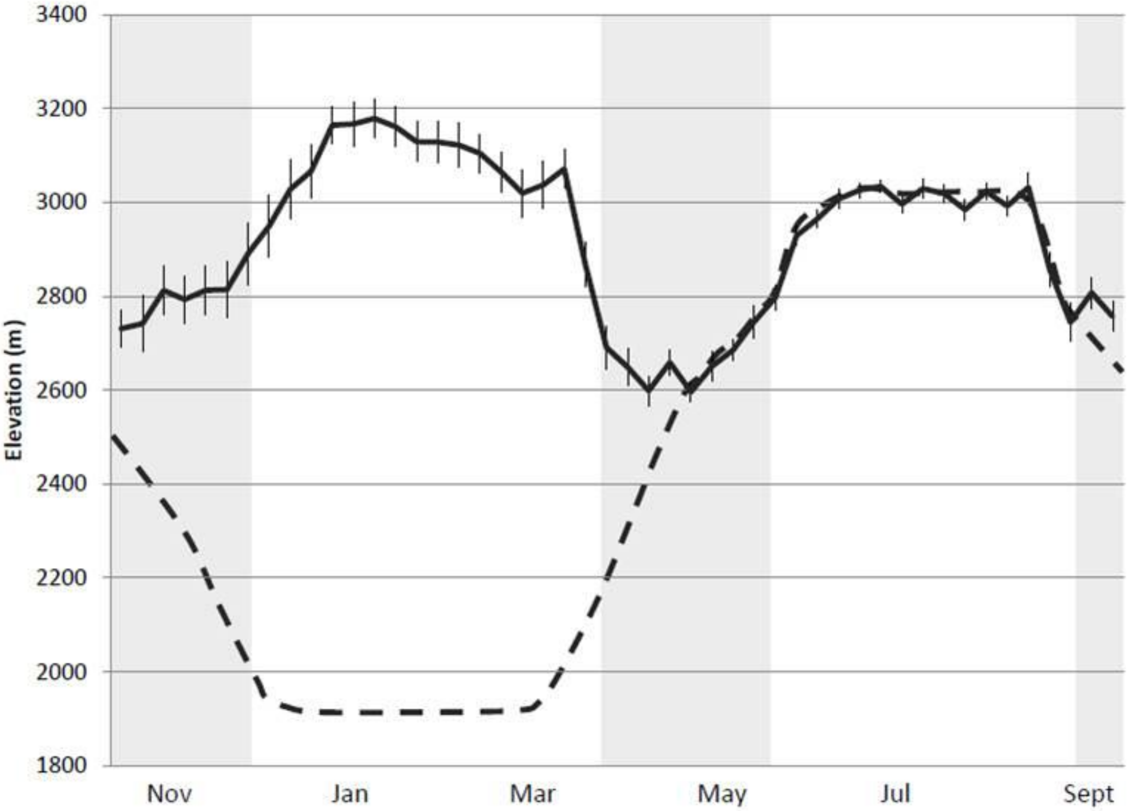


Figure 3. Average weekly elevation of GPS-collared bighorn sheep (mean ± SE) (solid line) and approximate historical elevations of bighorn sheep (dashed line) (from Whitfield 1983). Transparent gray boxes depict the historical spring and fall migration periods.

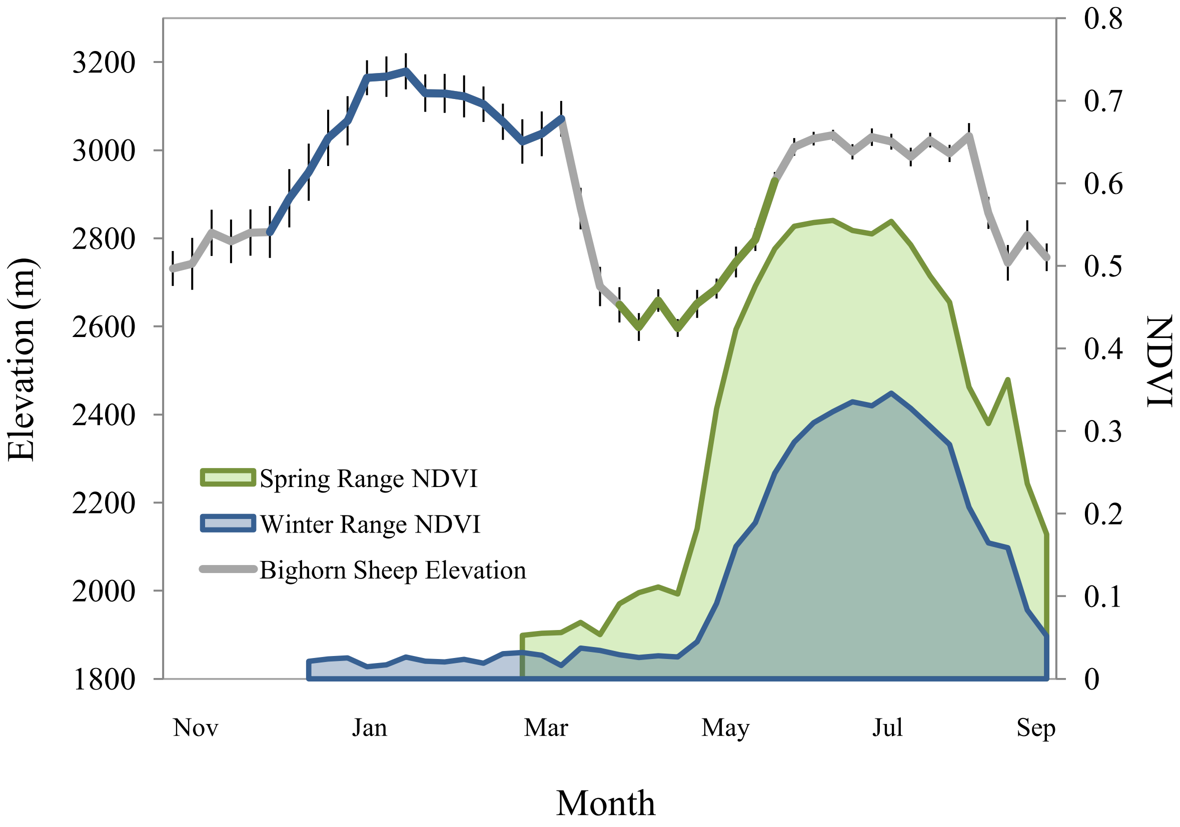


Figure 4. Average weekly elevation of GPS-collared bighorn sheep (mean ± SE) (line) and weekly average normalized difference vegetation index for spring (green) and winter (blue) bighorn sheep ranges (mean ± SE). Blue and green portions of the line correspond to winter and spring seasons.

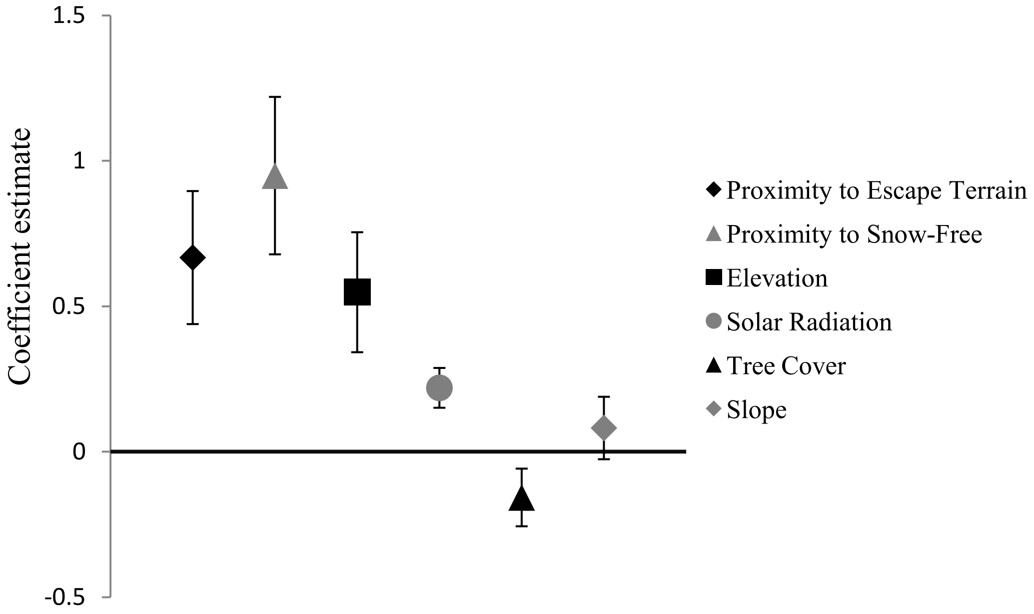


Figure 5. Averaged coefficients for the winter population-level resource selection function. Bars represent 95% confidence intervals for each coefficient, based on individual model (n = 23) estimates. Coefficients with bars that do not overlap zero indicate significant selection (+) or avoidance (-).

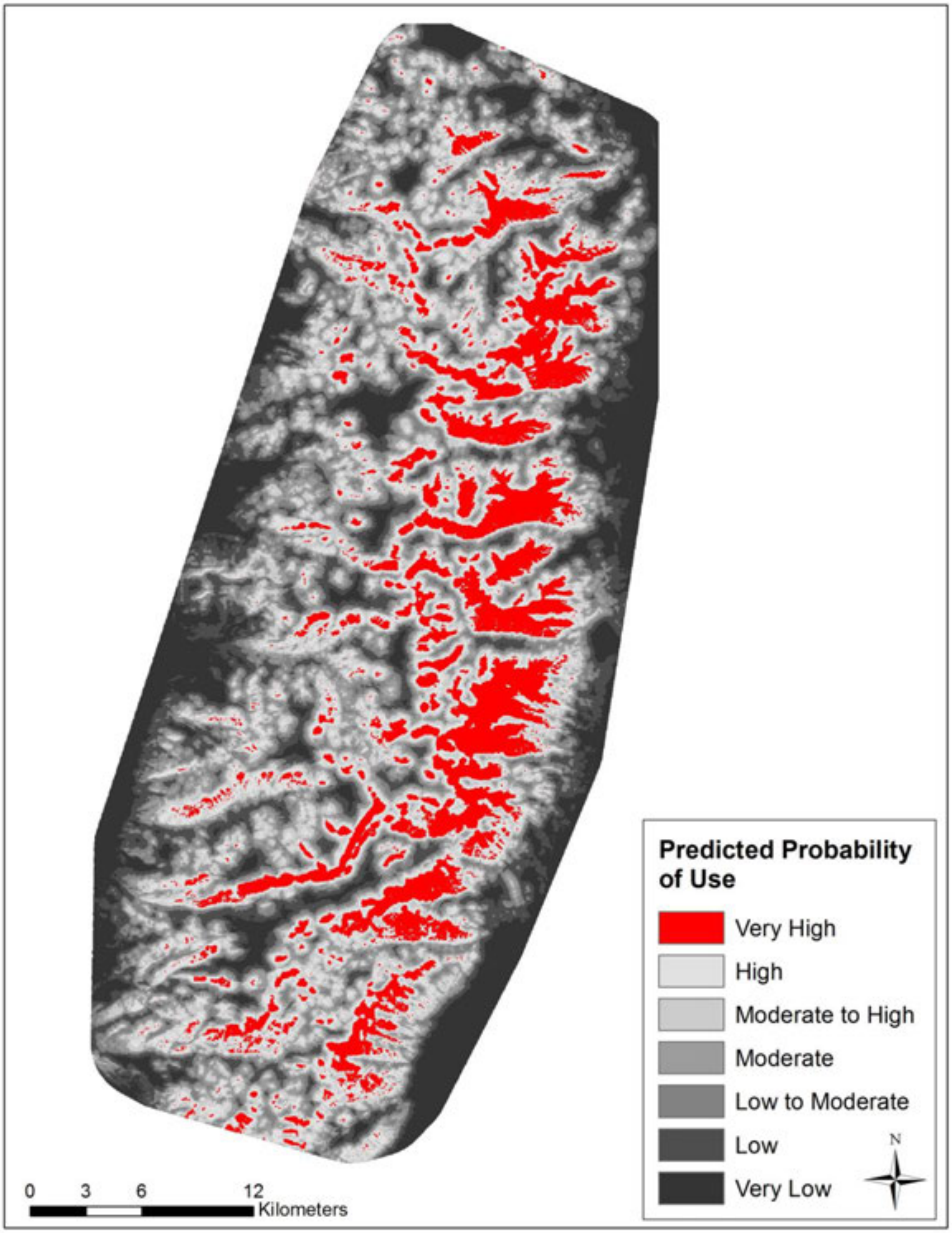


Figure 6. Predicted probabilities of bighorn sheep use during winter in the Teton Range from very low (dark grey) to very high (red) categories.

Table 1. Habitat use coefficients averaged among GPS-collared bighorn sheep for winter model ($n = 23$) and summer model ($n = 19$). Significance is indicated by bold-face (95% confidence intervals does not overlap zero).

	Winter Model				Summer Model	
	RSF Coefficients		Probability of Detection Coefficients		RSF Coefficients	
Covariate	β	95% CI	β	95% CL	β	95% CI
Prox. Escape Terrain	**0.667**	0.439, 0.896			**0.950**	0.745, 1.155
Prox. Snow-Free	**0.949**	0.679, 1.220				
Elevation	**0.549**	0.342, 0.755			**0.336**	0.295, 0.376
Solar Radiation	**0.220**	0.151, 0.288				
Tree Cover	**-0.157**	-0.256, -0.058	3.985	-0.746, 8.716	**-0.451**	-0.545, -0.356
Slope	0.082	-0.026, 0.189	**-0.465**	-0.893, -0.037	**0.516**	0.405, 0.628
Prox. Mineral Licks					0.074	-0.006, 0.154

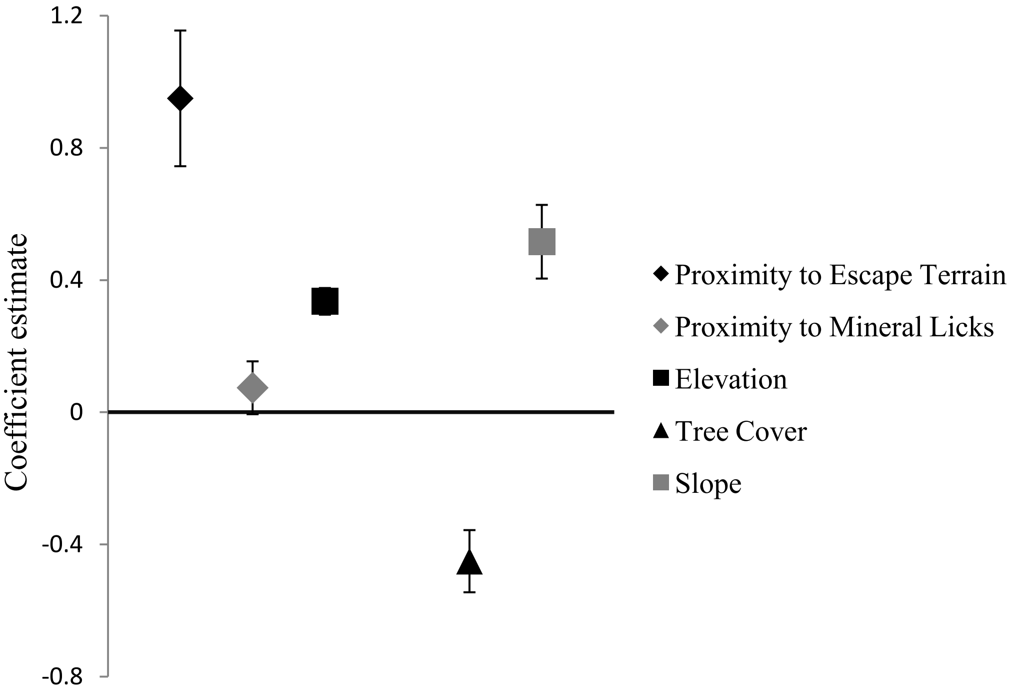
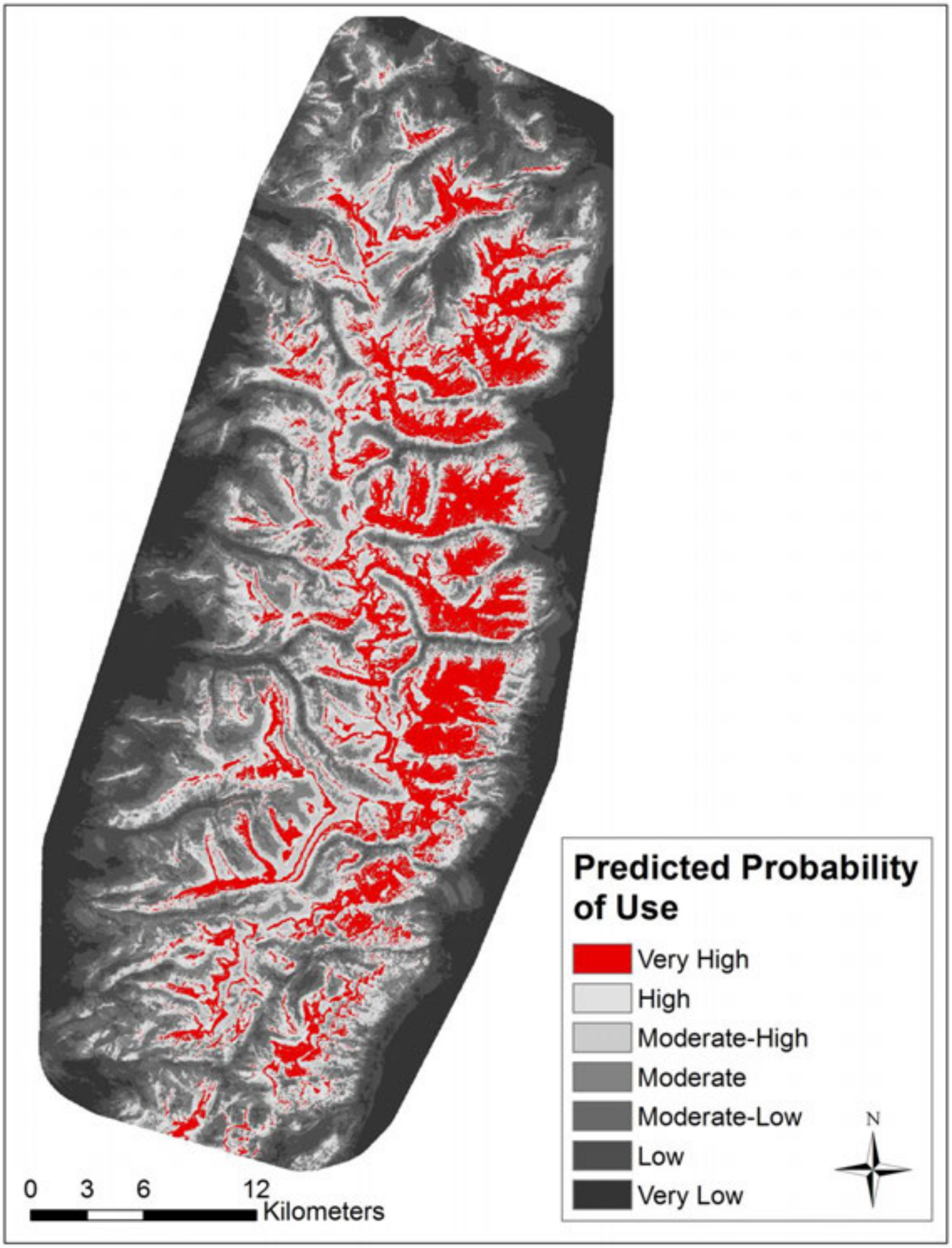


Figure 7. Averaged coefficients for the summer population-level resource selection function. Bars represent 95% confidence intervals for each coefficient, based on individual model (n = 19) estimates. Coefficients with bars that do not overlap zero indicate significant selection (+) or avoidance (-).

Figure 8. Predicted probabilities of bighorn sheep use during summer in the Teton Range from very low (dark grey) to very high (red) categories.



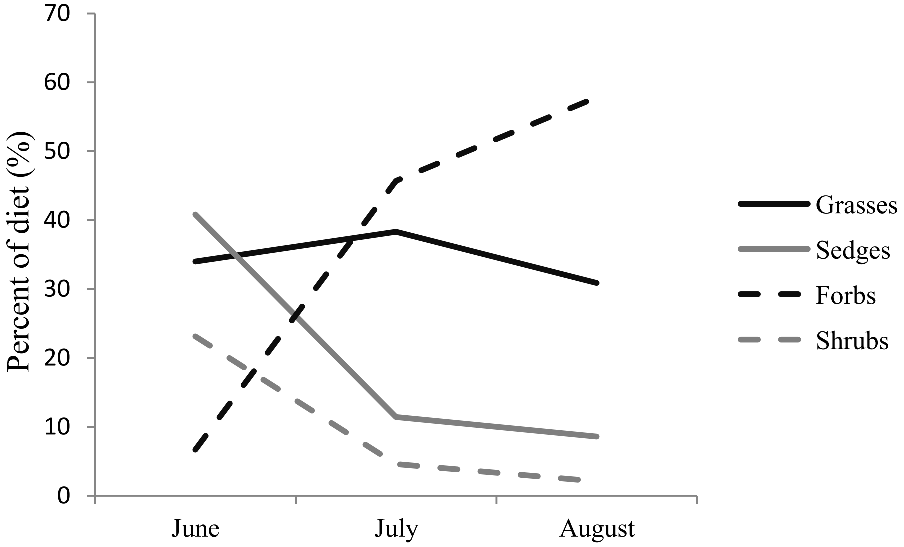


Figure 9. Percent occurrence of grasses, sedges, forbs, and shrubs in bighorn sheep diets during June, July, and August.

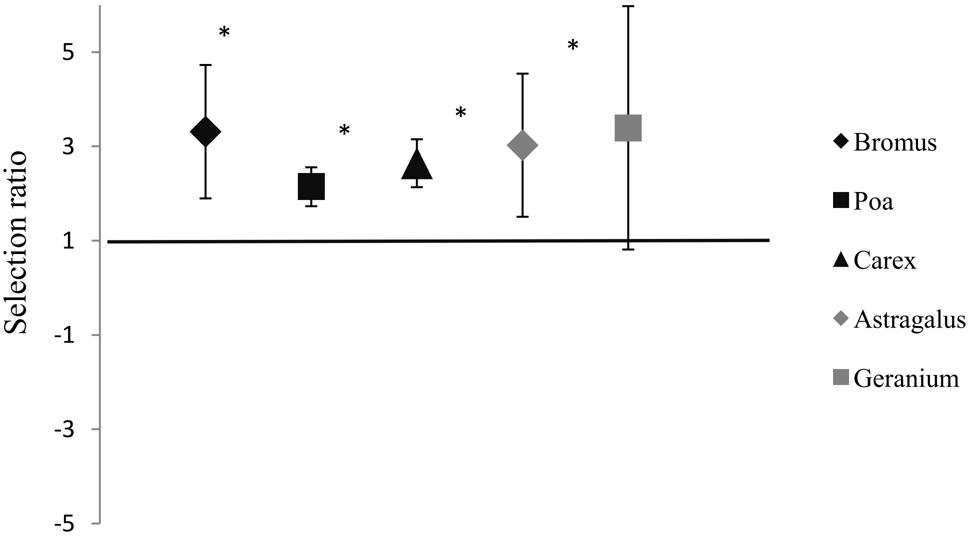


Figure 10. Average selection ratios for *Bromus*, *Poa*, *Carex*, *Astragalus*, and *Geranium* genera (n=3 for each genera), with 90% confidence intervals. Asterisks (*) indicate the 90% confidence interval does not overlap 1.0.

Plate 1. Photo of typical high elevation bighorn sheep winter range in the Teton Range (photo: A. Courtemanch).

CHAPTER II: IMPACTS OF NON-MOTORIZED WINTER BACKCOUNTRY RECREATION ON A BIGHORN SHEEP POPULATION IN NORTHWEST WYOMING

ABSTRACT

Expansion of human recreation into wildlands and backcountry areas is increasing worldwide, and its disturbance effects on wildlife are often overlooked. Immediate and short-term responses of wildlife to disturbance have been well-researched, but long-term effects such as avoidance of preferred habitats and altered movement patterns are less known, especially for ungulates. Relatively severe ungulate disturbance responses have been linked to off-trail, unpredictable forms of human recreation. We investigated the long-term behavioral responses of bighorn sheep (*Ovis canadensis*) to backcountry skiing and snowboarding in the Teton Range in northwest Wyoming, USA. We used global positioning system (GPS) data to evaluate winter habitat selection and movements of 28 adult female bighorn sheep and concurrent backcountry recreationist movements during winters 2009 and 2010. Resource selection functions revealed that Teton bighorn sheep relied on small patches of high elevation, windswept ridges and slopes for winter habitat. However, bighorn sheep avoided areas of backcountry recreation, even if those areas were otherwise relatively high quality habitat. Avoidance behavior resulted in up to a 30% reduction in available high quality habitat for some individuals. Bighorn sheep avoided areas with both low and high recreation use. Individual bighorn sheep exposed to high levels of recreation exhibited increased daily movement rates and home range sizes compared to sheep exposed to low or no recreation. These results reveal that bighorn sheep appear to be sensitive to forms of recreation which people largely perceive as having minimal impact to wildlife, such as backcountry skiing. Understanding these impacts is critical to design appropriate management strategies to ensure continued coexistence with this small bighorn sheep population.

Key-words: bighorn sheep, recreation, disturbance, *Ovis canadensis*, Teton Range, Wyoming, habitat selection

INTRODUCTION

Ecotourism and recreation in wildlands are increasing worldwide (Knight & Cole, 1995, Oliff et al. 1999). Expansion of human presence into wildlands represents an often overlooked source of disturbance to wildlife, and may exert additional pressures on already vulnerable populations. It is well established that human recreation can evoke stress responses in wildlife due to the ubiquitous perception of humans as potential predators (MacArthur et al. 1972, Knight & Cole 1995, Frid & Dill 2002, Arlettaz et al. 2007). Repeated disturbance can cause wildlife to accumulate high energetic costs (Béchet et al. 2004, Neumann et al. 2010, Cassirer et al. 1992) and avoid preferred habitats (Béchet et al. 2004, George & Crooks 2006, Thiel et al. 2008), with the potential to influence survival and abundance (Phillips & Alldredge 2000, Müllner et al. 2004, Bejder et al. 2006, Patthey et al. 2008). The effects of human disturbance on wildlife are complex, and depend on the type of disturbance, frequency, life history of the species, availability of alternative habitats, and other factors (Knight & Cole 1995, Papouchis et al. 2001, Stankowich 2008, Naylor et al. 2009). Why some individuals and populations seem to tolerate disturbance while others exhibit more extreme responses is still poorly understood, yet is critical for future conservation and management.

The behavioral mechanisms whereby human activity disturbs wildlife have been well established (Knight & Cole 1995, Frid & Dill 2002, Beale & Monaghan 2004). Disturbance from recreation can cause both short and long-term responses. Short-term responses have been documented for a variety of taxa and include flight behavior, elevated stress levels, and increased vigilance when recreationists are present (MacArthur 1972, Hamr 1988, Cassirer et al. 1992, Fowler 1999, Papouchis et al. 2001, Taylor & Knight 2003, Arlettaz et al. 2007, Neumann et al. 2010). Energetic costs from short-term disturbance events can be high. Neumann et al. (2010) estimated that energetic usage by female moose (*Alces alces*) increased by 48% and calves by 61% during the one hour following disturbance by skiers. Elk (*Cervus elaphus*) in Yellowstone National Park in Wyoming, USA expended 5.5% of their average daily energy budget when moving away from cross country skiers (Cassirer et al. 1992). Long-term responses include abandonment of preferred habitats (Foster & Rahs 1983, Hamr 1988, Béchet et al. 2004, Thiel et al. 2008) and altered movement and activity patterns to avoid human activity (Foster & Rahs 1983, George & Crooks 2006, Pauli & Buskirk 2007). Long-term displacement from preferred habitats and altered movement and activity patterns are more difficult to quantify, especially for animals such as ungulates with extensive home ranges. Studies that have sought to document these effects have found mixed conclusions (Hamr 1988, Cassirer et al. 1992, Papouchis et al. 2001, Neumann et al. 2010, Cadsand 2012). Hamr (1988) found that chamois (*Rupicapra rupicapra*) vacated suitable habitats for prolonged periods during intense periods of off-trail recreational activity by hikers, downhill skiers, and low-flying aircraft, but tolerated lower levels of activity. Desert bighorn sheep (*Ovis canadensis nelsoni*) avoided road corridors with both low and high levels of human activity, foregoing an average of 20.2% of their available habitat in the low use area and 35.5% in the high use area (Papouchis et al. 2001). However, other studies involving moose (Neumann et al. 2010), elk (Cassirer et al. 1992), and mountain goats (*Oreamnos americanus*) (Cadsand 2012) did not find prolonged abandonment of preferred habitats.

Much attention has been paid to the effects of motorized disturbance on ungulates (Côté, 1996, Preisler et al. 2006, Sawyer et al. 2006, Seip et al. 2007, Cadsand 2012) and hunting disturbance (Kilgo et al. 1998, Pauli & Buskirk, 2007); however non-consumptive, non-motorized recreation has been studied far less. These forms of recreation, such as hiking, backcountry skiing, cross-country skiing, mountaineering, and paragliding, are commonly perceived by the public as having minimal or no impact on wildlife (Taylor & Knight 2003). However, several studies have demonstrated that non-motorized recreation, especially occurring off-trail, can cause severe disturbance to ungulates (Hamr 1988, Papouchis et al. 2001, Reimers et al. 2003). For example, Reimers et al. (2003) found that mountain reindeer (*Rangifer tarandus tarandus*) in southern Norway exhibited longer movement distances following provocation by skiers (average 970 m) compared to snowmobiles (average 660 m). Hikers caused the most severe and prolonged responses in desert bighorn sheep, causing sheep to flee 100 m farther and remain alert 10 minutes longer than when disturbed by vehicles or mountain bikers (Papouchis et al. 2001). Notably, the unpredictability of a disturbance and the distance at which an animal first notices it, appear to be important in determining the severity of the response (Hamr 1988, Papouchis et al. 2001). Non-motorized, off-trail recreationists can often approach animals at closer distances before they are detected (Papouchis et al. 2001). Indeed, some wildlife can become habituated to predictable, repeated disturbances, such as vehicle traffic on roads or heavily used hiking trails (Hamr 1988). However, activities that occur away from established roads or trails often elicit stronger disturbance effects than activities confined to predictable routes (Miller et al. 2001). In addition, several studies have found that the presence of dogs with recreationists heightens wildlife responses. Miller et al. (2001) found that mule deer (*Odocoileus hemionus*) fled at greater distances and moved farther when approached by a pedestrian and dog than by a pedestrian alone.

Previous studies have indicated that disturbance during sensitive times of year is especially detrimental to wildlife, such as the nesting period for birds (Müllner et al. 2004) and the denning periods for mammals (Magoun & Copeland 1998, Linnell et al. 2000). Winter is a demanding time of year for temperate ungulates, during which individuals rely on their fat reserves and limited forage to meet the energetic demands of thermoregulation and gestation (Parker et al. 2009). Additional energetic demands caused by disturbance or avoidance of preferred habitats have the potential to influence the energy balance of individuals. Few studies have successfully linked disturbance from non-motorized recreation to long term changes in habitat use and movement patterns of ungulates. We investigated these questions using a bighorn sheep (*Ovis canadensis*) population in the Teton Range in northwest Wyoming, USA. The Teton Range bighorn sheep population is small and isolated, spending summers and winters in alpine habitats above 3,000 m after losing its traditional migration routes over 60 years ago to residential development, construction of roads and fences, and widespread livestock grazing. Previous work has demonstrated that high elevation, wind-swept ridgelines and slopes serve as critical habitat for the population during winter (see Chapter 1), however these areas are small and scattered across the landscape. The town of Jackson, Wyoming is a popular destination for winter sports enthusiasts, and backcountry skiing and snowboarding make up the majority of winter recreation in the study area. We developed two main predictions based on previous studies of ungulate responses to recreation. First, we predicted that bighorn sheep would alter their winter habitat use in areas with high intensities of off-trail recreation activity. We expected that bighorn sheep would tolerate lower levels of recreation activity due to the importance of their limited winter habitat. Second, we predicted that bighorn sheep exposed to high recreation intensities would exhibit increased daily movement rates and larger home range sizes.

METHODS

Study area

We studied bighorn sheep habitat selection and human backcountry recreation patterns during winters 2008/2009 and 2009/2010 in the Teton Range, located within the Greater Yellowstone Ecosystem (GYE) 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 approximately 10 km southeast of the study area. The Teton Range stretches north to south for approximately 60 km, with elevations ranging from 2,000 m in the foothills to 4,197 m at the summit of the Grand Teton. The area is typified by rugged, rocky peaks and steep canyons that cut east-west throughout the range. Vegetation varies considerably across elevational and topographical gradients. Surrounding valleys are mostly comprised of mesic sagebrush steppe habitat. In the foothills, aspen (*Populus tremuloides*) stands are intermixed with conifers, including Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and Douglas fir (*Pseudotsuga menziesii*), often with dense shrub understories. At mid-elevations, south-facing slopes are relatively open and support complex mountain shrub or forb/grassland communities containing snowberry (*Symphoricarpus* spp.), serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus* spp.), geranium (*Geranium* spp.), columbine (*Aquilegia* spp.), and brome (*Bromus* spp.) with scattered Douglas fir stands. Higher elevations are characterized by dry and wet alpine meadows and talus slopes, with a diversity of forbs and grasses such as milk-vetch (*Astragalus* spp.), sweet-vetch (*Hedysarum* spp.), buttercups (*Ranunculus* spp.), cinquefoil (*Potentilla* spp.), groundsel (*Senecio* spp.) and bluegrass (*Poa* spp.). Other ungulates in the study area include elk, mule deer, and moose. The study area supports a suite of predators, including mountain lion (*Puma concolor*), coyote (*Canis latrans*), golden eagle (*Aquila chrysaetos*), wolverine (*Gulo gulo*), black bear (*Ursus americanus*), grizzly bear (*Ursus arctos*), and wolf (*Canis lupus*).

The Teton Range bighorn sheep population is a small, native bighorn sheep herd that numbers approximately 100-150 individuals and resides in the Teton Range year-round. Historically, this population migrated seasonally between high elevation summer range and low elevation winter range in the surrounding valleys and canyons (Whitfield 1983). However, permanent human settlement in the area, which began in the late 19th century, had a rapid and lasting impact on the population's migration patterns. The cumulative effects of road and fence construction, residential development, widespread domestic sheep grazing, and wildfire suppression on low elevation winter ranges caused the population to abandon its migration by around 1950 (Whitfeld 1983). Consequently, the population now survives year-round on its traditional, high elevation summer range.

The town of Jackson is a premier destination for winter sports, particularly skiing. Winter recreation has increased rapidly in the Teton Range during the past two decades; cross country and backcountry skiing has tripled in GTNP (National Park Service 2014). Since the majority of the Teton Range is designated Wilderness, where motorized recreation is prohibited, recreation is dominated by backcountry skiing and snowboarding, with ice climbing and mountaineering occurring less frequently. Backcountry skiing was popularized in the early 1970s, and the Jackson area was at the forefront of the sport (Turiano 1995). Recent technological advances in equipment have enabled backcountry skiers to travel faster, go longer distances, and accomplish highly technical routes. The Teton Range is regularly featured in backcountry ski magazines and videos, attracting large numbers of both amateur and elite backcountry skiers. There are two ski resorts that operate on National Forest lands in the Teton Range, Jackson Hole Mountain Resort (JHMR), which opened in 1965 on BTNF, and Grand Targhee Resort, which opened in 1969 on CTNF. Both resorts provide ski lift service to out-of-bounds backcountry areas, making access to high elevation, alpine areas relatively easy for large numbers of recreationists.

Bighorn sheep capture

We used helicopter net-gunning to capture 20 female bighorn sheep during 14-15 February 2008 and 8 female bighorn sheep during 12-13 March 2009 in the Teton Range. The population is segregated into a northern and southern group, separated by approximately 15 km. Very little winter recreation occurs in the northern portion of the study area; the majority is concentrated in the southern portion. Of the sheep we captured, 10 were in the northern group and 18 were in the southern group. We fitted individuals with store-on-board global positioning system (GPS) collars (model TGW-3500, Telonics, Inc., Mesa, Arizona, USA), programmed to acquire a fix every 5 hours and automatically release after 29 months (for 2008 capture) or 17 months (for 2009 capture). All animal captures were conducted according to protocols approved by the University of Wyoming’s Institutional Animal Care and Use Committee.

Backcountry recreation data

We sought to collect concurrent movement data from backcountry recreationists and GPS-collared bighorn sheep during winters 2009 and 2010. We monitored the movements of backcountry recreationists originating from 10 backcountry access points in the Teton Range from January – April 2009 and 2010 (Fig. 2). Recreationists were randomly intercepted at each access point according to a sampling protocol of random days stratified by weekends and weekdays (D'Antonio et al. 2010). One recreationist from each group was asked to voluntarily participate by carrying a GPS unit (Garmin GPS 60, Garmin International, Inc., Olathe, Kansas, USA) that was programmed to automatically collect a GPS fix every 5 seconds while traveling in the backcountry. Sampled access points included Bradley-Taggart and Death Canyon trailheads in GTNP, Upper Rock Springs, Lower Rock Springs, and Headwall/Granite backcountry gates on JHMR on BTNF, Fish Creek Road on BTNF, Grand Targhee Resort backcountry gate on CTNF, and Teton Canyon, Darby Creek, and Fox Creek trailheads on CTNF (Fig. 2). In addition, we worked with a local business that manages three backcountry yurts on CTNF to send GPS units with their clients. We did not sample recreationists at Teton Pass, a popular backcountry access point on BTNF, because minimal bighorn sheep winter habitat exists in that area and sheep use is infrequent. We were interested in identifying general recreation patterns, thus we sampled trailheads and recreationists at random. Overall, we collected a total of 760 usable GPS movement paths from backcountry recreationists.

To account for any possible positional error associated with GPS measures, calibration techniques were employed (D'Antonio et al. 2010). A high accuracy GPS point was recorded using a Trimble GeoXT GPS unit (Trimble Navigation Limited, Sunnyvale, California, USA) at each backcountry access point. At the start of each sampling day, a Garmin 60 GPS unit was randomly selected and 75 points were recorded at the same location at which the calibration point was recorded. A Euclidean distance was then calculated from each point recorded by the Garmin 60 GPS units to the calibration point; these values were averaged to determine the overall positional error.

To estimate relative intensities of recreation use (numbers of recreationists), we deployed TrailMaster^{TM} 1550 active infrared trail counters (Goodson & Associates, Inc., Lenexa, Kansas, USA) at 5 backcountry access points from January – April 2010. These points were Bradley-Taggart, Death Canyon, Upper Rock Springs, Lower Rock Springs, and Teton Canyon. Trail counters were located on backcountry uphill skin tracks, sometimes over 3 miles from a parking lot, to avoid counting frontcountry users such as snowshoers and cross country skiers. We deployed several trail counters at some backcountry access points to account for multiple routes. Trail counter data was visually inspected for erroneous readings caused by snowstorms or wind, and data from these events were removed. We corrected for double-counts (recreationists passing the trail counter on their way out and back from the backcountry) by estimating the frequency of occurrence of double-counts by recreationists sampled with GPS units. Trail counters supplied estimates of intensities of use, whereas GPS units identified backcountry routes and provided spatial patterns of use.

To evaluate the spatial influence of backcountry recreation routes on bighorn sheep habitat use, we developed a winter recreation variable for inclusion in a resource selection function (RSF). We mapped all GPS tracks collected from recreationists in a geographical information system (GIS) (ESRI ArcGIS 10). We treated all recreation routes the same, regardless of the amount of use. Data from trail counters and GPS units showed that recreation routes had a range of use, from less than 10 people (some technical routes in GTNP) to more than 5,500 people (Rock Springs Canyon on BTNF) in winter 2010. We expected that bighorn sheep exposed to low levels of recreation would fail to exhibit avoidance of recreation in their individual habitat selection models, whereas bighorn sheep exposed to higher levels of use would exhibit avoidance.

Because bighorn sheep respond to human disturbance up to 400 m away (Papouchis et al. 2001), we created viewsheds around all GPS tracks extending up to that distance (Spatial Analyst, ESRI ArcGIS 10). Viewsheds were designed to take into account topography, tree cover, height of the recreationist (accounting for snow depth), and height of sheep. The resulting spatial layer, from here on referred to as the recreation footprint, represents the area around each recreation route where sheep and recreationists would be in view of each other, creating the potential for disturbance. This approach takes into account the reality that bighorn sheep and winter recreationists rarely directly cross paths because skiers and snowboarders utilize areas with deep snow, whereas sheep are usually confined to rocky, bare slopes or ridges. However, the recreation footprint approach captures the fact that these two types of areas occur in close proximity to each other throughout the Teton Range.

Bighorn sheep habitat use amid human disturbance

To assess bighorn sheep avoidance of backcountry recreation routes, we evaluated the influence of landscape features and winter recreation activity on winter habitat use. We used each GPS-collared bighorn sheep in the southern portion of the study area as the sampling unit (n=11), and utilized a discrete choice resource selection function (RSF) (Manly et al. 2002) to estimate coefficients for each individual. We excluded sheep that survived for less than 1 month or had no recreation activity recorded in their area of availability for the model. Winter was defined as January 1 – April 15 for both models to coincide with the majority of backcountry recreation activity. We developed two models, one with only landscape covariates and one including the addition of a recreation covariate. Landscape covariates were the same used in the winter RSF in Chapter 1: distance to rugged escape terrain, distance to snow-free areas, elevation, solar radiation, tree cover, and slope. We combined terrain ruggedness and escape terrain into one variable, defined as "rugged escape terrain" that had a slope > 30º, terrain ruggedness index > 0.001 (Sappington et al. 2007), and patch-size >= 1 hectare (Dicus 2002, DeCesare & Pletscher 2006). To spatially delineate consistently snow-free areas, we used a new technique utilizing the normalized difference snow index (NDSI) with Landsat satellite imagery from 1993 – 2011 (U.S. Geological Survey, http://glovis.usgs.gov) (see Chapter 1). Elevation and slope covariates were derived from a 10-m digital elevation model (DEM) (U.S. Geological Survey). Percent tree cover was derived from a 30-m National Land Cover Database for Wyoming (2001). Winter solar radiation was estimated using the Spatial Analyst solar radiation function (ESRI ArcGIS 10) (Kumar et al. 1997, Dicus 2002, DeCesare & Pletscher 2006). We created proximity to rugged escape terrain and proximity to snow-free areas rasters using the Spatial Analyst distance function (ESRI ArcGIS 10). The winter recreation covariate was created using the recreation footprint layer. We created a raster where cells inside the recreation footprint received a value of 1 and cells outside received a value of 0. We conducted a Pearson's pairwise correlation analysis before modeling to identify multicolinearities, but found that no variable combinations exceeded $|r| > 0.60$.

We developed a slightly different winter model than was used in Chapter 1 by using the modified date range and only bighorn sheep in the southern portion of the study area ($n = 11$) to evaluate the influence of recreation on habitat selection. We created a sampling grid of 100 m x 100 m cells that was clipped to each sheep's local convex hull polygon of winter locations. 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. We estimated habitat use coefficients for each individual animal and then averaged coefficients to develop population-level inference. To evaluate significance, we calculated mean and 95% confidence intervals for each covariate from the population-level model. Significance of averaged coefficients was determined based on whether confidence intervals overlapped zero (Marzluff et al. 2004).

To evaluate the spatial distribution of winter habitat and the effect of winter recreation on winter habitat predictions, we mapped the predicted probability of bighorn sheep habitat use from each population-level model, with and without recreation. We applied the model estimates using Raster Calculator (ESRI ArcGIS 10) on a grid of 30 m x 30 m cells. The model prediction for each cell was assigned a value of 1 to 7 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 bighorn sheep use.

Influence of recreation on movement rates and home range sizes

To evaluate the impact of winter recreation on individual bighorn sheep, we analyzed diurnal sheep movement rates in relation to recreation intensity. We found that GPS-collared bighorn sheep were exposed to various levels of recreation within their home ranges, ranging from virtually none to daily incursions, as determined by GPS tracks of recreationists and trail counters. We aimed to quantify the intensity of recreation activity within each bighorn sheep home range for each winter for both northern and southern sheep ($n = 30$) during the core recreation period, January 1 – April 15. The home range of each sheep in each winter was defined using a 95% kernel polygon (ESRI ArcGIS 10). We mapped all recreation footprints that intersected each home range, calculated the proportion of the home range covered by each route and its footprint, and assigned each route an intensity weight based on the proportion of the total number of recreationists carrying GPS units that used that route (Fig. 3). We used the following formula to calculate a recreation intensity value (RIV) for each sheep for each winter, where i = a recreation route and n = total routes within the home range:

$$\text{RIV} = \sum_{i=1}^{n} (\text{Proportion of home range area} * \text{Proportion of total GPS units})_i$$

The RIV is a dimensionless value that indexes the relative amount of recreation disturbance within the home range of each bighorn sheep during each winter. All northern sheep were assigned a RIV of zero; they were exposed to none or very little recreation, therefore we did not sample recreationists in their home ranges. We used the RIVs to classify each sheep for each winter into high, low, or no recreation categories. Individuals with winters that had RIV > 0.5 were assigned to the high recreation class (n = 8), RIV < 0.5 to low recreation (n = 11), and sheep with zero (all northern sheep) to no recreation (n = 11).

We quantified the average diurnal movement rate (m/day) of each sheep for each winter by summing each step length between GPS fixes between the hours of 700 and 1,600 and taking the average for all days between January 1 and April 15. We treated each winter as a separate sampling period under the assumption that sheep may exhibit different movement rates each winter due to maternal status, body condition, or winter snow conditions (Shackleton et al. 1999). We averaged the diurnal movement rates for sheep in each of the recreation intensity categories, high, low, and no recreation. We compared means between categories using a one-way analysis of variance (ANOVA) and Tukey's honest significant difference (HSD) test.

We calculated home range sizes for each sheep for each winter using 95% kernel polygons (ESRI ArcGIS 10). We averaged home range sizes for sheep within each recreation intensity category and compared means between categories using a one-way ANOVA and Tukey’s HSD test.

RESULTS

Recreation patterns and intensities

We collected 760 usable GPS tracks from recreationists during January – April 2009 and 2010. These were distributed among Bradley-Taggart (*n* = 124), Death Canyon (*n* = 48), Upper Rock Springs (*n* = 332), Lower Rock Springs (*n* = 86), Headwall/Granite Canyon (*n* = 49), Fish Creek Road (*n* = 2), Teton Canyon (*n* = 43), Grand Targhee (*n* = 31), Darby Creek (*n* = 5) and Fox Creek (*n* = 2) backcountry access points. We also collected 38 GPS tracks from recreationists utilizing backcountry yurts. We sampled recreationists on 140 separate days over the two winters. Average distance travelled by recreationists in one day was 10.0 km, but several groups travelled over 25.0 km. The average elevation gained by recreationists was 913.0 m, and the maximum was 1776.0 m.

The amount of use from various backcountry access points differed widely throughout the Teton Range. The most heavily used access points were the Upper and Lower Rock Springs backcountry gates at the JHMR on BTNF (8,712 and 3,181 backcountry recreationists, respectively). Trailheads in GTNP had less use, with 2,225 backcountry recreationists recorded at Bradley-Taggart and 1,005 at Death Canyon. Two-hundred and nine visits were recorded at Teton Canyon trailhead on CTNF (Fig. 4). We did not have trail counters at every backcountry access point, but it was obvious that we collected data for the areas with the majority of the use. Data from the trail counters showed that approximately 78% of backcountry recreationists in the study area originated from JHMR through backcountry gates that were accessed via ski lifts, while the remaining 22% of use originated from parking lots in GTNP and CTNF. Based on observations we made while recruiting recreationists to carry GPS units, other backcountry access points received far less use. The exception was the Headwall/Granite Canyon access point from JHMR, where a moderate amount of use occurred but it was logistically too difficult to establish reliable trail counters.

The response rate from recreationists to participate in the study was 77%, but differed substantially between recreationists entering the backcountry from ski resorts (70% participation) compared to outside of ski resorts (91% participation). Ninety-eight percent of recreationists contacted were backcountry skiing or snowboarding and 2% were ice climbing. GPS positional error averaged 3.7 meters for the Garmin GPS 60 units, which we deemed to be inconsequential at the spatial scale of our analysis.

Bighorn sheep winter habitat use in a recreated landscape

We have previously shown that Teton bighorn sheep select for proximity to rugged escape terrain, proximity to consistently snow-free areas, high elevation, and south-facing slopes, and avoid dense tree cover during winter (see Chapter 1). We found the same results when using a revised winter model with only southern sheep during the core recreation period (Table 1, Fig. 5). When we included a recreation covariate, we found that sheep avoided recreation footprints ($\beta = -0.247$; Table 1, Fig. 5). Interestingly, we found that all individual sheep exhibited avoidance of recreation footprints, regardless of whether recreation intensity was low or high.

Areas of relatively high quality winter habitat for Teton bighorn sheep are fragmented and patchy on the landscape, surrounded by a matrix of unsuitable habitat (Fig. 6; also see Chapter 1). The predicted probability maps show that bighorn sheep avoidance of recreation footprints results in an overall reduction in suitable habitat (Figs.6 - 8). Across the study area, the models predict that there is a 4% loss of the highest probability habitat with the addition of the recreation covariate (Fig. 6). However, the difference is much greater within some individual sheep home ranges, ranging from a 15-31% reduction in highest probability habitat for some individuals (Fig. 7). Interestingly, sheep that winter primarily in winter closure areas were also affected, losing up to 10% of their highest probability habitat from the influence of recreation routes adjacent to the closures and incursion events into the closures (Fig. 8).

Bighorn sheep movement rates and home range sizes

We found that bighorn sheep exposed to various recreation intensities exhibited different daily movement rates (m/day) ($F = 5.218$, df = 2, 24, $p = 0.013$; Fig. 9). Post-hoc comparisons using Tukey's HSD test indicated that bighorn sheep exposed to high recreation intensities had higher daily movement rates ($M = 374.2$, ± 40.3 SE) when compared to sheep exposed to low ($M = 256.7$, ± 23.6 SE, $p = 0.038$) or no recreation ($M = 249.1$, ± 23.2 SE, $p = 0.016$). Movement rates did not differ between the low and no recreation areas ($p = 0.982$). Over the course of a winter (90 days), the additional daily movements for sheep in high recreation areas accumulate to approximately 11.25 km per individual.

We found that bighorn sheep also exhibited different home range sizes (km^2) depending on recreation intensity ($F = 4.395$, df = 2, 24, $p = 0.024$; Fig. 10). Post-hoc comparisons using Tukey's HSD test indicated that bighorn sheep exposed to high recreation intensities had larger home ranges ($M = 22.3$, ± 3.59 SE) when compared to sheep exposed to low ($M = 14.3$, ± 0.62 SE, $p = 0.042$) or no recreation ($M = 14.8$, ± 1.26 SE, $p = 0.039$). Home range sizes did not differ between the low and no recreation areas ($p = 0.985$).

DISCUSSION

Few studies have successfully linked disturbance from non-motorized recreation to long-term changes in ungulate habitat use and movement patterns. We found that bighorn sheep avoided winter backcountry recreation routes, even where they overlapped with predicted high quality winter habitat. Our findings did not support our prediction that bighorn sheep would only avoid routes with high intensities of human use and tolerate low levels of use due to the importance of access to limited winter habitat. Instead, bighorn sheep appeared highly sensitive to backcountry recreation, because they avoided routes with both low and high intensities of use. Our results supported our second prediction, that individual bighorn sheep exposed to high levels of recreation would exhibit increased daily movement rates and larger home ranges than individuals exposed to less recreation. Overall, these results suggest that bighorn sheep in this system are highly sensitive to human disturbance, changing their habitat use and movement patterns even during a season when resources are limited.

Influence of recreation on bighorn sheep habitat use

Having lost access to their traditional migration routes and low-elevation winter range, Teton bighorn sheep now winter exclusively on high elevation windswept ridgelines and south-facing slopes in the Teton Range (see Chapter 1). These areas of winter habitat are small and patchy across the landscape, fragmented by a matrix of unsuitable habitat comprised of deep snow and tree cover (Fig. 6). Previous work has suggested that winter habitat is a limiting factor for this population, and that sheep do not seem to be able to increase their summer foraging to offset the cost of poor winter habitat (see Chapter 1). Aside from two ski resorts, backcountry skiing and snowboarding make up the majority of human activity in bighorn sheep winter habitat (Plate 1).

We found that these types of backcountry recreation are widespread and pervasive across the Teton Range, and perhaps most importantly, occur in an off-trail manner. Most recreation occurs in a diffuse, "spider web" pattern across the landscape (Fig. 2). Other studies have shown that this type of off-trail, unpredictable human activity elicits a stronger behavioral response from ungulates than does activity on established, predictable routes (Hamr 1988, Papouchis et al. 2001, Enggist-Dublin & Ingold 2003). Papouchis et al. (2001) found that desert bighorn sheep fled in 61% of instances when hikers approached from off-trail, compared to less than 20% when mountain bikers and vehicles approached on established trails and roads. Chamois tolerated hikers and cross-country skiers as long as they stayed on known trails (Hamr 1988). Unpredictable disturbances such as people traveling off-trail likely elicit strong responses in ungulates because they are analogous to predation stimuli (Frid & Dill 2002, Beale & Monaghan 2004). Previous studies have found that ungulates do not habituate to this type of off-trail recreation and may instead become increasingly sensitized (Foster & Rahs 1983, Côté 1996, Enggist-Dublin & Ingold 2003).

Our results are consistent with the idea that off-trail, unpredictable human activity represents a disturbance to wintering sheep through a heightened perception of predation risk (Frid & Dill 2002). Teton bighorn sheep exhibited avoidance of backcountry recreation footprints (both routes and viewsheds extending up to 400 m away), regardless of recreation intensity of use (Fig. 5). In the Teton Range, most backcountry skiing and snowboarding routes are located in areas with deep snow, which can be directly adjacent to more rugged, windblown slopes that characterize bighorn sheep habitat. Bighorn sheep rely on their visual acuity to detect predators, which may explain why sheep exhibit disturbance responses even when recreationists are in adjacent areas within sight distance (Shackleton et al. 1999). This result highlights the importance of considering viewsheds when evaluating potential disturbance to wildlife.

Surprisingly, sheep did not use habitat within recreation footprints, even during times when recreationists were absent, despite limited winter habitat availability. Other authors have suggested that animals will tolerate disturbance when alternative habitats are unavailable or limited (Gill, et al. 2001, Stankowich 2008, Cadsand 2012), but this does not appear to be the case with Teton bighorn sheep. This avoidance behavior resulted in up to a 30% reduction in the predicted highest quality habitat for some individuals that wintered in high recreation areas (Fig. 7). This effective loss of winter habitat could potentially lead to less available forage, density-dependence effects, and demographic consequences (Beale & Monaghan 2004, Pauli & Buskirk 2007), although evaluating these effects was outside of the scope of this study. Because Teton bighorn sheep have already been restricted to one seasonal range through migration loss, the behavioral avoidance of backcountry recreation illustrates how migration loss can heighten the effect of other stressors acting on animals occupying non-traditional range.

Few studies have been able to identify these types of long-term effects on ungulates from recreation (Stankowich 2008, Cadsand 2012). However, studies involving other taxa have documented avoidance of recreation areas and heightened stress levels (Fowler 1999, Arlettaz et al. 2007, Thiel et al. 2008). Thiel et al. (2008) found that capercaillie (*Tetrao urogallus*) avoided ski routes during peak recreation periods but returned when recreationists were absent. Our study is one of the first to document long term avoidance of non-motorized recreation areas by ungulates, even if those areas are otherwise relatively high quality habitat.

Movement rates and home range sizes

Bighorn sheep exposed to relatively high levels of recreation exhibited increased movement rates and larger home ranges than individuals exposed to low or no recreation (Fig. 9, Fig. 10). Interestingly, these findings suggest that despite avoiding recreation footprints through habitat selection, individuals still exhibit disturbance effects through movement. Increased movement rates could be caused by, 1) fleeing events caused by human disturbance, and/or 2) foraging in sub-optimal habitats. Regardless of the cause, increased movement rates, especially during winter, can increase daily energetic costs (Daily & Hobbs 1989). Because temperate ungulates are already in a net energy balance during winter, such costs have the potential to scale up to influence nutritional dynamics and demographic fates of individuals (Parker et al. 2009).

Restricting human activity in critical wildlife habitat is a commonly used management tool (Knight & Cole 1995), and our results suggest that existing winter closures in GTNP are effective at buffering individual bighorn sheep from disturbance effects. Bighorn sheep that spent most of the winter within the closures experienced low recreation exposure and exhibited the same daily movement rates and home range sizes as sheep in the northern portion of the study area that experienced little to no recreation disturbance (Fig. 9, Fig. 10). However, although most recreationists complied with the closures, some incursions were documented. Bighorn sheep appeared to avoid these incursion routes, even though human activity was infrequent (Fig. 8). In addition, recreation activity adjacent to the closures caused a small loss of habitat caused by the recreation footprint extending into the closures. This result highlights the potential importance of considering viewsheds when designing wildlife closures. Our results suggest that in order for closures to be effective, there needs to be very minimal or no incursions to prevent displacement of bighorn sheep from preferred habitats.

Management implications

The Teton bighorn sheep population has experienced numerous changes to its habitats and migration patterns due to residential development, construction of roads and fences, historical livestock grazing, and wildfire suppression, culminating in the population abandoning its traditional low elevation winter ranges (Whitfield 1983). Currently, the population is small and appears to be limited by winter habitat quality and availability (see Chapter 1). Our study suggests that winter habitat is further constricted by backcountry skiing and snowboarding activity and that bighorn sheep likely incur additional energetic costs in areas of high recreation activity. Disturbance from diffuse and unpredictable patterns of backcountry recreation represents an added pressure to this small, isolated population.

Since bighorn sheep appear to be affected by all levels of recreation intensity, seasonal closures to human activity would maximize protection of bighorn sheep. However, seasonal closures may not be an option in all areas. Other studies have suggested that restricting recreation to certain, predictable routes may potentially mitigate disturbance (Hamr 1988), however others have found that ungulates may never habituate (Fairbanks & Tullous 2002). Reducing overall numbers of recreationists would likely produce little benefit since bighorn sheep exhibit avoidance of low use recreation areas.

Bighorn sheep are an iconic species of the Greater Yellowstone Ecosystem, one that is associated with its deepest wilderness areas. However, continued human expansion and use of wildlands likely represents on additional stress on this species. Unexpectedly, bighorn sheep appear to be sensitive to forms of recreation which people largely perceive as having minimal impact to wildlife, such as backcountry skiing. Understanding these impacts is critical to design appropriate management to ensure continued human-wildlife coexistence in wildlands.

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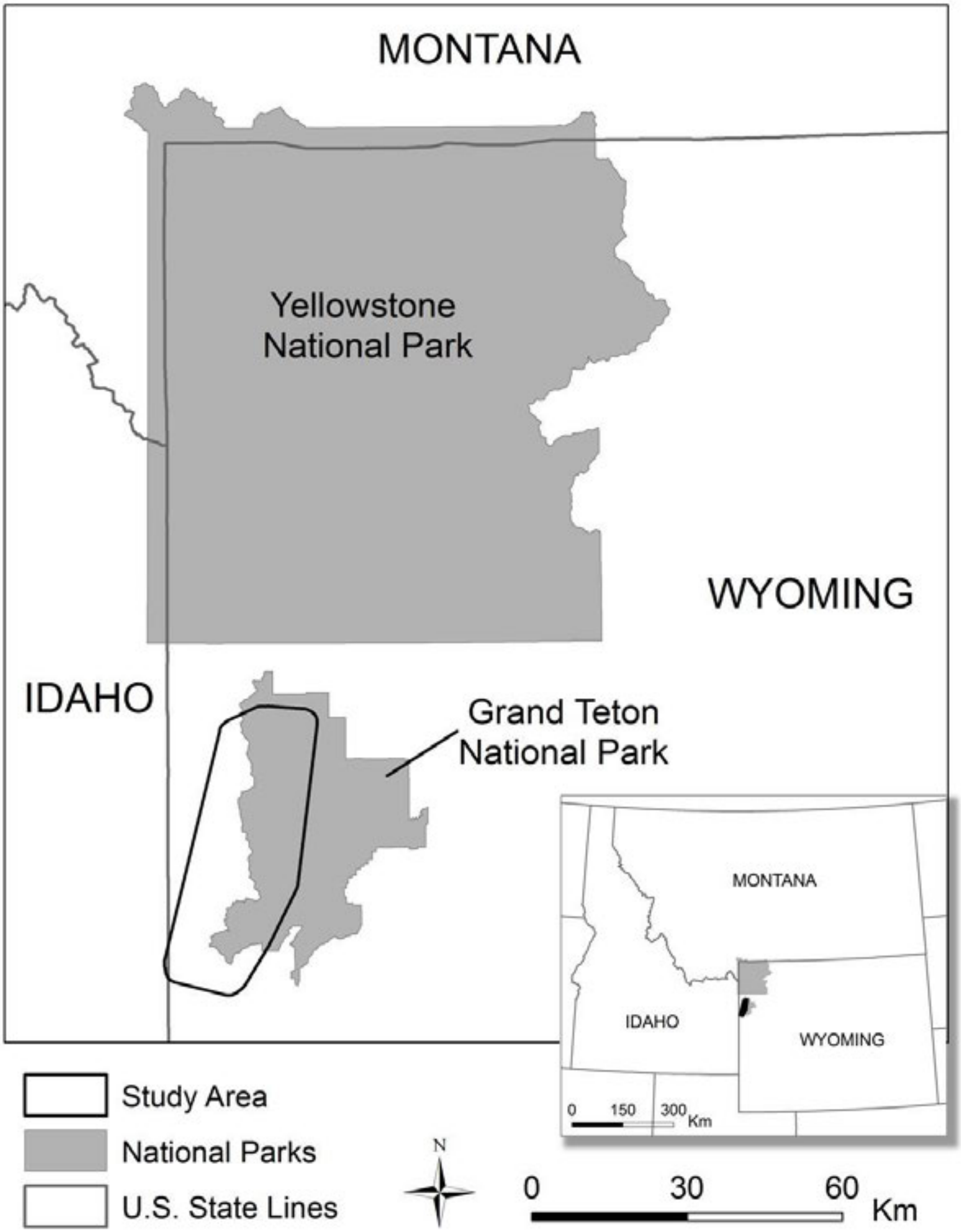

Figure 1. Study area in the Teton Range in northwest Wyoming, USA.

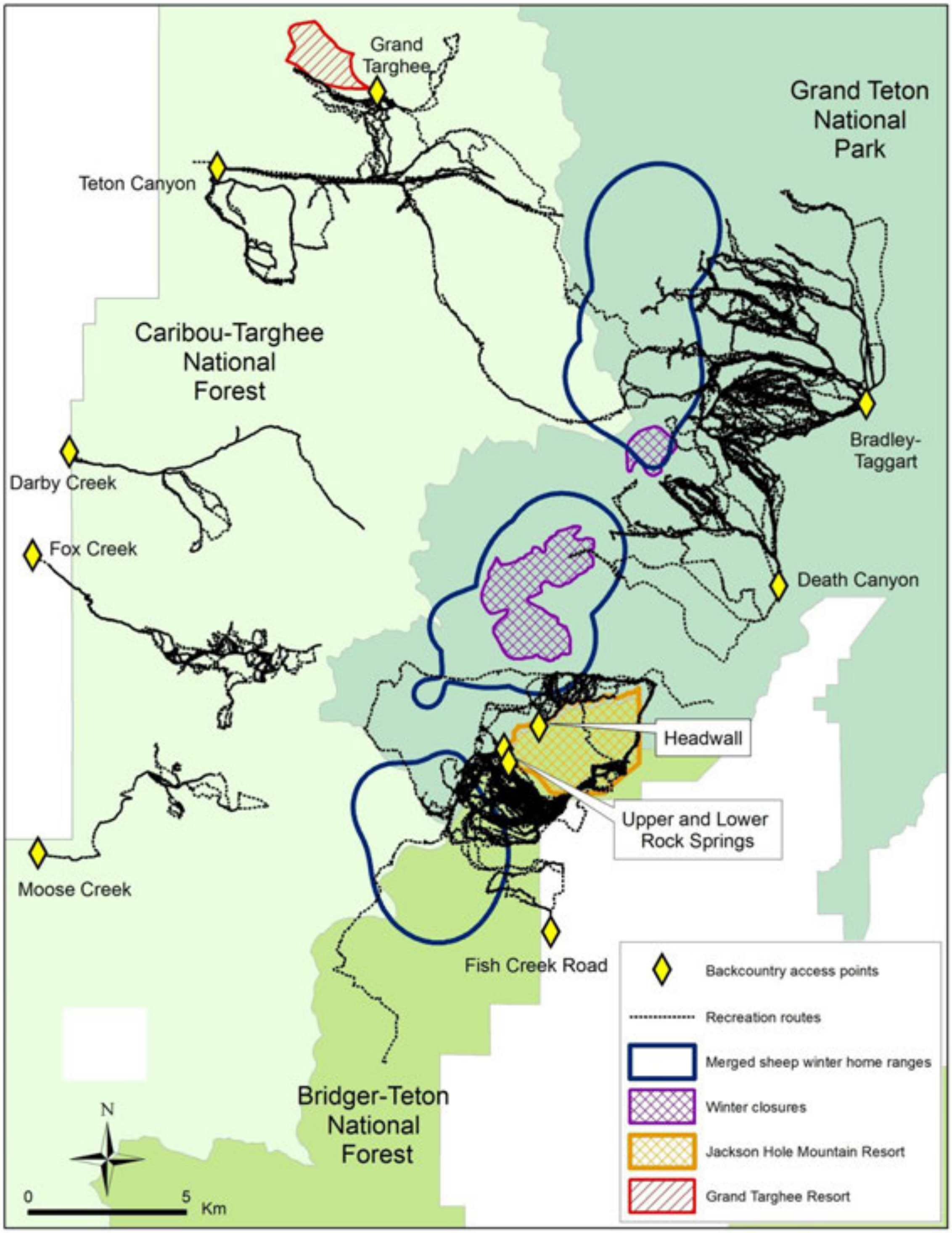

Figure 2. Backcountry access points (yellow diamonds), backcountry recreation routes (black dashed lines), merged bighorn sheep winter home ranges (blue polygons), winter closures (purple hatched polygons), ski resorts (red and orange hatched polygons), and public lands in the Teton Range.

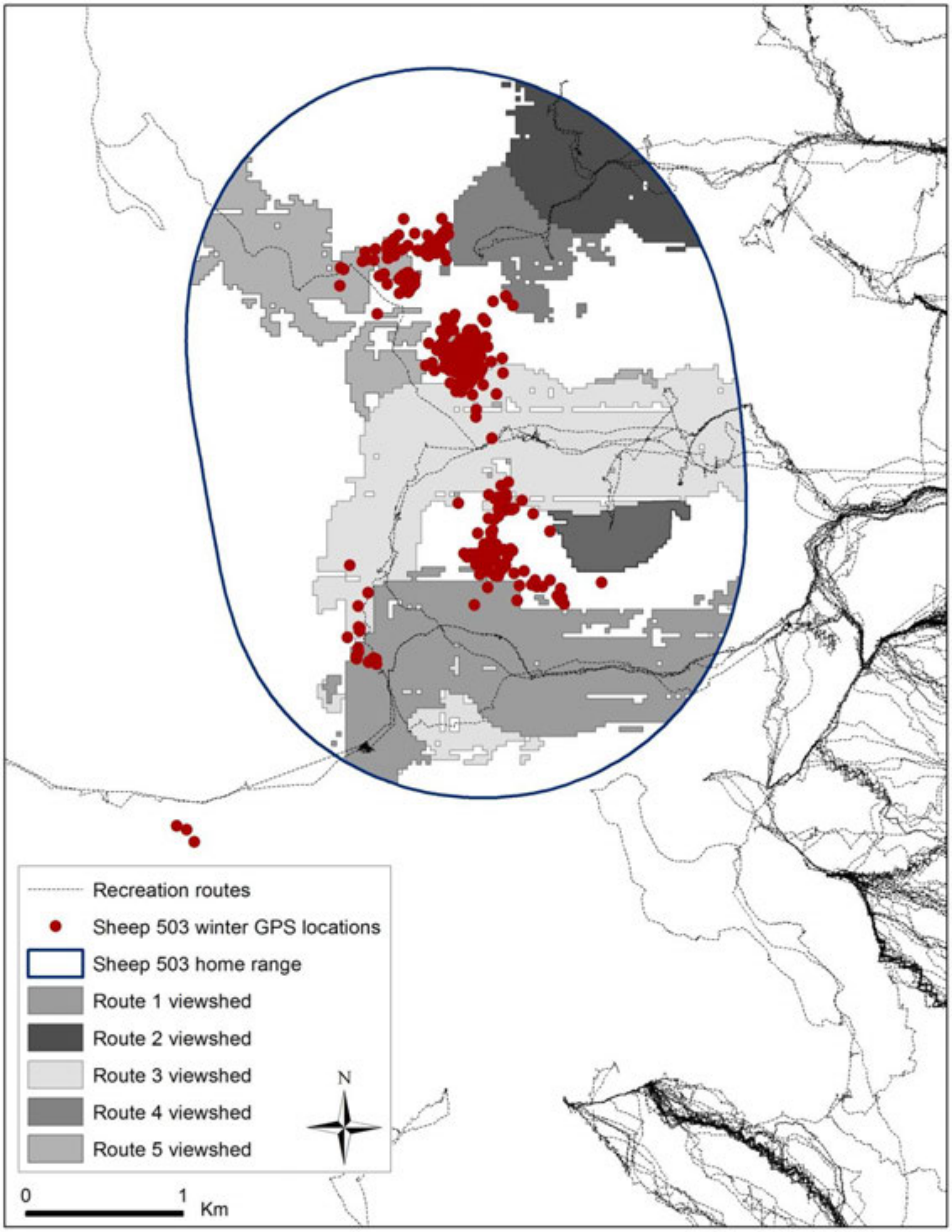

Figure 3. Example of the spatial data included in the recreation intensity value calculation for a bighorn sheep. The area of each recreation route viewshed (grey shaded polygons) within a bighorn sheep's winter home range (black polygon) is used in the calculation.

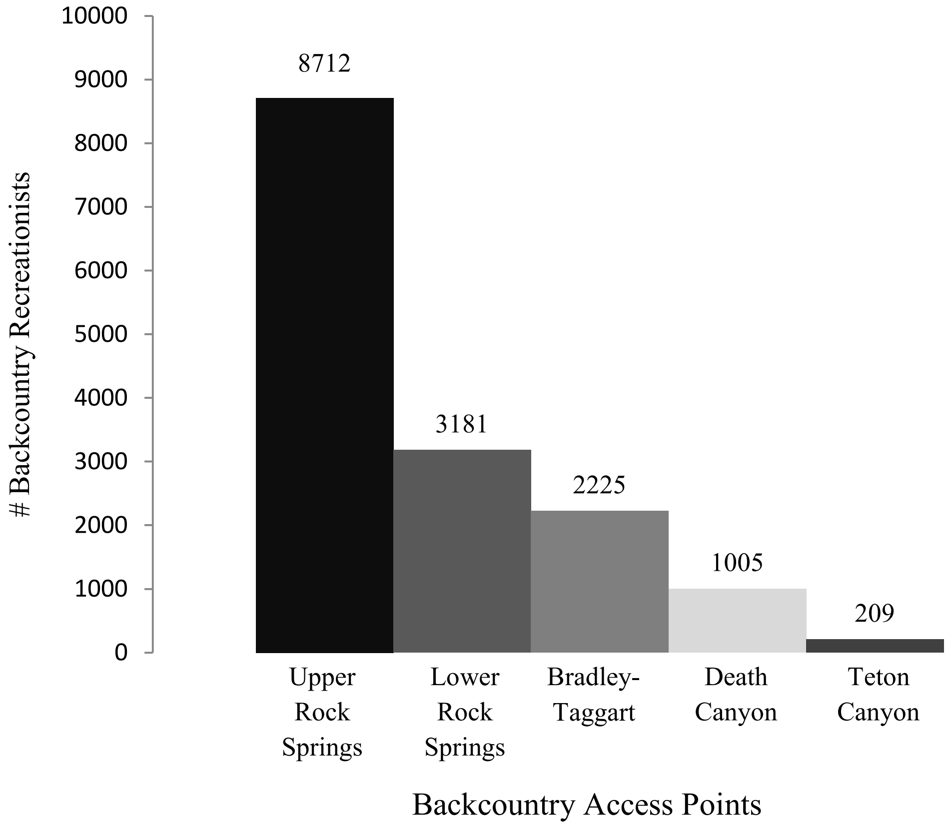

Figure 4. Total number of backcountry recreationists recorded on trail counters at five major recreation access points in the Teton Range in winter 2010.

Table 1. Habitat selection coefficients averaged among GPS-collared bighorn sheep for winter model without recreation (*n* = 11) and winter model with recreation (*n* = 11). Significance is indicated by bold-face (95% confidence interval does not overlap zero).

	Winter model without recreation		Winter model with recreation	
	RSF coefficients		RSF coefficients	
Covariate	β	95% CI	β	95% CI
Proximity to escape terrain	**0.894**	0.295, 1.493	**0.821**	0.368, 1.273
Proximity to snow-free	**0.792**	0.237, 1.347	**0.800**	0.327, 1.274
Elevation	**0.904**	0.500, 1.308	**0.926**	0.515, 1.337
Solar radiation	**0.151**	0.025, 0.277	**0.147**	0.020, 0.273
Tree cover	**-0.237**	-0.461, -0.014	**-0.230**	-0.456, -0.004
Slope	0.060	-0.120, 0.231	0.048	-0.127, 0.224
Winter recreation			**-0.247**	-0.383, -0.112

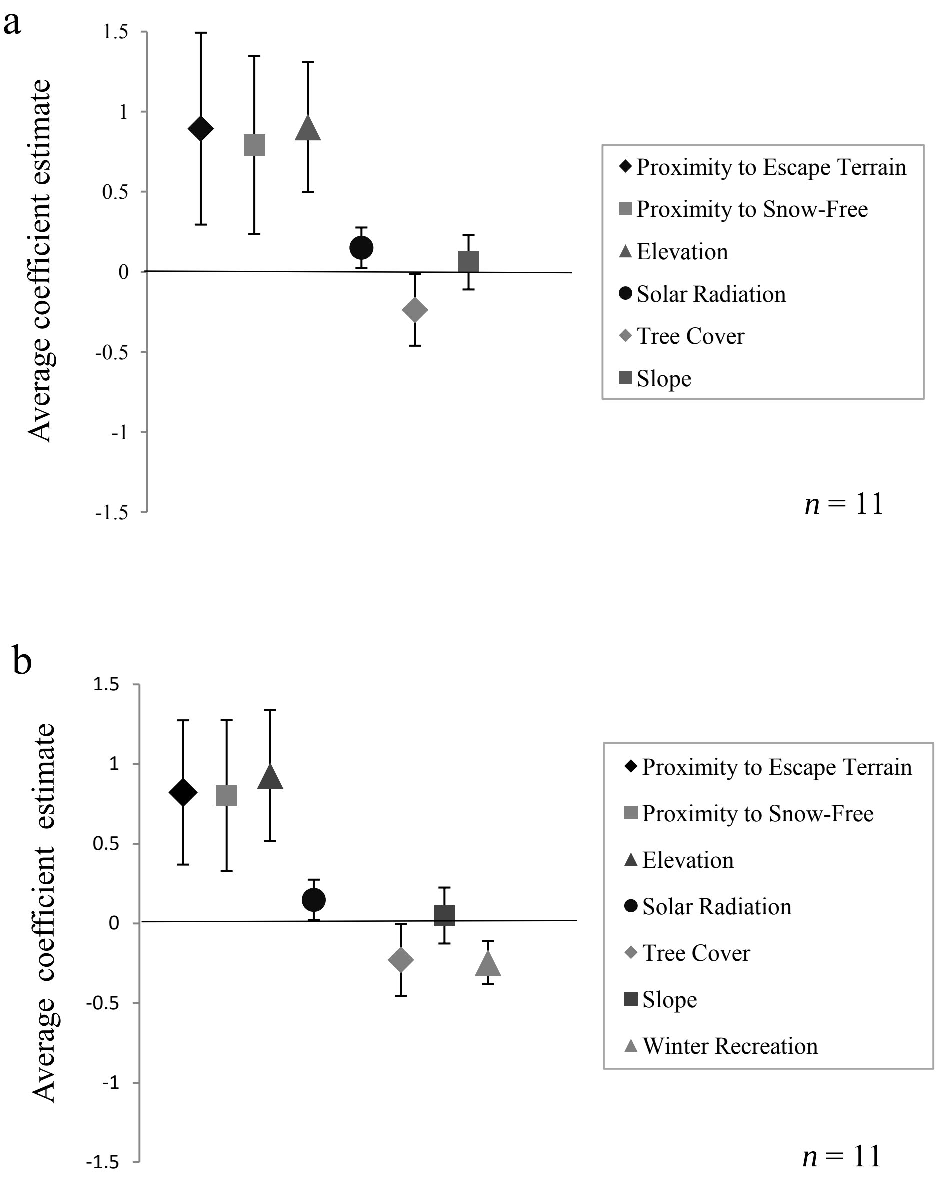

Figure 5. Results from bighorn sheep winter resource selection model without recreation (a), and with recreation covariate (b). Capped bars represent 95% confidence intervals around averaged coefficients of each covariate from individual sheep models (*n* = 11). Coefficients with bars that do not overlap zero indicate significant selection (+) or avoidance (-).

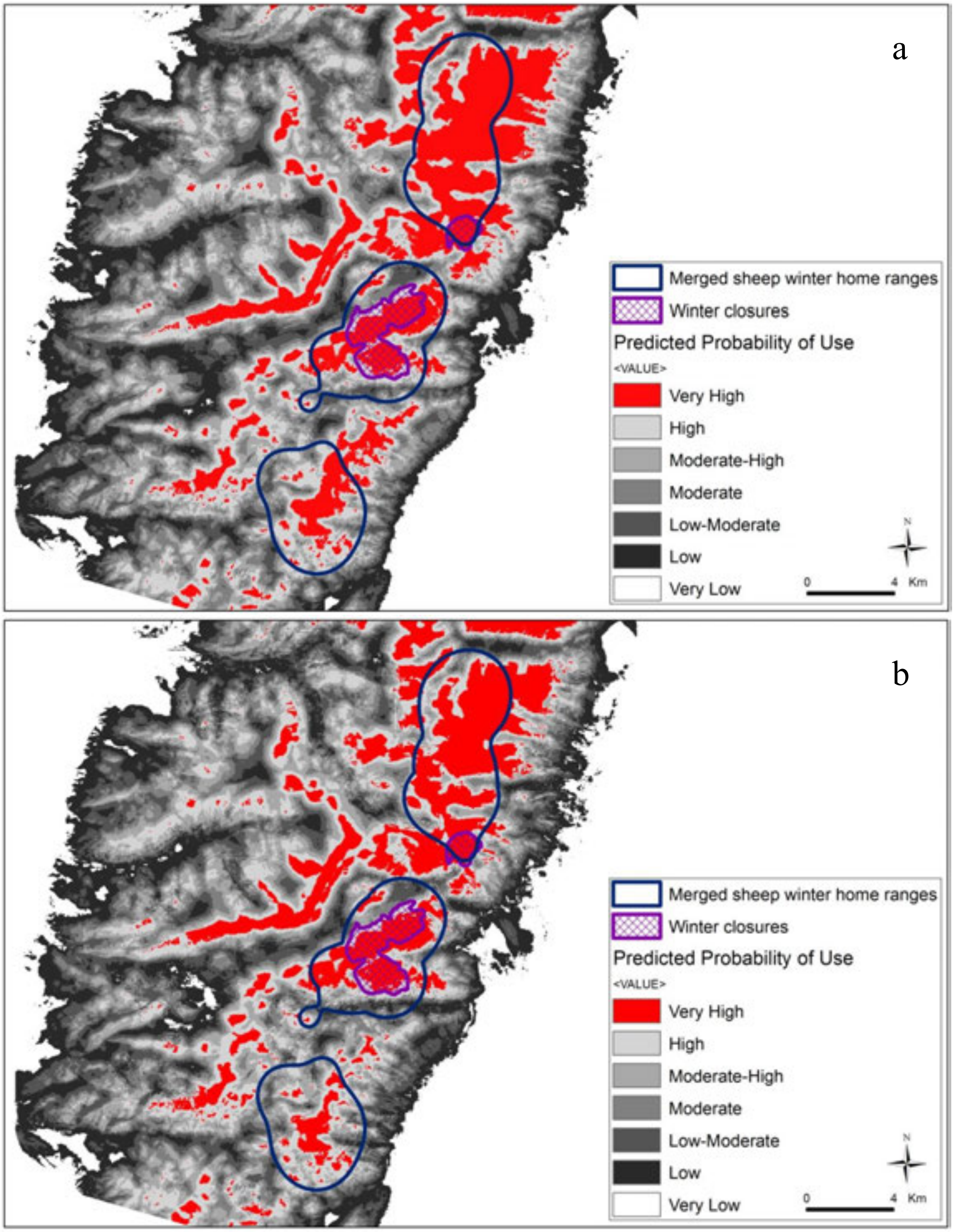

Figure 6. Predicted probabilities of bighorn sheep use during winter in the southern Teton Range from the winter model without recreation (a), and the winter model with recreation (b). Categories range from low (dark grey) to very high probability (red). Merged bighorn sheep winter home ranges and winter closures are shown.

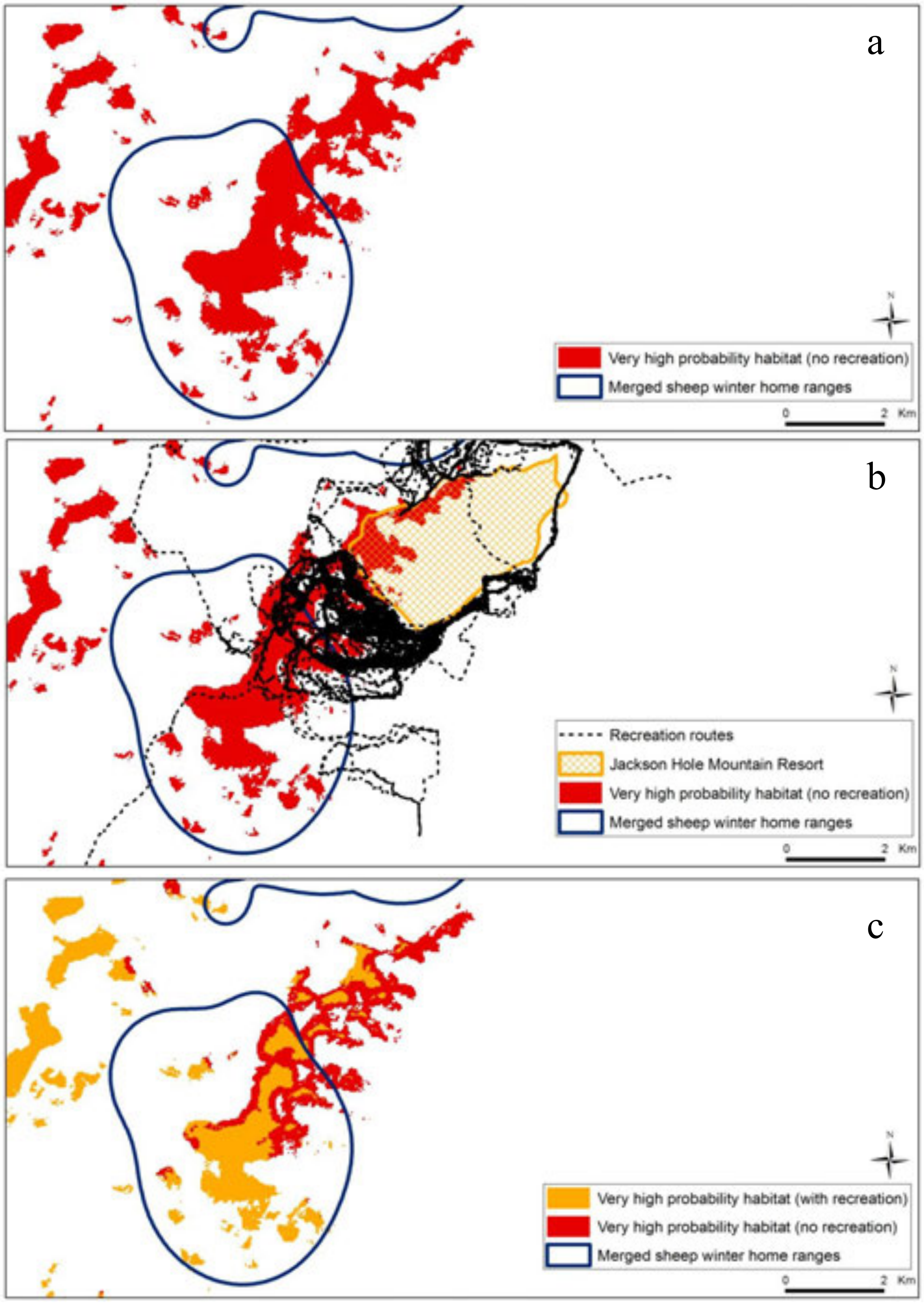

Figure 7. Predicted highest probability habitat from the winter model without recreation (red) and merged bighorn sheep home ranges (blue polygons) in the southern Teton Range (a). These are overlayed with winter backcountry routes and the location of the Jackson Hole Mountain Resort (b), and predicted highest probability habitat from the winter model with recreation (c). In (c), red areas denote predicted reduction highest quality habitat when recreation is considered.

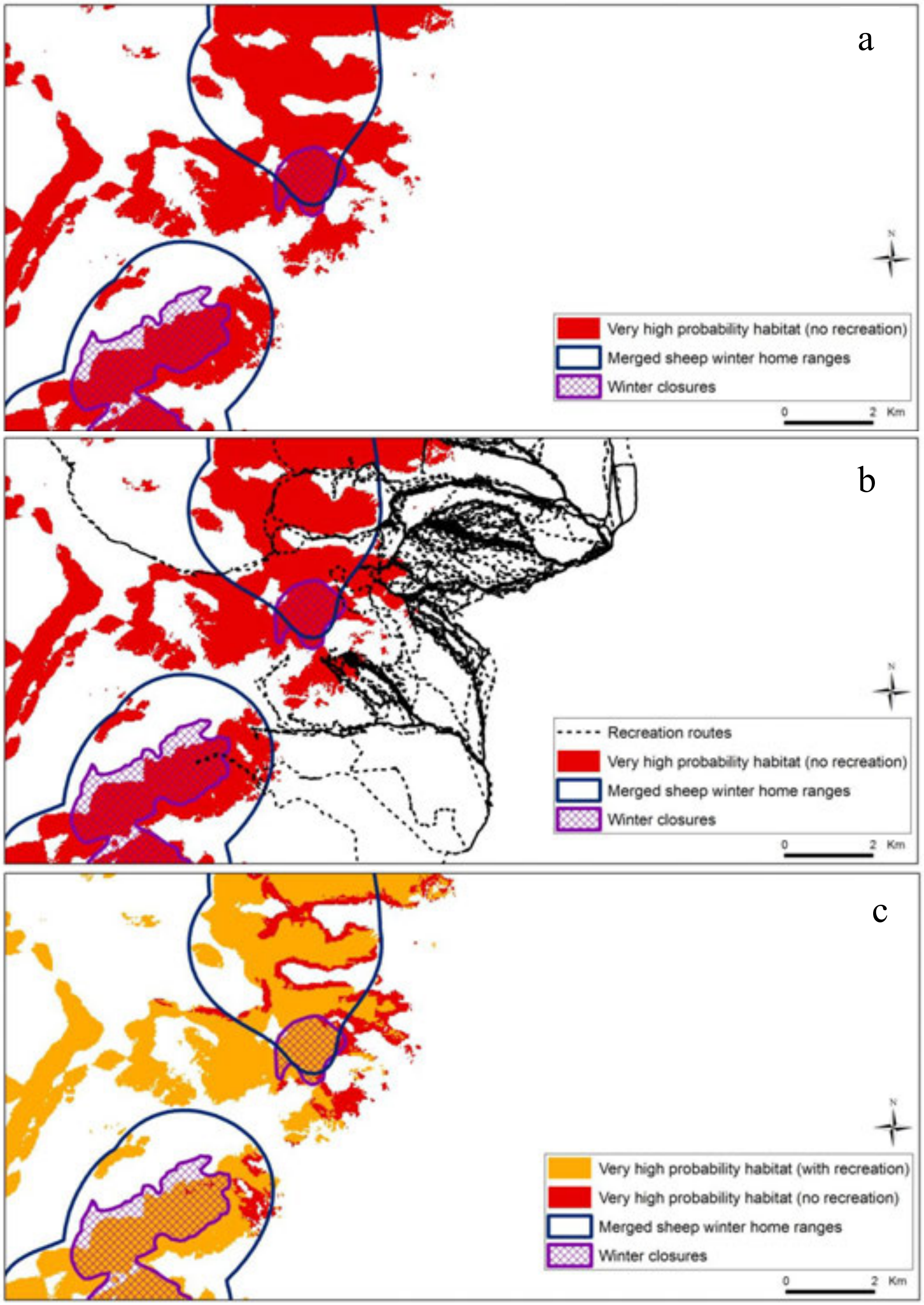

Figure 8. Predicted highest probability habitat from the winter model without recreation (red), merged bighorn sheep home ranges (blue polygons), and winter closures (purple) (a), in a portion of Grand Teton National Park. These are overlayed with winter backcountry recreation routes (b) and predicted highest probability habitat from the winter model with recreation (c). In (c), red areas denote predicted reduction highest quality habitat when recreation is considered.

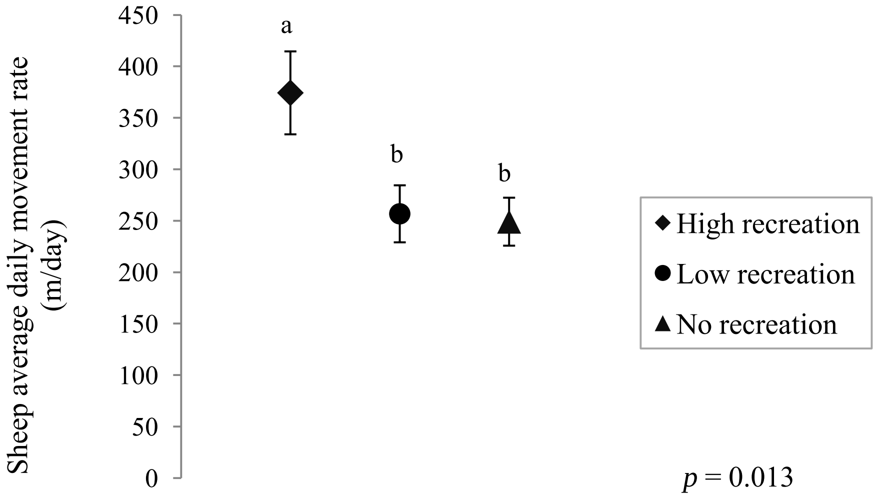

Figure 9. Average winter daily movement rates (m/day) of bighorn sheep exposed to relatively high ($n = 8$), low ($n = 8$), and no recreation activity ($n = 11$). Capped bars represent ± 1 standard error. Letters indicate significant difference.

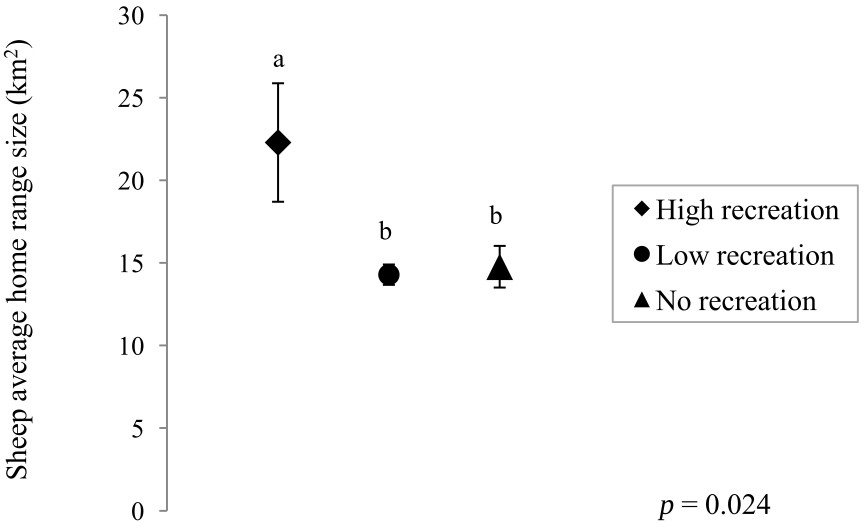

Figure 10. Average home range sizes (km^2) of bighorn sheep exposed to relatively high ($n = 8$), low ($n = 8$), and no recreation activity ($n = 11$). Capped bars represent ± 1 standard error. Letters indicate significant difference.

Plate 1. Backcountry ski tracks in high elevation bighorn sheep winter habitat in the Teton Range, Wyoming (photo: A. Courtemanch).

MANAGEMENT RECOMMENDATIONS

- Mid-elevation spring habitats appear to be particularly important for the Teton Range bighorn sheep population, especially with regards to the abbreviated migration they now exhibit. Improving and expanding spring habitat would benefit bighorn sheep. Management could include reducing conifer and shrub encroachment, improving forage quality using prescribed or wildland fire, increasing connectivity to winter and summer habitats, and limiting human activity in these areas. In addition, competition with other ungulates species for spring habitat and forage should be identified and reduced when feasible.

- Winter habitat is likely a limiting factor for the Teton Range bighorn sheep population. Our results indicate that even low levels of human activity cause bighorn sheep to avoid areas of suitable winter habitat. Thus, excluding human activity from winter habitats and areas adjacent to winter habitats would increase their availability for bighorn sheep. Other factors that could displace bighorn sheep from winter habitats in the future, such as competition with other ungulate species, should be minimized to the greatest extent possible.

- Maintaining and improving identified movement corridors between the northern and southern groups within the population would keep the potential for genetic interchange in the future.

- Our results indicate that this small population has been exposed to very few diseases, including bacterial pathogens associated with pneumonia. Due to domestic sheep allotment retirements and subsequent closures, the population has low risk of disease transmission from domestic sheep. Other potential routes of disease transmission, including from bighorn sheep or mountain goats immigrating from surrounding herds, should be mitigated whenever possible.

- The Teton bighorn sheep population appears to be small, but stable. Continued surveys of the population, both from the ground and air are important to track population trends and be able to identify signs of population decline.

- Future research on the Teton bighorn sheep population would be beneficial. Suggested future research includes: 1) evaluating bighorn sheep expanded use of mid-elevation areas and response to habitat treatments and domestic sheep allotment retirements; 2) monitoring disease prevalence in the herd using improved detection techniques; and 3) evaluating the effects of wintering at high elevation and the abbreviated migration strategy on seasonal body condition dynamics and reproduction.

SUPPLEMENTAL INFORMATION

APPENDIX I: New remote sensing method for identifying consistently snow-free areas

Similar to the normalized difference vegetation index (NDVI), the normalized difference snow index (NDSI) utilizes certain wavelengths from satellite imagery to identify areas covered with snow or ice (Dozier 1989, Hall et al. 1995). While snow is highly reflective of visible wavelengths, it absorbs mid-infrared (MIR) wavelengths, leading to the NDSI:

$$(TM2 - TM5)/(TM2 + TM5)$$

where TM2 is the visible wavelengths in Band 2 (0.52 – 0.60 μm) and TM5 is the mid-infrared wavelengths in Band 5 (1.55 – 1.75 μm) on Thematic Mapper sensors. The NDSI produces values ranging from -1.0 to 1.0, where negative values indicate rock or vegetation and positive values indicate various levels of snow cover (Hall et al. 1995). The benefits of the NDSI are that it successfully identifies snow in rugged terrain, in shadows, and discriminates snow from cloud cover (Hall et al. 1995).

We were interested in mapping consistently snow-free areas at a relatively fine spatial scale across many winters. We selected 30 cloud-free satellite images from 1993 - 2011 during the winter period (November 15 – April 15) (http://glovis.usgs.gov/) from both the Landsat 5 Thematic Mapper (TM) sensor ($n = 19$) and Landsat 7 Enhanced Thematic Mapper Plus (ETM+) sensor ($n = 11$), which have 30x30 m spatial resolution. Since the study area falls in the center of Landsat scenes, we were able to utilize images from the Landsat 7 ETM+ scan-line corrector-off (SLC-off) satellite despite a malfunction on its SCL in May 2003, which only affects the scene edges. Due to frequent winter cloud-cover in the Teton Range many satellite images are unusable, so the ability to use both the Landsat 5 TM and Landsat 7 ETM+ increased our temporal resolution for image acquisition.

We performed the NDSI analysis using ERDAS Image 9.3 software. We used the Map Algebra tool (ESRI ArcGIS 10) to average the NDSI values from each pixel across all images. This produced a single raster of average NDSI values (i.e. snow cover) across all winters for each pixel. We performed an unsupervised classification on this raster and used *a priori* knowledge of the study area and winter flight photos to assign a threshold NDSI value for snow cover. Due to local atmospheric effects, there is not an exact NDSI threshold for snow, but a reliable threshold can be established using *a priori* knowledge of the study area and ground-truthing (Hall et al. 1995). Hall et al. (1995) identified pixels with NDSI values over 0.45 as having least 60% snow cover, but reported that NDSI thresholds for snow cover varied between landscapes. Silverio & Jacquet (2005) noted that NDSI values for glaciers were different for the same study site in different years (≥0.52 in 1987 and ≥0.40 in 1996), which was likely due to atmospheric effects or debris covering portions of the glaciers. Based on *a priori* knowledge of the study area, winter flight photos, and NDSI values from the literature, we selected a threshold of ≤ 0.5 for snow-free areas.

We found that many areas that were tree covered exhibited NDSI values below the 0.5 threshold because of tree canopy. Since we were interested in identifying snow-free areas without significant tree cover, we excluded areas with >30% tree cover using the 30-m National Land Cover Database for Wyoming (2001).

We further confirmed the 0.5 NDSI threshold by conducting ground-truthing surveys with a simultaneous Landsat 7 satellite fly-over on 16 January 2010. Ground crews visited 20 sites in the Teton Range on that day and estimated percent snow cover in 90 m^2 areas (representing nine 30-m Landsat pixels), which were compared to the NDSI snow cover classification for the paired satellite image. Snow cover was identified correctly on 18 of the 20 sites (90% accuracy) using the NDSI threshold of ≤ 0.5. This approach was successful at mapping snow-free versus snow-covered portions of the study area.

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APPENDIX II: Comparison of modified discrete choice and discrete choice winter resource selection results

Comparison of results from winter modified discrete choice and discrete choice resource selection functions. Average coefficient is the average of estimated coefficients from individual sheep models (*n* = 23) and SD is standard deviation. T-values and p-values are from two-tailed Student's t-tests (df = 44).

Variable	**Modified Discrete Choice**		**Discrete Choice**		**t-Value**	**P-Value**
	Average Coefficient	**SD**	**Average Coefficient**	**SD**		
Proximity to Escape Terrain	0.668	0.124	0.745	0.578	-0.463	0.646
Proximity to Snow-Free	0.949	0.133	0.964	0.702	-0.071	0.944
Elevation	0.549	0.139	0.615	0.513	0.440	0.662
Solar Radiation	0.220	0.033	0.213	0.158	-0.133	0.895
Tree Cover	-0.157	0.054	-0.255	0.527	-0.814	0.420
Slope	0.082	0.054	0.034	0.257	-0.625	0.535
P[Detection] Variable						
Slope	-0.465	1.048				
Tree Cover	3.985	11.576				

APPENDIX III: Bighorn sheep disease sampling methods and results

Blood and fecal samples and ear, tonsil, and nasal swabs were collected from all GPS-collared bighorn sheep at time of capture (n = 28). Testing was conducted for ovine progressive pleuropneumonia, epizootic hemorrhagic disease virus, *Mycobacterium* paratuberculosis (Johne’s disease), bluetongue virus, parainfluenza virus, respiratory synctial virus, bovine viral diarrhea, infectious bovine rhinotracheitis, *Brucella ovis*, and *Psoroptes* mites (scabies) at the Wyoming State Veterinary Laboratory, Laramie, Wyoming, USA. Tonsil and nasal swabs were cultured for identification of respiratory bacteria, such as *Mannheimia haemolytica*, *Mycoplasma ovipneumoniae*, and *Bibersteinia trehalosi*. All samples were negative for ovine progressive pleuropneumonia, epizootic hemorrhagic disease virus, *Brucella ovis*, bluetongue virus, *Mycobacterium* paratuberculosis (Johne’s disease), and *Psoroptes* mites. Titers were very low, indicating no previous exposure, for parainfluenza (< 1:4), bovine viral diarrhea (< 1:4), respiratory synctial virus (< 1:4), and infectious bovine rhinotracheitis (< 1:8). One tonsil swab produced cultures of *Mannheimia* spp., which was further deduced to likely be *Mannheimia glucosida*. This species is not usually associated with pneumonia in bighorn sheep, but the cultured sample did contain a leukotoxin. The individual ewe from which the sample was collected never exhibited symptoms of pneumonia and survived through the study.

Unlike neighboring migratory bighorn sheep populations, we found that Teton bighorn sheep have very low disease prevalence. Sampling efforts of the neighboring Jackson bighorn sheep herd in 2012 revealed the presence of *Mannheimia haemolytica*, *Mycoplasma ovipneumoniae*, *Bibersteinia trehalosi*, and *Pasteurella multocida* from tonsil and nasal swabs (H. Edwards, *pers. comm.*). Also, it is highly unusual to find ungulates in Wyoming that have not been previously exposed to parainfluenza (H. Edwards, *pers. comm.*). Residing at high elevation year-round appears to buffer Teton bighorn sheep against co-mingling with domestic sheep and other bighorn sheep populations that may carry disease. It is well-established that pneumonia-causing pathogens can be transmitted from domestic sheep (*Ovis aries*) to bighorn sheep (Lawrence et al. 2010), with the potential to cause population-level die-offs. Until recently, the active Forest Service domestic sheep allotments in the Teton Range posed a disease risk to Teton bighorn sheep. As a result of the allotment retirements that occurred in the early 2000s, the disease risk to bighorn sheep from domestic sheep has been virtually eliminated. Currently, the closest active Forest Service domestic sheep allotment is 17 km away. While the neighboring Jackson population has undergone at least two documented pneumonia outbreaks (2001-2002 and 2011-2012) (Wyoming Game and Fish Department 2012), our data suggest the Teton population has remained unusually disease-free.

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APPENDIX IV: Genetic variation and isolation of the Teton Range bighorn sheep population

While Teton Range bighorn sheep historically shared a common winter range with the neighboring Jackson bighorn sheep population (Whitfield 1983), recent evidence indicates that these two populations are now genetically differentiated from one another (Kardos et al. *in prep*). This genetic differentiation, pointing to a lack of successful dispersal and interbreeding, likely occurred after the Teton population lost its historical migration and became resident. Fitzsimmons et al. (1995) found that the Teton population had a small effective population size ($N_e = 33$) and high inbreeding coefficient ($F = 0.014$), although the sample size was small ($n = 4$). Despite occasional observations of young rams in areas between the two populations' ranges (Wyoming Game and Fish Department, *unpublished data*), there is no genetic evidence of successful dispersal and interbreeding ($F_{ST} = 0.18$) (Kardos et al. *in prep*). Furthermore, there is evidence of substantial genetic differentiation between the northern and southern groups within the Teton Range population ($F_{ST} = 0.12$) (Kardos et al. *in prep*). This is surprising, due to the apparent habitat connectivity that exists between the northern and southern groups and the fact that we documented one GPS-collared ewe that moved twice between these areas during our study, although returned to the north for the breeding season each time (Figure A1). Although it appears possible for bighorn sheep to move between these two groups, perhaps strong philopatry predisposes individuals to return to their natal areas to breed, preventing genetic connectivity. In addition, there is genetic evidence of a severe bottleneck in recent history (e.g. 2 - 15 generations ago) in the northern group of the Teton Range population (Kardos et al. *in prep*). The apparent genetic isolation from the Jackson population, low genetic variation, genetic differentiation between the northern and southern groups, and the small population size raise substantial concern for future population persistence (Berger 1990). Heterozygosity and allelic diversity can be very important to individual fitness (Hogg et al. 2006) and disease and parasite resistance (Rijks et al. 2008).

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APPENDIX V. GPS-collared bighorn sheep information

GPS-collared bighorn sheep information: sheep ID, capture date, general capture location, estimated age at time of capture (from horn rings), lamb presence (X) or absence (blank) in summers 2008, 2009, and 2010 (grey box denotes sheep was not collared that summer; question marks denote unknown lamb presence/absence), cause of mortality if applicable, date of mortality, and fate of GPS collar. South group are sheep with home ranges in the southern portion of the study area and north group are sheep with home ranges in the northern portion.

SOUTH GROUP

Sheep ID	Capture Date	Capture Location	Estimated Age	Lamb at Heel			Cause of Mortality	Mortality Date	GPS Collar Fate
				2008	2009	2010			
211	2/15/2008	Icefloe Lake	2						downloaded
261	2/15/2008	Snowdrift Lake	8	X	X	X			VHF battery died; not recovered
493	2/14/2008	Prospectors Mountain	5	▨	▨	▨	Avalanche	Apr. 2008	downloaded
503	2/15/2008	Open Canyon	4			X			downloaded
543	2/15/2008	Static Peak	6		▨	▨	Avalanche	Dec. 2008	downloaded
553	2/14/2008	Prospectors Mountain	2		X	X			downloaded
633	2/15/2008	Indian Lake	7	▨	▨	▨	Avalanche	Mar. 2008	downloaded
662	2/15/2008	Jensen Canyon	1	X		X			downloaded
683	2/14/2008	Prospectors Mountain	4	X		X			downloaded
743	2/15/2008	Jensen Canyon	4		X	X			downloaded
753	2/15/2008	Prospectors Mountain	3						downloaded
763	2/14/2008	Mount Hunt	5	▨	▨	▨	Avalanche	May 2008	downloaded
773	3/13/2009	Jensen Canyon	2	▨	▨	▨	Mountain lion	Apr. 2009	downloaded
783	3/12/2009	Prospectors Mountain	4	▨		X			downloaded
893	3/13/2009	Mount Hunt	2	▨	X	X			downloaded
493B	3/12/2009	Mount Hunt	4	▨	X				downloaded
633B	3/12/2009	Prospectors Mountain	4	▨	X	X			downloaded
763B	3/12/2009	Mount Hunt	3	▨		X			failed to initialize; no data

NORTH GROUP

Sheep ID	Capture Date	Capture Location	Estimated Age	Lamb at Heel			Cause of Mortality	Mortality Date	GPS Collar Fate
				2008	2009	2010			
161	2/15/2008	Elk Mountain	5		▨	▨	Unknown	Dec. 2008	downloaded
351	2/15/2008	Elk Mountain	1		X				downloaded
463	2/15/2008	Elk Mountain	5	X					downloaded
473	2/15/2008	Doane Peak	5		▨	▨	Unknown	Nov. 2008	downloaded
482	2/15/2008	Ranger Peak	7	X	X				downloaded
563	2/15/2008	Doane Peak	4	X	X	?			downloaded
623	2/15/2008	Elk Mountain	2			?			VHF battery died; not recovered
653	2/15/2008	Colter Canyon	7	X	X	▨	Unknown	Nov. 2009	downloaded
723	3/12/2009	Elk Mountain	4	▨	X				downloaded
543B	3/12/2009	Doane Peak	3	▨	X				downloaded

APPENDIX VI. List of plant genera present in Teton bighorn sheep summer diets

Genera were identified from summer fecal samples from 2008-2010.

Genus

Achillea
Agoseris
Agrostis
Anemone
Arabis
Arenaria
Arnica
Artemesia
Aster
Astragalus
Balsamorhiza
Bromus
Carex
Castilleja
Cerastium
Collinsia
Delphinum
Deschampsia
Epilobium
Erigeron
Erysimum
Fragaria
Geranium
Hedysarum
Koeleria
Lomatium
Lupinus
Paxistima
Penstemon
Poa
Polygonum
Potentilla
Ranunculus
Salix
Sedum
Senecio
Symphoricarpos

Genus cont.

Taraxacum
Trifolium
Vaccinium

APPENDIX VII. List of plant common names and genera observed on Teton bighorn sheep summer ranges during summers 2008-2010

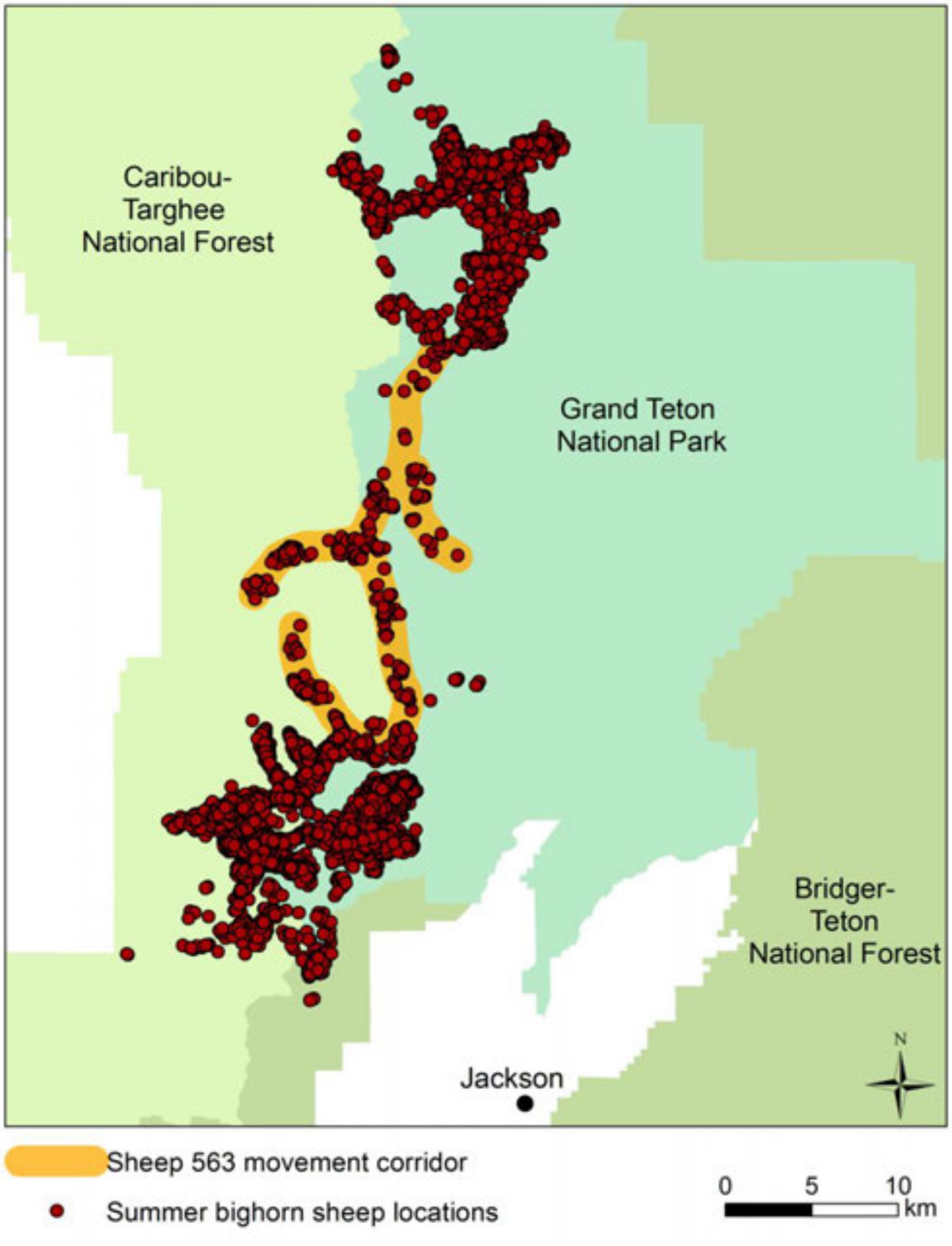
Common Name	Genus
Mountain maple	*Acer*
Yarrow	*Achillea*
Agoseris	*Agoseris*
Serviceberry	*Amelanchier*
Pearly everlasting	*Anaphalis*
Northern rock jasmine	*Androsace*
Cut-leaved anemone	*Anemone*
Alpine pussytoes	*Antennaria*
Columbine	*Aquilegia*
Hairy rockcress	*Arabis*
Lyall's rockcress	*Arabis*
Sandwort	*Arenaria*
Alpine arnica	*Arnica*
Heart-leaved arnica	*Arnica*
Seep-spring arnica	*Arnica*
Prairie Sage	*Artemesia*
Alpine sage	*Artemisia*
Sagebrush	*Artemisia*
Alpine aster	*Aster*
Arctic aster	*Aster*
Thick-stemmed aster	*Aster*
Alpine milk vetch	*Astragalus*
Prickly milk vetch	*Astragalus*
Arrow-leaved balsamroot	*Balsamorhiza*
Brome	*Bromus*
Common harebell	*Campanula*
Sedges	*Carex*
Red paintbrush	*Castilleja*
Yellow paintbrush	*Castilleja*
Chickweed	*Cerastium*
Rabbitbrush	*Chrysothamnus*
Thistle	*Cirsium*
Springbeauty	*Claytonia*
Leather flower	*Clematis*
Blue-eyed Mary	*Collinsia*
Steer's head	*Dicentra*
Pretty shootingstar	*Dodecatheon*
Arctic fleabane	*Erigeron*
Purple fleabane	*Erigeron*
Subalpine fleabane	*Erigeron*

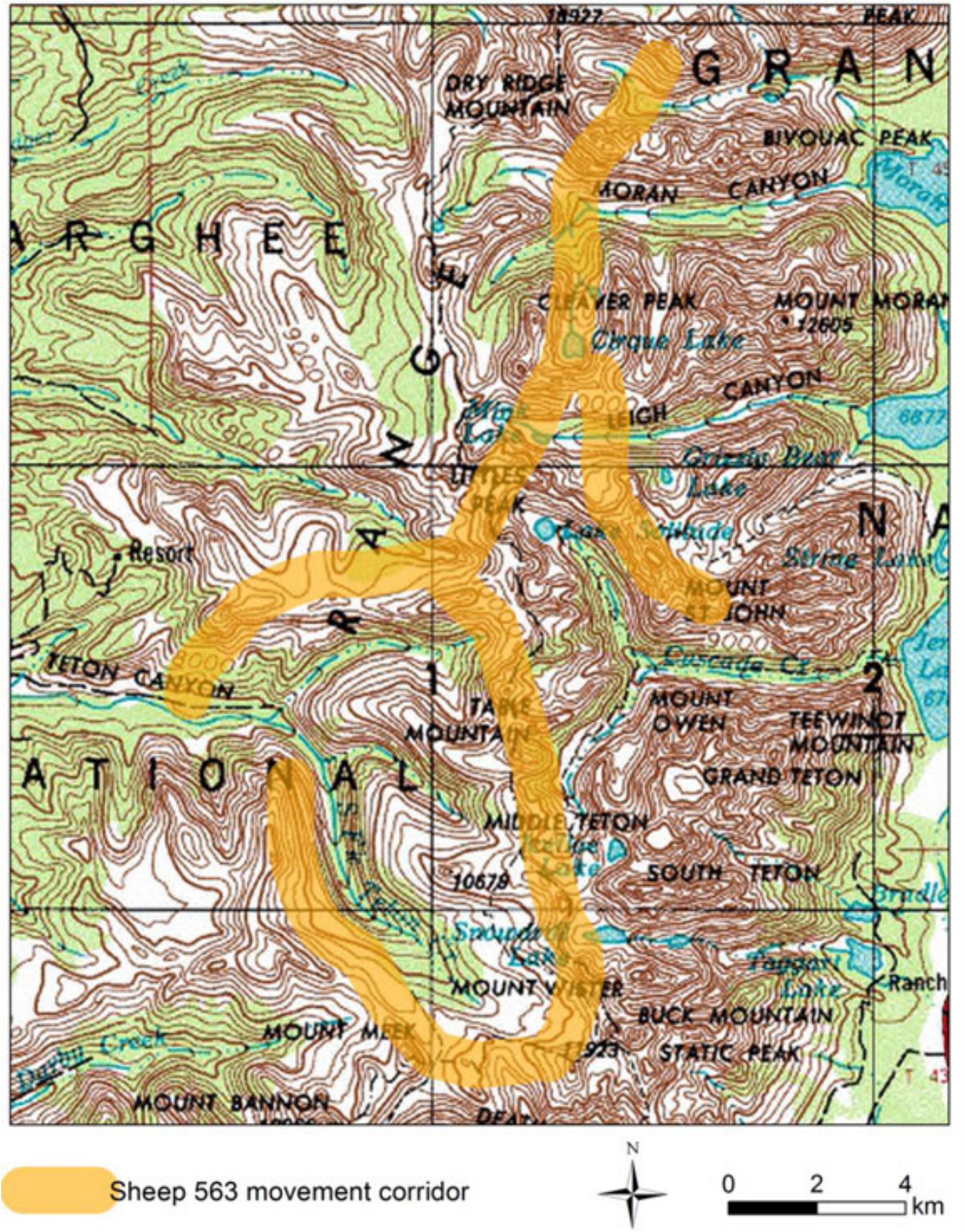
Cushion buckwheat	*Eriogonum*
Sulfer buckwheat	*Eriogonum*
Wild strawberry	*Fragaria*
Green gentian	*Frasera*
Mountain bog gentian	*Gentiana*
Sticky purple geranium	*Geranium*
Stickseed	*Hackelia*
Northern sweet vetch	*Hedysarum*
Alpine sweet vetch	*Hedysarum*
Goldeneye	*Heliomeris*
Waterleaf	*Hydrophyllum*
Alpine ivesia	*Ivesia*
Junegrass	*Koeleria*
Wild blue flax	*Linum*
Woodland star	*Lithophragma*
Yellow Puccoon	*Lithospermum*
Desert parsley	*Lomatium*
Lupine	*Lupinus*
Oregon grape	*Mahonia*
False Solomon's seal	*Maianthemum*
Mountain boxwood	*Paxistima*
Bracted lousewort	*Pedicularis*
Coil-beaked lousewort	*Pedicularis*
Elephant's head lousewort	*Pedicularis*
Fern-leaf lousewort	*Pedicularis*
Oeder's lousewort	*Pedicularis*
Sickletop lousewort	*Pedicularis*
Slender blue penstemon	*Penstemon*
Shrubby cinquefoil	*Pentaphylloides*
Scorpionweed	*Phacelia*
Cushion phlox	*Phlox*
Bluegrass	*Poa*
Alpine bistort	*Polygonum*
American bistort	*Polygonum*
Diverse-leaved cinquefoil	*Potentilla*
Snow cinquefoil	*Potentilla*
Sticky cinquefoil	*Potentilla*
Currant	*Ribes*
Raspberry	*Rubus*
Willow	*Salix*
Red-stemmed saxifrage	*Saxifraga*
Lance-leaved stonecrop	*Sedum*
Roseroot	*Sedum*
Alpine groundsel	*Senecio*
Arrow-leaved groundsel	*Senecio*

Butterweed groundsel	*Senecio*
Dwarf mountain groundsel	*Senecio*
Rayless alpine groundsel	*Senecio*
Rock groundsel	*Senecio*
Western groundsel	*Senecio*
Woolly groundsel	*Senecio*
Moss campion	*Silene*
Spike-like goldenrod	*Solidago*
Long-stalked starwort	*Stellaria*
Northern starwort	*Stellaria*
Snowberry	*Symphoricarpos*
Dandelion	*Taraxacum*
Meadowrue	*Thalictrum*
Mountain huckleberry	*Vaccinium*
Sitka valerian	*Valeriana*
Subalpine valerian	*Valeriana*
Violet	*Viola*
Mountain death camas	*Zigadenus*

Appendix VIII: Bighorn sheep movement corridor between the northern and southern groups in the Teton Range

Maps showing movement corridor identified by one GPS-collared bighorn sheep. Sheep 563 was captured in the northern group, but travelled between the northern and southern groups during August and September 2009 and 2010. She always returned to the north to breed and spend the winter and spring.




10927
PEAK
G R A N
DRY RIDGE MOUNTAIN
BIVOUAC PEAK
MORAN CANYON
A R G H E E
CLEAVER PEAK
MOUNT MORAN
12605
Cirque Lake
CANYON
LEIGH
Mica Lake
6877
R A N G E
Grizzly Bear Lake
LITTLES PEAK
Lake Solitude
N A
String Lake
Resort
MOUNT ST JOHN
9000
Cascade Cr
TETON CANYON
1
2
TABLE MOUNTAIN
MOUNT OWEN
TEEWINOT MOUNTAIN
A T I O N A L
GRAND TETON
MIDDLE TETON
Bradley Lake
10678
SOUTH TETON
Snowdrift Lake
Taggart Lake
Ranch
MOUNT WISTER
BUCK MOUNTAIN
MOUNT MEEK
10923
STATIC PEAK
Darby Creek
MOUNT BANNON
DEATH
Sheep 563 movement corridor
N
0
2
4
km