

Navigating snowscapes: scale-dependent responses of mountain sheep to snowpack properties

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Abstract. Winters are limiting for many terrestrial animals due to energy deficits brought on by resource scarcity and the increased metabolic costs of thermoregulation and traveling through snow. A better understanding of how animals respond to snow conditions is needed to predict the impacts of climate change on wildlife. We compared the performance of remotely sensed and modeled snow products as predictors of winter movements at multiple spatial and temporal scales using a data set of 20,544 locations from 30 GPS-collared Dall sheep (*Ovis dalli dalli*) in Lake Clark National Park and Preserve, Alaska, USA from 2005 to 2008. We used daily 500-m MODIS normalized difference snow index (NDSI), and multi-resolution snow depth and density outputs from a snowpack evolution model (SnowModel), as covariates in step selection functions. We predicted that modeled snow depth would perform best across all scales of selection due to more informative spatiotemporal variation and relevance to animal movement. Our results indicated that adding any of the evaluated snow metrics substantially improved model performance and helped characterize winter Dall sheep movements. As expected, SnowModel-simulated snow depth outperformed NDSI at fine-to-moderate scales of selection (step scales < 112 h). At the finest scale, Dall sheep selected for snow depths below mean chest height (<54 cm) when in low-density snows (100 kg/m³), which may have facilitated access to ground forage and reduced energy expenditure while traveling. However, sheep selected for higher snow densities (>300 kg/m³) at snow depths above chest height, which likely further reduced energy expenditure by limiting hoof penetration in deeper snows. At moderate-to-coarse scales (112–896 h step scales), however, NDSI was the best-performing snow covariate. Thus, the use of publicly available, remotely sensed, snow cover products can substantially improve models of animal movement, particularly in cases where movement distances exceed the MODIS 500-m grid threshold. However, remote sensing products may require substantial data thinning due to cloud cover, potentially limiting its power in cases where complex models are necessary. Snowpack evolution models such as SnowModel offer users increased flexibility at the expense of added complexity, but can provide critical insights into fine-scale responses to rapidly changing snow properties.

Key words: animal movement; MODIS; mountain sheep; resource selection; snow cover; snow depth; SnowModel; snowpack evolution; step selection function.

INTRODUCTION

Snow enshrouds up to one-third of the global land mass annually (Lemke et al. 2007) and influences the demography and movements of animals that reside in these “snowscapes,” defined here as landscapes covered by snow. Snowscapes offer benefits for some species in the form of a protective subnivium critical to overwinter survival (Pauli et al. 2013). For many animals, however, snow signals a period of caloric stress brought on by limited access to

high-quality forage and increased metabolic demands associated with thermoregulation and impaired mobility (Parker et al. 1984, 2009, Robinson and Merrill 2012, Gilbert et al. 2017). Conditions such as deep snow or icing caused by rain-on-snow events (Stien et al. 2010) can severely limit the ability of herbivores to access ground forage, decrease efficiency of movement (Parker et al. 1984), and increase predation risk (Hebblewhite et al. 2005, Sand et al. 2006, Brodie et al. 2014, Lendrum et al. 2017). Thus, the snow-covered period is often limiting for terrestrial mammals living in temperate and Arctic regions (Parker et al. 2009), with strong selective forces linking environmental conditions, animal behavior, and fitness (Boutin and Lane 2014).

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Snowscapes may have especially strong effects on wildlife in Arctic and boreal ecosystems where snow cover persists for much of the year (Callaghan et al. 2011a, Pozzanghera et al. 2016). The Arctic is warming at twice the rate of lower latitudes and is predicted to experience elevated levels of precipitation with a higher proportion falling as rain (Olsen et al. 2011, Bintanja and Selten 2014, Bring et al. 2016, Vihma et al. 2016). As a consequence, the snow-covered season is shortening, spring conditions are becoming more variable, and rain-on-snow events are increasing in frequency (Putkonen et al. 2009, Jeong and Sushama 2017, Langlois et al. 2017, Mallory and Boyce 2017). These changes in temperature and hydrology are transforming northern ecosystems, with profound implications for wildlife that are not well understood (Callaghan et al. 2004, 2011b, Chapin et al. 2004, Post et al. 2009). In addition, changes in climate are altering human-wildlife interactions in subsistence communities at high latitudes via direct effects on human mobility (e.g., snowmobile travel) and indirect effects on the distribution and abundance of game species (Berman and Kofinas 2004, Brinkman et al. 2016). The paucity of knowledge regarding the response of animal populations to dynamic snowscapes represents a critical gap in understanding and mitigating the vulnerability of natural systems to climate change.

Snowscapes are highly dynamic, with properties (e.g., presence, depth, density, and stratification) varying considerably in space and time due to both short-term (e.g., diurnal cycles or single-storm events; Heilig et al. 2015) and long-term climatic patterns (e.g., seasonal phenology, annual temperature trends, decadal cycles; Sproles et al. 2013, Heilig et al. 2015). In addition, topography and vegetative cover can shape microclimates and further contribute to fine-scale spatial variation in snowscapes (Hiemstra et al. 2006, Liston and Elder 2006a). Thus, quantifying spatially and temporally heterogeneous snowscapes is key to understanding how animals navigate such dynamic landscapes (Watson et al. 2008).

Movement-based resource selection models are effective tools for evaluating animal movement in response to both static and dynamic spatial features (Thurfjell et al. 2014). Step selection functions (SSF) comprise a class of movement-based resource selection models that partition an individual's movement path into discrete steps taken over uniform intervals of time (Compton et al. 2002, Fortin et al. 2005). Selection in such cases is quantified using conditional logistic regression, where spatial covariates for observed steps (i.e., "used" locations or GPS fixes) are compared to those from random steps (i.e., "available" locations) defined by an individual or population's movement patterns (Thurfjell et al. 2014). Sampling random steps are achieved through random draws from modeled or empirical distributions of displacement distances and turning angles derived over constant intervals of time, which is often the finest interval between observed animal locations (Thurfjell et al. 2014). By doing so, resource availability is constrained by an individual's current location in space and time and spatial covariates (e.g., snow depth) change dynamically in "step" with animal trajectories. Thus, the time interval between steps (hereafter referred to as the "step scale") can be adjusted to test for scale-dependent responses to spatial

covariates, whereby increases in step intervals will permit longer distance movements and expand both the temporal and spatial extent of the domain available to an individual.

Snow data products are readily available, but they may not capture relevant snow properties at spatial and temporal resolutions that match the needs of animal movement and resource selection studies. Satellite-derived measures of snow cover offer extensive spatial and temporal coverage (Painter et al. 2009, Hall and Riggs 2016), but measuring snow characteristics such as depth, density, and thaw/refreezing conditions across broad landscapes over time is far more challenging. NASA's Moderate-resolution Imaging Spectroradiometer (MODIS) instruments offer moderate spatial (≥ 500 -m grid for snow cover) and high temporal (daily) resolution multispectral imagery with global coverage (Hall and Riggs 2016) and are commonly used in ecological studies as a means of representing temporally dynamic landscapes (Bischof et al. 2012, Rose et al. 2015, Stoner et al. 2016). Yet, MODIS products, such as MODIS normalized difference snow index (NDSI), may be too coarse spatially for the purposes of fine-scale animal movement modeling (e.g., 500-m grid). Landsat is another satellite-borne, multispectral instrument that measures fractional snow-covered area at much finer spatial grains (30 m), but it has relatively poor temporal resolution (8- or 16-d coverage intervals), and, like MODIS products, suffers from data gaps due to cloud cover (Zhu and Woodcock 2014). Additional space-borne or aerial instruments for measuring snow properties exist, including passive microwave (Walker and Goodison 1993, Kim et al. 2015), radar (Nagler and Rott 2000, Marshall and Koh 2008), and light detection and ranging (LIDAR; Deems et al. 2013, Eitel et al. 2016). Yet, the data products from each of these instruments are often insufficient for studying the effects of changing snowpack properties on animal movement because of limited spatial resolution (>500 -m grid), temporal resolution (weekly, annual, or single event), and/or spatial and temporal extent. Thus, current snow products derived using remote sensing may have limited utility in the study of animal movement.

Physical snowpack models can also be used to simulate a wide array of snow properties at relevant temporal and spatial scales (NOHRSC 2004, Hiemstra et al. 2006, Watson et al. 2008). These models simulate the physical processes involved in surface mass-energy exchange using inputs such as meteorological data, topography, and vegetation. Compared to remote sensing products, snowpack models offer a more detailed characterization of snow conditions and can also vary in extent, temporal and spatial resolution, and derived snow metrics (Liston and Elder 2006a, Watson et al. 2006a, Brennan et al. 2013). Such models include the Snow Data Assimilation System (SNODAS, daily 1-km grid coverage across the conterminous United States from 2004 through present day NOHRSC 2015), SnowModel (Liston and Elder 2006a, b), and several other snow hydrologic models (Watson et al. 2006b, Messer et al. 2008, Geremia et al. 2014). SnowModel, in particular, offers users tremendous flexibility as a spatially distributed, multi-layer snow-evolution modeling system scalable down to 1-m spatial and 10-min temporal resolutions and can derive over 100 unique snow metrics, including snow depth and snow density (Liston and Elder 2006a, b). As such, SnowModel could be an

ideal tool for investigating the influence of snowpack properties on animal movement and resource selection. Although SnowModel has been used extensively for climate and hydrological applications worldwide (Hiemstra et al. 2006, Liston and Hiemstra 2011, Semmens et al. 2013, Sproles et al. 2013, Højlund et al. 2016), it has been used in only a small number of wildlife studies to date (Liston et al. 2016, Lendrum et al. 2017, Reinking et al. 2018). Snowpack models offer many attractive features for the purposes of animal movement and resource selection, though several factors may limit their utility relative to more user-friendly remote-sensing products. Apart from SNODAS, snowpack models require specialized knowledge of physical systems and programming to perform the computationally intensive snowpack simulations. In addition, physically based snow evolution models require meteorological inputs derived through direct measurement or atmospheric models that may not exist in some areas or at the required resolution. The resulting model products are thus subject to uncertainty in model specification, meteorological inputs, and derived estimates that can lead to systematic biases (e.g., SNODAS; Brennan et al. 2013, Hedrick et al. 2015), which may be exacerbated at finer spatiotemporal resolutions (Daly 2006).

Here, we examine the response of Dall sheep (*Ovis dalli dalli*) in Lake Clark National Park and Preserve, Alaska, USA (Lake Clark NPP) to multiple snowpack metrics using a movement-based analysis of resource selection (Fig. 1). As a medium-sized ungulate requiring year-round access to forage along alpine slopes (Nichols and Bunnell 1999, Roffler et al. 2017), Dall sheep may be especially sensitive to changes in snow depth and density (Simmons 1982, Nichols 1988). Dall sheep often seek windblown patches with exposed forage or sufficiently shallow (or soft) snow to permit excavation, most commonly occurring along the windward side of ridges or along ridgetops (Simmons 1982, Nichols and Bunnell 1999). Their populations have declined by 21% range wide since 1990, with declines of more than 70% in some populations forcing emergency harvest closures (Alaska Department of Fish and Game 2014). Changing snow conditions may be playing a role in the observed declines, yet no quantitative analyses have examined how Dall sheep navigate complex snowscapes. In addition, with Dall sheep hunting opportunities being a highly contentious issue among some user groups (Alaska Department of Fish and Game 2014), further information on the effects of changing snowscapes on Dall sheep movements is needed to inform conservation and management. Here, we compare the relative abilities of SnowModel outputs and remotely sensed MODIS data products to predict Dall sheep space use in winter across spatiotemporal scales. Because snow conditions may influence Dall sheep via several mechanisms (e.g., energetics of movement or access to forage) and across multiple spatial and temporal scales, we conducted our analyses with three broad hypotheses in mind. First, we predicted that including any snowscape metric, whether remotely sensed or modeled, would improve our ability to describe Dall sheep movement and space use. Second, we predicted that SnowModel-simulated snow depth would outperform NDSI as a predictor of Dall sheep movement. Our reasoning was that NDSI would have insufficient variation during winter to capture movement decisions made by Dall sheep.

Third, we predicted Dall sheep would select for shallow, low-density snows that should facilitate snow excavation when foraging and improve efficiency of movement (Parker et al. 1984, Dailey and Hobbs 1989). Our approach illustrates a novel framework to understand how wildlife navigate changing snowscapes across multiple scales and may enhance wildlife managers' ability to predict how climate change will affect the movements of valued game species such as Dall sheep.

METHODS

Study animal

Dall sheep are endemic to the mountainous regions of Alaska and northwestern Canada, where snow cover persists for eight to nine months of the year and is characterized by fine-scale heterogeneity associated with complex landscapes. Dall sheep prefer rugged terrain at elevations above tree line (Nichols and Bunnell 1999, Roffler et al. 2017), which facilitates evasion of natural predators such as wolves (*Canis lupus*), coyotes (*Canis latrans*), and brown bears (*Ursus arctos*; Geist 1971, Frid 1997) and extends the growing seasons of key forage species as a consequence of the topographic heterogeneity (Nichols and Bunnell 1999, Myrsetrud et al. 2001). Dall sheep require year-round access to forage in the form of grasses (*Festuca* spp. and *Poa* spp.) and sedges (*Carex* spp.). Sheep often exhibit seasonal migratory movements along an elevation gradient, moving higher in summer and lower in winter (Data S1: Fig. S1). Dall sheep are a medium-sized ungulate with mean chest heights of 54 cm (Telfer and Kelsall 1984). However, as with many ungulates, they are sexually dimorphic in that males are generally taller and heavier than females (Nichols and Bunnell 1999). Although Dall sheep are social, herds are sexually segregated except during the rut in late fall and early winter (Rachlow and Bowyer 1998, Nichols and Bunnell 1999).

We captured 30 adult Dall sheep (12 male, 18 female) using helicopter net-gunning without chemical immobilization during three capture events from fall of 2005 through spring of 2008. We fitted each individual with a global positioning system (GPS) collar (Telonics TGW-3500/TGW-3580; Telonics, Mesa, AZ, USA) programmed to acquire locations every seven hours and released animals at the site of capture.

Study area

Lake Clark National Park and Preserve (NPP; Figs. 1, 2) is at the intersection of the Alaska and Aleutian Ranges along the Chigmit Mountains in south-central Alaska and at the southern extent of the Dall sheep range. Lake Clark NPP is characterized by a diversity of elevation-dependent ecotypes, with boreal conifers (*Picea glauca* and *P. mariana*) and interspersed white birch (*Betula neoalaskana*) along south slopes and at lower elevations, as well as alder (*Alnus viridis*) along riparian corridors. Alpine tundra and barren ground dominate as elevation increases, transitioning into persistent snow cover and glaciers at the highest elevations. The park's maritime climate varies considerably by year, proximity to the coast, and elevation. Winter temperatures average -10°C in the interior (Remote Automated Weather



FIG. 1. This photograph of a Dall sheep ewe and three lambs highlights the spatial heterogeneity in snowscapes, particularly along ridgelines, within the Dall sheep native range. Photo credit: Laura Prugh; Wrangell Mountains, Alaska, USA.

Stations, RAWS; Port Alsworth from 2005 to 2008) and -1.5°C along the coast (RAWS; Silver Salmon Lakes from 2013 to 2017), with occasional minimum temperatures falling below -40°C in the interior (data *available online*).¹ Winter precipitation is also heaviest along the coast, with monthly averages of 90.1 ± 12.0 mm (mean \pm SE) and 18.2 ± 3.77 mm along the coast and in the interior, respectively.

Landscape covariates

We included landscape covariates that are expected to influence Dall sheep movements based on previous studies (Dailey and Hobbs 1989, Rachlow and Bowyer 1998, Roffler et al. 2017; Table 1). By doing so, we were able to evaluate the relative improvement in model fit when including snow compared to more traditional, landscape-based resource selection models. We characterized topographic heterogeneity by deriving elevation, slope, aspect, vector ruggedness measure (VRM; Sappington et al. 2007), terrain ruggedness index (TRI; Riley et al. 1999), and proximity to escape terrain (distance in meters to slopes $>60\%$; McKinney et al. 2003) from LANDFIRE and the United States Geological Survey National Elevation Dataset (NED, 30-m re-gridded to 25-m). Terrain metrics have been used to characterize sheep habitat due to their value in describing seasonal migrations, refuge from predators, and variation in forage (Rachlow and Bowyer 1998, Nichols and Bunnell 1999).

¹ <https://raws.dri.edu/>

However, to avoid redundancy, we only considered models where proximity to escape terrain, slope, TRI, and VRM were considered independently. Because of strong associations between snow properties and aspect, we did not include aspect in models with snow. We also included proximity to glacier as an index of moisture continuum and forage accessibility (*sensu* Berger et al. 2015) and proximity to barren ground and shrubs given the importance of both in providing access to ground forage. Proximity to glacier, barren ground, and shrub land was derived from the USGS National Land Cover Database classification scheme on a 30-m grid (NLCD; Homer et al. 2015).

Snow covariates

We simulated snow depth and snow density using SnowModel (Liston and Elder 2006a) at 1-d increments for the period our GPS collars were deployed (1 September 2005 through 31 August 2008; 1,096 d). SnowModel is composed of four sub-models that estimate surface energy exchanges (EnBal; Liston et al. 2000), snow depth and water-equivalent evolution (SnowPack; Liston and Mernild 2012), snow redistribution by wind (SnowTran-3D; Liston et al. 2007), and assimilate both available field (*i.e.*, weather stations) and remote sensing data sets (SnowAssim; Liston and Hiemstra 2008). SnowModel simulates numerous processes, including snow accumulation; blowing-snow redistribution and sublimation; interception, unloading, and sublimation within forest canopies; snow density evolution; and

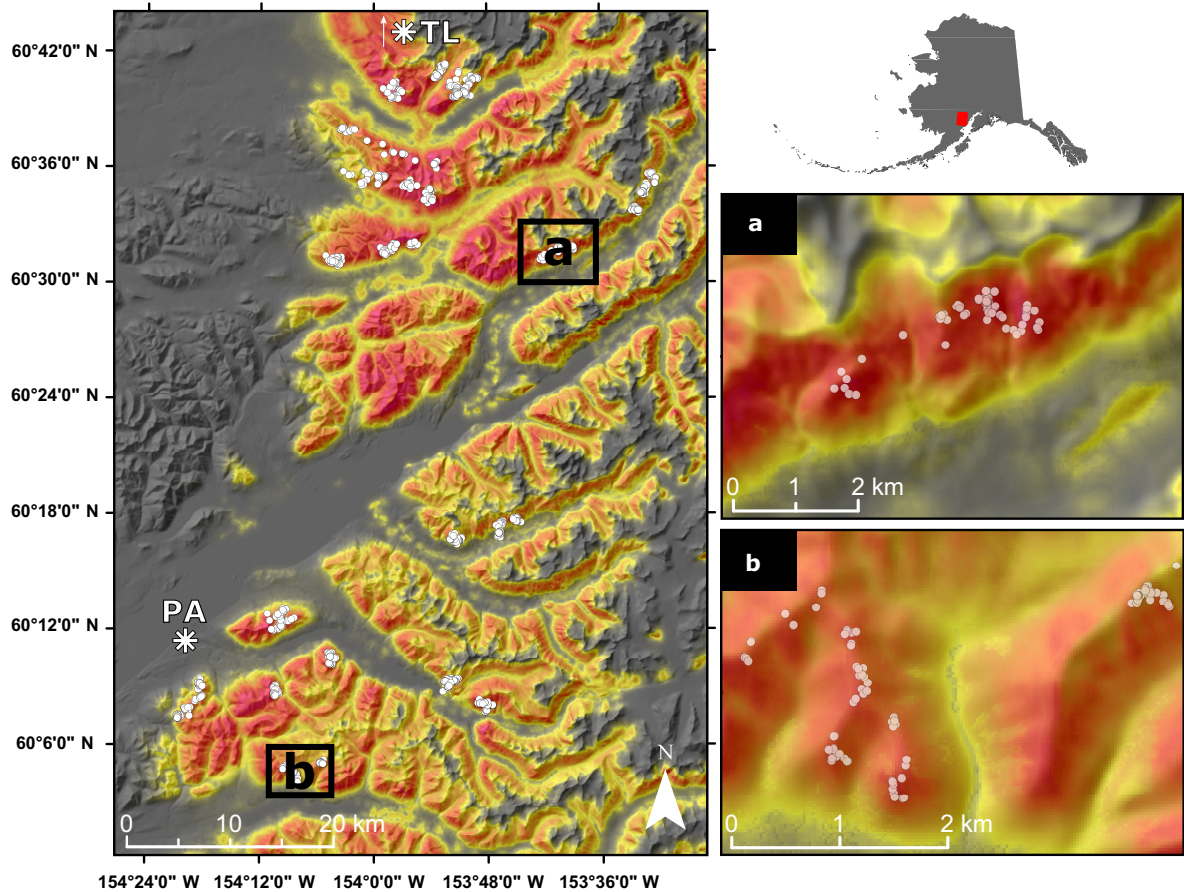


FIG. 2. The western face of the Chigmit Mountains in Lake Clark National Park and Preserve, Alaska. White points are locations from multiple Dall sheep from 27 March through 5 April 2006. The base heatmap depicts the relative, conditional probability of use on 1 April 2006 as predicted by the best model from our second, fine-scale analysis. Hotter colors correspond to higher relative probabilities of use by sheep. White asterisks denote SNOTEL stations as meteorological inputs in SnowModel (PA, Port Alsworth; TL, Telaquana Lake, 15 km north of map edge). The two insets (a, b) were arbitrarily chosen to depict model predictions of space use along east-west and north-south gradients.

snowpack ripening and melt (including thaw/refreezing). To do so accurately, the model requires data inputs for temporally variant precipitation, air temperature, wind speed and direction, solar and longwave radiation, and relative humidity obtained from meteorological stations and/or atmospheric models located within or near the simulation domain, and spatially distributed, time-invariant topography and land cover.

We used empirical meteorological data from two remote automated weather stations (RAWS; Port Alsworth and Stoney) and 25 grid points from NASA's Modern Era Retrospective-Analysis for Research and Applications (MERRA-2; Gelaro et al. 2017) data product. We incorporated each in MicroMet (Liston and Elder 2006b) to aggregate the original hourly, 10-m air temperature, specific humidity, u and v wind components, surface pressure, and precipitation variables into daily atmospheric forcing distributions required by SnowModel (see Liston and Elder [2006b] for additional details). In addition, we used SnowAssim to assimilate snow depth observations from the Port Alsworth and Lake Telaquana Snow Telemetry (SNOTEL) sites in the Lake Clark NPP region (Fig. 2). Last, we incorporated topographic and vegetation data using NED and

NLCD as discussed above, but we reclassified NLCD to match SnowModel's defined vegetation classes (see Appendix S1; Liston and Elder 2006b) and rescaled each to the appropriate simulation resolution (e.g., 25 m, 100 m, 500 m, 2 km, and 10 km). Our choice of SnowModel resolutions reflected the finest resolution possible with existing input data (e.g., 25 m derived from DEM and land cover). The coarser resolutions were motivated by potential comparisons with 500-m MODIS NDSI (e.g., 500-m grid) and two publicly accessible SnowModel data sets on 2- and 10-km grids for all of Alaska (G. E. Liston, *unpublished data*) and the pan-Arctic (Liston and Hiemstra 2011), respectively. We simulated each of the coarser grids by rescaling the original 25-m topography and land cover inputs to the coarser resolutions. Given the sensitivity of snow evolution models to quantity and quality of meteorological input data, we validated SnowModel outputs by comparing observed and modeled estimates of temperature, wind speed, and snow depth using available SNOTEL data (Appendix S1: Fig. S3, S4). In addition, we qualitatively compared observed and simulated snow distributions using Landsat imagery (Appendix S1: Fig. S5), including a comparison of the presence of glaciers with areas where

TABLE 1. Covariate descriptions and summary statistics used in a Dall sheep step selection function.

Variable	Description	Used			Available		
		Mean	Median	Range	Mean	Median	Range
Escape terrain	proximity (m) to >60% slope	60.8 (76.0)	90.0	0.0–805.0	93.7 (160.1)	90.0	0.0–5,048.0
Barren	proximity (m) to talus (NLCD 31)	79.1 (134.2)	30.0	0.0–1,420.7	124.9 (214.5)	30.0	0.0–3,559.7
Shrub	proximity (m) to dwarf, low, tall shrub/scrub (NLCD 51,52)	52.8 (87.9)	30.0	0.0–839.2	66.5 (120.7)	30.0	0.0–2,676.4
Glacier	proximity (m) to glacier (NLCD 12)	5,123.5 (3,783.1)	3,575.2	108.0–14,955.2	5,130.2 (3,800.1)	3,638.4	0.0–17,706.2
VRM	Vector Ruggedness Measure; see Sappington et al. (2007)	0.5 (0.3)	0.6	0.0–1.0	0.5 (0.3)	0.6	0.0–1.0
TRI	Terrain Ruggedness Index	11.6 (3.7)	12.0	0.2–37.7	11.0 (3.9)	11.5	0.0–41.6
Slope	degrees (0–90)	30.4 (8.4)	32.0	0.2–62.3	29.0 (9.1)	30.9	0.0–64.6
Elevation	25-m grid, elevation (m)	1,008.5 (237.7)	1,006.9	141.5–2,046.2	979.2 (277.4)	986.0	77.0–2,199.6
Snow density (25 m)	kg/m ³ ; 25-m grid SnowModel	201.3 (152.4)	223.5	0.0–550.1	199.8 (152.5)	223.1	0.0–550.1
Snow density (500 m)	kg/m ³ ; 500-m grid SnowModel	197.5 (150.1)	224.5	0.0–550.0	197.9 (151.4)	224.9	0.0–550.1
Snow density (2 km)	kg/m ³ ; 2-km grid SnowModel	196.7 (152.1)	225.4	0.0–550.0	196.5 (152.2)	225.4	0.0–550.1
Snow density (10 km)	kg/m ³ ; 10-km grid SnowModel	209.2 (159.1)	245.7	0.0–550.0	209.0 (159.2)	245.4	0.0–550.0
Snow depth (25 m)	cm, 25-m grid SnowModel	30.0 (32.3)	21.1	0.0–258.6	28.7 (31.1)	20.1	0.0–307.1
Snow depth (500 m)	cm, 500-m grid SnowModel	27.5 (28.6)	21.0	0.0–128.9	27.5 (28.8)	20.7	0.0–138.8
Snow depth (2 km)	cm, 2-km grid SnowModel	26.9 (28.5)	20.0	0.0–126.7	26.8 (28.4)	19.7	0.0–133.7
Snow depth (10 km)	cm, 10-km grid SnowModel	38.1 (42.0)	25.3	0.0–199.0	37.9 (42.0)	25.1	0.0–199.0
NDSI	daily normalized difference snow index, 500-m grid MODIS	40.9 (30.4)	53.0	0.0–91.0	41.8 (30.6)	54.0	0.0–92.0

Notes: The summary statistics are derived from the complete winter data set and decomposed into used and available location data for qualitative comparisons of sheep resource selection. Values in parentheses are SD.

SnowModel indicated snow persistence. Appendix S1 contains additional information about the SnowModel simulation methods.

In addition to SnowModel outputs, we acquired MODIS snow cover through the National Snow and Ice Data Center using the Center's file transfer protocol (e.g., MOD10A1) and custom R code (*available online*).² We specifically used estimates of normalized difference snow index (NDSI, an index of fractional snow cover) on a 500-m grid (MOD/MYD10A1, version 6; Hall and Riggs 2016). Daily MODIS products suffer from cloud cover and misclassification, resulting in large proportions of empty pixels within some regions. Thus, we implemented a two-step gap-filling procedure to increase the number of cloud-free observations within our data set. First, we filled MODIS Terra (MOD10A1) with Aqua observations (MYD10A1) given the temporal lag in satellite passage, which provided an opportunity for gap-filling as cloud cover evolved throughout a given day (Parajka and Blöschl 2008). Second, we filled cloud-obscured or missing pixels with the nearest

high-quality measurement within buffers of 5 and 10 d (sensu Hall et al. 2010; Table 2).

Step selection process

We used a step selection function (SSF; Fortin et al. 2005) to evaluate the influence of landscape metrics and time-varying snow conditions on Dall sheep resource selection from January through mid-May (i.e., winter). We selected

TABLE 2. The size of winter data sets used in a Dall sheep step selection function based on the inclusion of MODIS normalized difference snow index (NDSI) and the temporal cloud fill interval.

Subset	N_{used}	N_{avail}
MODIS: no cloud fill	457	1,847
MODIS: 5-d cloud fill	2,812	12,460
MODIS: 10-d cloud fill	3,674	16,900
Complete data set	20,554	102,770

Note: N_{used} , number of used points; N_{avail} , number of available points.

² <ftp://n5eil01u.ecs.nsidc.org/SAN/MOSA/>

this period to avoid potentially confounding behaviors such as the rut (mid October through mid December) and parturition (May through June; Rachlow and Bowyer 1991). Although we did not have exact parturition dates for sampled ewes, we used median displacements and elevations from sheep locations to characterize when this transition likely occurred (Data S1: Fig. S1). We derived movement distributions for each individual during winter at eight step scales from 7 h through 896 h (or approximately five weeks) using increments in proportion to our finest GPS fix rate (i.e., 7 h). Each distribution was composed of observed movements (i.e., empirical step lengths and turning angles) and used to generate five random displacements from “used” locations at time t_{step} , and therefore local “availability” at time $t_{\text{step}} + 1$, at every step made by an individual for each of the eight-step scales. We annotated both observed (Used = 1) and random steps (Used = 0) with each of the spatial covariates described above. We conducted conditional logistic regression using the `clogit` function in R package `survival` (version 2.39-5; Therneau 2015). Conditional logistic regression can pair used locations with matched random locations through a stratifying variable, in this case, a step identifier that is unique across all steps made by all individuals (Fortin et al. 2005). We also clustered by animal year in order to account for the lack of independence between steps made by the same individual for a given winter, which represents a robust and conservative approach for estimating coefficient variances provided more than 30 clusters are present (Prima et al. 2017).

Model selection and evaluation

We assessed collinearity and variance inflation in all covariates using R package `usdm` (version 1.1-5; Naimi 2015), and either removed one or considered collinear variables independently within model sets (cutoffs: $r > 0.70$ or $\text{VIF} > 4$; Menard 2002). We ranked models by the Quasi-likelihood Under Independence Criterion (QIC; Pan 2001), a conservative information theoretic for evaluating relative fit in conditional step selection models (Craiu et al. 2008). In general, smaller QIC values indicate improved relative model fit. As the data sets change across step scales, both in terms of the number of locations and the sample of availability, comparisons of relative fit were limited to within step scale model sets. Many snow metrics were also strongly correlated (e.g., SnowModel snow depth at 500 m and NDSI at 500 m, $r = 0.593\text{--}0.634$; Data S1: Table S1), necessitating a two-stage model selection process for each of the eight-step scales considered. First, we used QIC to identify the most parsimonious model representing base (or null) resource selection for Dall sheep by considering all possible combinations of landscape covariates (except elevation and models with redundant terrain metrics; Table 1). Candidate models included simple second-order polynomials for all continuous metrics to reflect possible non-linearities in Dall sheep response to those covariates (Boyce 2006, Manly et al. 2007). Our justification for doing so was that all continuous landscape covariates were based either on proximity metrics or terrain ruggedness and likely to elicit non-linear responses in sheep. For example, the strength of an individual’s response to land cover should decline with distance.

Similarly, we might predict sheep would avoid flat terrain due to the associated risks of predation while also avoiding the most rugged terrain due to the absence of forage, leading to selection for some intermediate ruggedness.

For the second stage, we created a model set for each step scale whereby each model consisted of the top-ranked base model and a single snow covariate from the suite of snow metrics we evaluated. This approach allowed us to evaluate the relative fit of each snow covariate at each step scale, while accounting for confounding relationships with landscape metrics and avoiding statistical problems associated with collinearity between snow metrics (Hosmer et al. 2013). As with the landscape covariates in the first stage, we considered simple second-order polynomials to reflect possible non-linearities in sheep response to snow. Given our specific interest in snow, we also included models with simple splines to test for more complex non-linearities (integrated in the `clogit` function call using the R package `splines`, version 3.3.2; R Core Development Team 2016). Our justification for including non-linear coefficients was the expectation that sheep would respond to snow in complex ways (e.g., strength of avoidance would increase non-linearly with snow depth up to some threshold before plateauing). In addition, we included models with elevation, either additively or as an interaction, to account for the confounding relationship between snow and elevation. Thus, model sets included the base models from the first stage, base models with a univariate snow metric, base models with polynomial or spline-based non-linearities in snow, and base models with snow–elevation interactions ($n = 139$ models evaluated for each step scale).

We examined model sets with three distinct hypotheses in mind: (1) adding snow metrics will improve model performance relative to models without snow, (2) SnowModel-simulated snow depth will outperform NDSI as a predictor of Dall sheep movement, and (3) Dall sheep will avoid deeper snow across all scales of selection and select for lower snow densities to facilitate snow excavation when foraging and improve efficiency of movement. To test the first hypothesis, we compared models with and without snow using QIC, expecting QIC to be lower for all models with snow covariates as compared to the base models. To test the second hypothesis, we evaluated the relative performance of snow metrics in describing Dall sheep resource selection across step scales using QIC. Models included NDSI at a 500-m grid or SnowModel-simulated snow depth at each of five spatial resolutions (25 m, 100 m, 500 m, 2 km, 10 km; Data S1: Fig. S2). Because we considered NDSI in this analysis, we restricted sheep locations to those included in the 5- or 10-d gap-filled data set in order to facilitate model comparisons between NDSI and all other snow metrics using information criterion (Table 2; Data S1: Tables S1–S3).

To test the third hypothesis, we evaluated Dall sheep resource selection in response to SnowModel-simulated snow conditions at the finest step scale (i.e., 7 h) using all available data (Table 2). In this case, we used snow depth and density simulated on a 25-m resolution grid. Due to differences in body mass and height between the sexes that could affect the way each responds to fine-scale snow conditions, we evaluated three distinct model sets: males only, females only, and all individuals pooled. We included

models allowing non-linearities in response to snow metrics as we did for the second hypothesis. However, because of the added power afforded the larger non-MODIS data set, we incorporated two- and three-way interactions based on combinations of snow depth, snow density, and elevation. Although three-way interactions add substantial complexity to the model sets, our biological justification for incorporating such complexity was to identify whether selection for snow density changed with snow depth per our hypothesis. In addition, we anticipated that selection for snow conditions might change with elevation or that selection for elevation would change with snow conditions.

Finally, we standardized all continuous metrics by centering on means and dividing by one standard deviation to facilitate comparison of effects and model convergence (Gelman et al. 2014; Table 1). We evaluated all models using an out-of-sample cross-validation procedure similar to k -folds cross-validation (Boyce et al. 2002), but where data were “folded” by iteratively withholding one individual as a test data set.

RESULTS

Base model of resource use

Model selection consistently supported the same suite of landscape covariates across all step scales (Fig. 3; Data S1: Table S2). In general, the top-ranked models with the lowest QIC indicated Dall sheep selected for high terrain ruggedness (TRI, unit-less 30–45) and proximity to barren ground and shrub, with increases in the magnitude of selection for each as step scale increased. However, there was some support for non-linearities indicating the magnitude of selection declined at greater distances from both vegetation classes and at the highest terrain ruggedness. Dall sheep avoided glaciers, selecting for intermediate distances (~8,500 m at mean estimates for all covariates), which reflected preference for rugged terrain while maintaining access to forage. All estimated coefficients for landscape covariates in the top-ranked base models were consistent within step scale regardless of which snow component was included, indicating our base model was not confounded by the type of snow metric (Data S1: Fig. S3). In addition, inference regarding landscape metrics was consistent between the models using the complete (non-MODIS) data set and the 10-d MODIS gap-filled subset (Data S1: Fig. S3). Therefore, we present the 10-d MODIS gap-filled results below given the added statistical power afforded the larger sample of sheep locations (Table 2).

Snow resolution across scales of selection

Including snow, in any form and at any spatial scale, markedly improved model fit relative to a base model with only time-invariant landscape metrics. All top models with and without snow exhibited excellent predictive potential for withheld (i.e., out-of-sample) individuals in a cross-validation context (Spearman’s Cross-Validation Score ≥ 0.84). At fine scales (≤ 14 -h), snow depth at 25 m was the best snow metric (Fig. 4; Data S1: Table S2). Support switched to snow depth measured on a 500-m grid at moderate step

scales (28 and 56-h). Interestingly, snow depth at 100 m performed considerably poorer than either snow depth at 25 and 500 m, without a continuous transition along a resolution gradient as step scale increased (Fig. 4). NDSI outperformed SnowModel’s snow depth and density as a predictor of Dall sheep movements at coarser step scales (≥ 112 h). Snow depth also consistently explained more variation in sheep movement than snow density (i.e., lower QIC for models with snow depth relative to snow density; Data S1: Table S2). When evaluating within snow covariate model sets (i.e., excluding all other snow covariate models), model selection generally supported an interaction between snow covariates and elevation, except for NDSI, within covariate-specific top models (i.e., lowest QIC within a single snow covariate model subset; Data S1: Table S2). In all cases, the interaction indicated an avoidance of snow depth and density with increasing elevation and a shift toward lower elevations when snow depth and density increased.

Movement at the finest scale

Using the complete data set without NDSI allowed us to evaluate more complex patterns in resource selection at the finest step scale, including the addition of three-way interactions between snow depth, snow density, and elevation. Because the results were consistent across sex-specific and pooled model sets, we show our results with the sexes pooled (Figs. 2, 5; for sex-specific results, see Data S1: Table S3, S4, Fig. S4). Our top model had robust support (next best Δ QIC > 33 , Spearman’s CV score = 0.94) and included a two-way interaction between non-linear snow depth (two-knot spline) and non-linear snow density (two-knot spline), along with additive non-linear terms for elevation (two-knot spline; Data S1: Table S5). This model indicated Dall sheep strongly selected for shallow, low-density snow up to depths of approximately 25 cm (or one-half of mean chest height) before declining precipitously to zero above mean chest height (54 cm, Fig. 5a). In addition, when snow depths exceeded mean chest height, sheep switched their selection for snow densities above 300 kg/m³ (Fig. 5b). The non-linear elevation coefficients indicated sheep selected for intermediate elevations.

DISCUSSION

We demonstrated that incorporating temporally dynamic and spatially heterogeneous snowpack metrics can substantially improve model performance in assessments of winter movement and resource selection using a population of Dall sheep in Lake Clark NPP, Alaska. Although their intended use may have been for non-biological purposes, existing snow products offer the potential for novel insights into how animals use snowscapes during a critical period for many species. Use of NDSI can improve our understanding of animal movement at broader scales and has the advantage of being a user-friendly and publically accessible data set. However, if fine-scale processes are of primary interest, a snowpack evolution model such as SnowModel will likely be needed.

Evaluating the mechanistic associations between climate, animal behavior, and demography necessitates matching

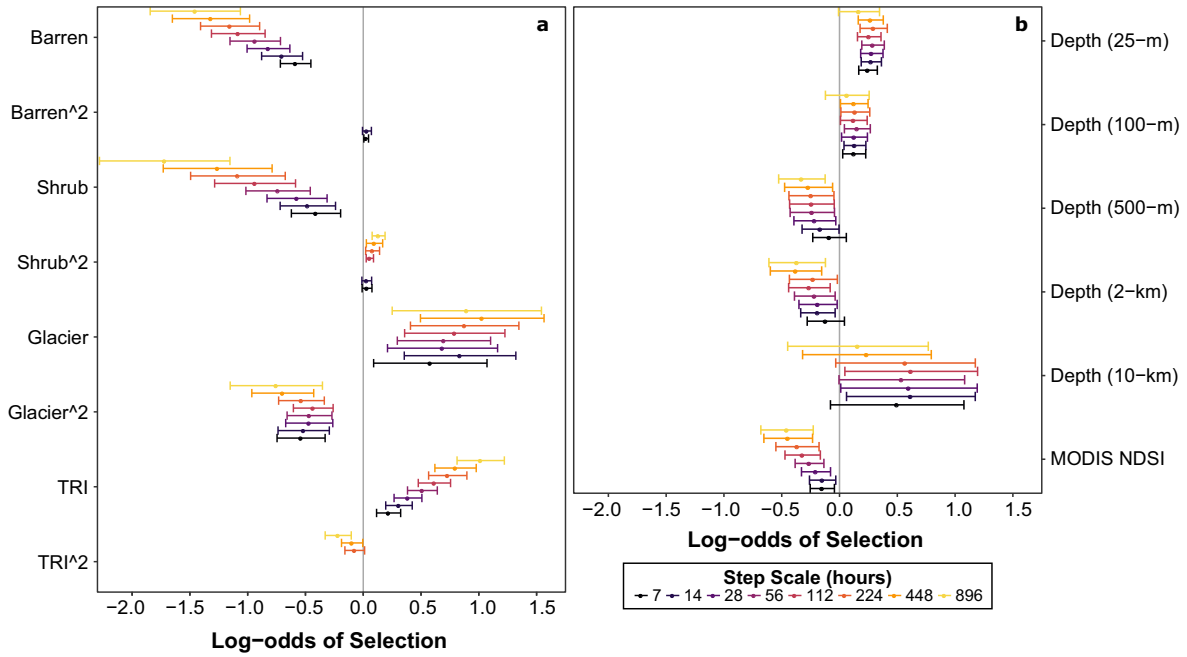


FIG. 3. The (a) estimates for base coefficients in the absence of snow and (b) independent snow coefficients at each of eight step scales in an assessment of Dall sheep resource selection. Error bars represent 95% confidence intervals. Positive values indicate avoidance for distance-based metrics and selection for all others. Variables are described in Table 1.

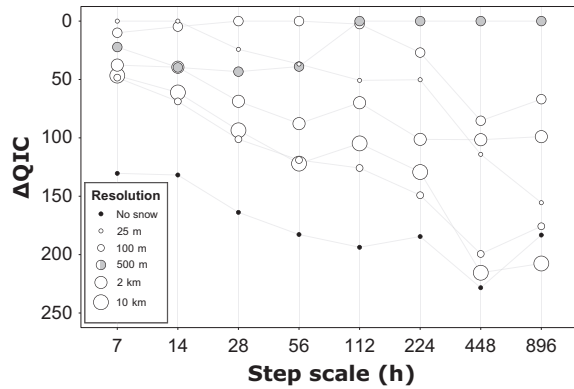


FIG. 4. A comparison of model performance between no snow (black), MODIS NDSI (gray), and snow depth (white) grouped by Dall sheep step scale. Δ QIC values equal to zero represent the best performing model overall for a given step scale (lowest quasi-likelihood under independence criterion [QIC]).

snow processes with behavior at relevant spatial and temporal scales (e.g., the inclusion of a blowing-snow process; Liston et al. 2007, 2016). For example, snow cover may influence forage accessibility, and therefore resource selection, at relatively fine scales (Hansen et al. 2011), whereas changes in snow cover may trigger migratory movements and variation in seasonal site selection at relatively large scales (Johnson et al. 2002, Cagnacci et al. 2011). The choice in scale, therefore, needs to be sufficiently fine to capture the desired ecological process and associated behavioral response (Thurfjell et al. 2014). Yet, the scale used to define resource selection behavior should not be confused with the scale used in spatial measurements (i.e., grains or

resolutions). If measured at too fine a resolution, spatial covariates may add noise, and therefore uncertainty, to the underlying process that elicit responses in animals, and if too coarse, informative spatial heterogeneity will be lost (Boyce 2006, Schaefer and Mayor 2007, Mayor et al. 2009, DeCesare et al. 2012). Although finer spatial and temporal resolutions in data are often desirable, the appropriateness and therefore benefit of current spatial data products is likely scale dependent with regard to animal movement and resource selection behavior.

Our results indicated the relative fit of various snow metrics was scale dependent across model sets, suggesting some metrics performed best at specific step scales (Fig. 4). In general, fine-scale movements (7- and 14-h) were predicted best by SnowModel snow depth on a 25-m grid, moderate-scale movements (28 through 56 h) by snow depth on a 500-m grid, and large-scale movements (≥ 112 h) by MODIS NDSI on a 500-m grid. However, selection coefficients were remarkably scale invariant (Fig. 3), suggesting the interpretation of each snow metric may be consistent across step scales. Thus, so long as a given snow metric sufficiently represents the ecological processes of interest, the metric could be informative regardless of the existence of better performing measures.

We predicted the finest resolution snow depth would outperform NDSI at all scales of selection because snow depth contains more information than snow cover and should be relevant to animal movement at all step scales. We likewise expected NDSI to inform animal resource use only at the broadest scales. Indeed, the finest resolution snow depth metrics (25 m) were more informative than the coarser NDSI (500 m) in characterizing Dall sheep movements at the finest step scales (7 and 14 h). The superior performance of SnowModel at the finest scales was likely due to three

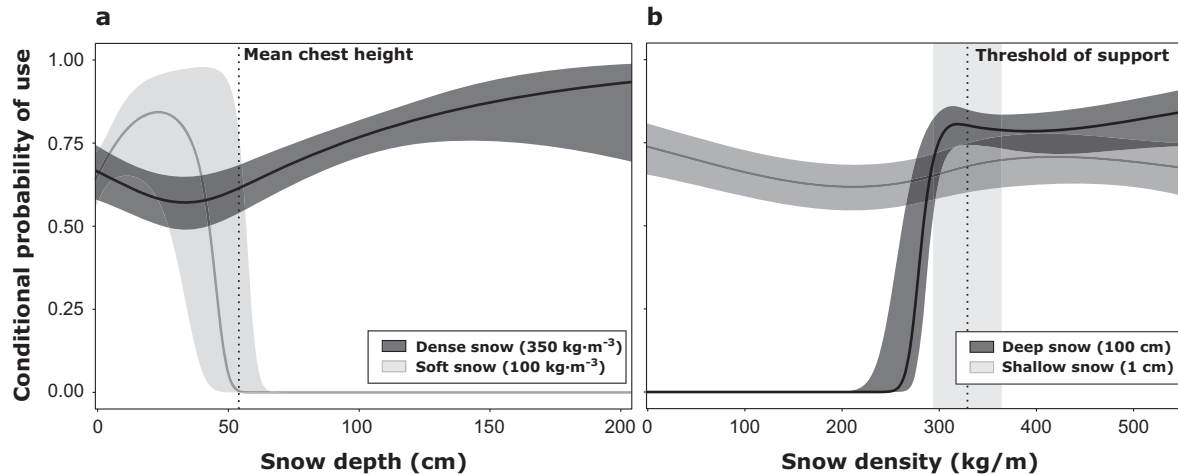


FIG. 5. The interactive effect of snow depth and density on conditional probability of use in Dall sheep. (a) The effect snow depth at two levels of density (soft snow, 100 kg/m^3 ; dense snow, 350 kg/m^3). (b) The effect of snow density at two levels of snow depth (shallow snow, 1 cm; deep snow, 100 cm). The dotted lines represent mean chest height (54 cm) and snow density threshold of support for the body mass of Dall sheep (329 kg/m^3 , $\text{SE} = 18$; Sivy et al., 2018) in panels a and b, respectively. All bands represent 95% confidence intervals.

main factors. First, snow depth on the 25 m SnowModel grid captured more variability in snow conditions than NDSI, particularly during the peak of winter when snow extent is greatest. Second, snow depth may directly reflect snow conditions affecting the energetics of animal movement and accessibility of forage and, thus, better predict space use than NDSI (Parker et al. 1984, Fancy and White 1987, Dailey and Hobbs 1989). Third, using SnowModel, we were able to simulate snow depth at a finer resolution than the typical short-distance movements of Dall sheep, as opposed to the fixed-resolution of a MODIS product. Winter movements of Dall sheep were characterized by a median distance of 140 m over a 7-h interval (Data S1: Fig. S1), which was larger than our finest SnowModel resolution of 25 m and smaller than NDSI fixed at 500 m.

Contrary to our expectations, NDSI outperformed snow depth as a predictor of Dall sheep movements at coarse step scales ($\geq 112\text{-h}$; Fig. 4). As a measure of sub-pixel snow patchiness (Hall and Riggs 2007), NDSI is capturing a spatially implicit snow distribution process that is not reflected in the pixel-level, point estimates of SnowModel outputs at the MODIS-equivalent 500-m scale. Although this implies NDSI is measuring a distinct characteristic of snowscapes at finer resolutions than the MODIS 500-m grid, NDSI also performed better than our finest resolution snow depth outputs (25 m) at these coarser step scales. This would suggest that sheep are indeed responding to lower fractional snow cover more so than snow depth at scales relevant to winter range selection (akin to second-order selection; Johnson 1980), and is consistent with observations of Dall sheep utilizing patches of wind-exposed forage above tree-line during winter (Nichols and Bunnell 1999). Thus, sheep may be selecting winter ranges with a higher preponderance of snow-free patches, rather than shallower snow depths, as a measure of access to forage within home ranges. However, because NDSI is based on actual observations rather than modeled processes, it may also provide a more accurate representation of snow distribution than SnowModel simulations at coarser resolutions.

Although NDSI performed well relative to the other snow metrics, two main factors may limit the utility of remotely sensed snow cover as a predictor of animal movements. First, in similar systems, problems with cloud cover and snow-cloud misclassification will likely necessitate excluding substantial amounts of animal location data due to the absence of an NDSI estimate for a given location in space and time. We could retain only 2.2% of sheep locations when including NDSI filtered by high-quality flags, which increased to 17.9% after performing a 10-d gap fill (Table 2). At worst, data loss can lead to systematic biases associated with spatial patterns in persistent cloud cover (Parajka and Blöschl 2008) and at best, substantially weaken one's inference regarding complex interactions among snow properties and other spatial covariates. Data losses may be greater in cases where additional quality filters are employed, such as the application of sensor azimuthal thresholds to limit the use of poor quality measurements at the boundaries of a satellite's path (Xin et al. 2012, Li et al. 2016). Although MOD10A1 (version 006) contains a flag for oscillating measurements akin to those described by Xin et al. (2012), in the absence of an azimuthal threshold, data may contain underestimates of NDSI in areas with extensive forest cover, heterogeneous terrain, or frequent shallow sensor passes (Xin et al. 2012, Li et al. 2016). Second, study systems with more homogenous landscapes may have insufficient heterogeneity in snow cover to inform animal resource selection (e.g., 100% snow cover throughout the study area all winter). In such cases, snowpack evolution models such as SnowModel may provide more variable snow metrics (e.g., snow depth and density) capable of informing animal space use. Despite these limitations, our results show that NDSI can improve animal movement and resource selection models compared to models lacking snow covariates.

The most appropriate snowscape metric for a given application will depend on the ecological process of interest and the scale at which it occurs (Thurfjell et al. 2014). Our results indicated the coarser Alaska-wide and pan-Arctic SnowModel Products (2 and 10 km, respectively) might not

be informative predictors of animal movement and resource selection, at least for species exhibiting similar short-distance movements as Dall sheep. NDSI, and perhaps the coarser SnowModel products (≥ 2 km), may be more appropriately used when addressing questions pertaining to large-scale movements in wide-ranging species such as wolverine (*Gulo gulo*; Aubry et al. 2007) or in classifying seasonal ranges of long-distance migrants such as caribou (*Rangifer tarandus*; Johnson et al. 2002). In addition, snow depth at 100 m performed considerably poorer than snow depth at 25 m and 500 m. Although not immediately intuitive, this outcome further highlights the importance of ecological process when considering scale-dependent responses to dynamic landscapes. The 25 m snow depth data likely provided sufficient resolution to capture complex, fine-scale responses of Dall sheep to snowscapes that influenced energetics and immediate access to forage. At coarser scales of selection (≥ 112 h), Dall sheep appeared to switch from more immediate energetic needs to simply ranging in areas with more exposed patches of forage (i.e., more patchy snow cover). Yet, the 100-m resolution snow depth data was inadequate for the purposes of both, with insufficient variation to support the added complexity observed at finer scales with 25-m data (≤ 14 h) and perhaps too noisy for the simpler patterns observed at coarser scales with 500-m data (≥ 28 h; Data S1: Table S2). Alternatively, because individuals navigate snowscapes with imperfect knowledge, exploratory movements may add noise and thus reduce the strength of selection for snow cover at the 100-m resolution. Further research examining the scale at which exploratory movements occur would improve inference regarding scale-dependent patterns of selection.

The utility of these snow metrics is not limited to the original products and can be used to derive additional snowscape properties that reflect specific spatial processes of interest. For example, NDSI and SnowModel snow depth can both be used to quantify snow disappearance dates (Dickerson-Lange et al. 2017) and snowline elevation (Parajka et al. 2017, Verbyla et al. 2017), which can be used to identify the timing of migration in ungulates and seasonal resource use in montane species. In addition, SnowModel can be used to generate fractional snow cover (Liston 2004) in cases where a coarse measure of snow distribution is hypothesized to influence animal movement.

We were also interested in fine-scale processes that influenced the energetics of movement and accessibility of forage. Many herbivores at higher latitudes experience chronic energy deficits as a consequence of limited access to and availability of high-quality forage during winter (Nichols and Bunnell 1999, Messer et al. 2008, MacNearney 2014). Thus, the energetic costs of moving through snow are likely to affect the way animals navigate snowscapes (Lundmark and Ball 2008, Avgar et al. 2013). As we predicted, Dall sheep selected for areas with shallower snow, corresponding to wind-blown ridges at moderate-to-high elevations (Fig. 2). Such selection patterns may help offset energy deficits by minimizing effort required to excavate ground forage under shallow snow (Nichols and Bunnell 1999). We also observed that sheep strongly avoided deeper snows at or above mean chest height (54 cm) when in softer snows (Fig. 5a). Contrary to expectations, however, Dall sheep

selected for higher snow densities when moving through deeper snows. Dall sheep should avoid deep snow unless sufficient density exists to support an individual's foot loadings, because the costs of traveling through deep snow increases exponentially with density below some threshold of support (Parker et al. 1984). This threshold of snow density for supporting Dall sheep was estimated to be 329.0 ± 18.0 kg/m³ (mean \pm SE; Sivy et al., 2018), which corresponds to the approximate density at which we found Dall sheep selected for denser snow in deep snow conditions (Fig. 5b). Although these results were for the sexes combined, the sex-specific responses to snow depth and density were consistent with known biological constraints. Males were willing to travel through deeper snows than females, up to a difference of approximately 10 cm (Data S1: Fig. S4a, c). Both sexes responded similarly to snow density, but males appeared to be more willing to travel through sub-optimal snow conditions based on model uncertainty in a male response to low density at elevated snow depths (Data S1: Fig. S4). These results imply a link between behavioral state and selection for specific snow conditions, whereby sheep select for shallow snow when foraging and dense snow when traveling. Ideally, we would have distinguished in-transit from foraging/resting states in an effort to better characterize state-dependent resource selection (McClintock et al. 2017), but this would have been difficult to achieve with the existing data set in the absence of accelerometer data or finer fix intervals (i.e., < 7 h). Future efforts to monitor space use should consider behavioral state more explicitly when evaluating movement and resource selection in response to dynamic snowscapes.

Climate change is altering snow conditions worldwide, with broad ecological implications for large-scale animal movements (Lundmark and Ball 2008, Cagnacci et al. 2011) and species' distributions (Sanecki et al. 2006, Matthews et al. 2010, Stien et al. 2010). Current climate projections for the contiguous United States and Alaska predict a 4–6% increase in precipitation, with an increase in snow during the winter and a greater proportion falling as rain annually (Wetherbee and Mast 2016). Snow cover is also expected to persist for longer at higher elevations relative to present day, although snow cover duration will be shorter on average (Wetherbee and Mast 2016). Our results indicate that these changes will likely affect Dall sheep movements in important and potentially predictable ways. Both females and males exhibited clear movement patterns in response to snow depth and density that match known thresholds in body size and support, respectively (Data S1: Fig. S4). Increased winter precipitation, particularly in the form of snow, is likely to reduce the overall availability of winter habitat for sheep (i.e., forage and navigable terrain) and limit the ability of individuals to mitigate energy deficits through behavioral modification. Thus, as these fine-scale movements are likely a means of minimizing energy costs associated with travel (Parker et al. 1984), increased late winter precipitation could be detrimental to survival during a critical period of the year for sheep (Rachlow and Bowyer 1991). If these movements are indeed linked to demographic processes, present increases in winter precipitation may already be contributing to recent declines in Dall sheep populations and may affect population persistence if current climate models are realized.

In contrast to the expected decline in winter habitat quality, the projected increase in winter precipitation may lead to more favorable conditions outside of the winter season. Warming temperatures and increased winter precipitation may translate to improved forage quality during parturition and summer (Myserud and Austrheim 2014) or overall shorter snow duration, which may offset the potential demographic costs of increased late winter precipitation. Our models can be used to map and predict trends in overwintering habitat based on current climate projections. Doing so will help managers to identify areas of high suitability during snow-covered periods, and to anticipate how these high-value areas will shift as the snowpack evolves through time (Hoefs 1984, Post and Stenseth 1999, Myserud and Saether 2011). For species that are harvested during winter, such as some deer and caribou populations, a snowscape modeling framework will also help managers better predict the movements of wildlife in relation to areas of high hunting activity, adding a new potential tool for adaptive harvest management (Allen and Singh 2016). Understanding the spatial requirements and resource needs of animals, while accommodating dynamic landscapes (e.g., snowscapes), will be critical in predicting how wildlife will respond to increasingly variable and severe environmental conditions resulting from climate change.

CONCLUSIONS

We demonstrate that the inclusion of existing snow products can substantially improve models of resource selection using Dall sheep in Lake Clark NPP as a case study. Our results provide statistical support for hypothesized drivers of Dall sheep movement (Nichols and Bunnell 1999) via the first movement-based assessment of Dall sheep resource selection. These results help refine our general understanding of how variable snow conditions shape animal movements across multiple spatial and temporal scales. Although current snow products may be sufficient for specific scale-dependent applications, we encourage further development of snowpack evolution models with an interest in generating snowpack metrics directly relevant to animal movement (e.g., snow collapse pressure; Hepburn 1978, Sheldon et al. 2007), as well as broader ecological processes such as resource selection, demography, and community dynamics. Because such models depend on accurate meteorological data that can be difficult to obtain in regions with sparse weather stations, we also encourage the development of new remote sensing instruments, or novel uses for existing remote sensing data, that can be used with snowpack evolution models to achieve more ecologically relevant metrics at biologically appropriate spatial and temporal scales. Doing so is essential to understanding how individuals, populations, and species will respond to changing snowscapes.

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LITERATURE CITED

- Alaska Department of Fish and Game. 2014. Trends in Alaska sheep populations, hunting, and harvests. Wildlife Management Report, Division of Wildlife Conservation, Fairbanks, Alaska, USA.
- Allen, A. M., and N. J. Singh. 2016. Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution* 3:155.
- Aubry, K. B., K. S. McKelvey, and J. P. Copeland. 2007. Distribution and broadscale habitat relations of the wolverine in the contiguous United States. *Journal of Wildlife Management* 71:2147.
- Avgar, T., A. Mosser, G. S. Brown, and J. M. Fryxell. 2013. Environmental and individual drivers of animal movement patterns across a wide geographical gradient. *Journal of Animal Ecology* 82:96–106.
- Berger, J., G. B. Schaller, E. Cheng, A. Kang, M. Krebs, L. Li, and M. Hebblewhite. 2015. Legacies of past exploitation and climate affect mammalian sexes differently on the roof of the world—the case of wild yaks. *Scientific Reports* 5:8676.
- Berman, M., and G. Kofinas. 2004. Hunting for models: grounded and rational choice approaches to analyzing climate effects on subsistence hunting in an Arctic community. *Ecological Economics* 49:31–46.
- Bintanja, R., and F. M. Selten. 2014. Future increases in Arctic precipitation linked to local evaporation and sea-ice retreat. *Nature* 509:479–482.
- Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Myserud. 2012. A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave? *American Naturalist* 180:407–424.
- Boutin, S., and J. E. Lane. 2014. Climate change and mammals: evolutionary versus plastic responses. *Evolutionary Applications* 7:29–41.
- Boyce, M. S. 2006. Scale for resource selection functions. *Diversity and Distributions* 12:269–276.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Brennan, A., P. C. Cross, M. Higgs, J. P. Beckmann, R. W. Klaver, B. M. Scurlock, and S. Creel. 2013. Inferential consequences of modeling rather than measuring snow accumulation in studies of animal ecology. *Ecological Applications* 23:643–653.
- Bring, A., I. Fedorova, Y. Dibike, L. Hinzman, J. Mård, S. H. Mernild, T. Prowse, O. Semenova, S. L. Stuefer, and M. K. Woo. 2016. Arctic terrestrial hydrology: a synthesis of processes, regional effects, and research challenges. *Journal of Geophysical Research: Biogeosciences* 121:621–649.
- Brinkman, T. J., W. D. Hansen, F. S. Chapin, G. Kofinas, S. BurnSilver, and T. S. Rupp. 2016. Arctic communities perceive climate impacts on access as a critical challenge to availability of subsistence resources. *Climatic Change* 139:413–427.
- Brodie, J. F., E. Post, J. Berger, and F. Watson. 2014. Trophic interactions and dynamic herbivore responses to snowpack. *Climate Change Responses* 1:4.

- Cagnacci, F., et al. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos* 120:1790–1802.
- Callaghan, T. V., et al. 2004. Effects of changes in climate on landscape and regional processes, and feedbacks to the climate system. *Ambio* 33:459–468.
- Callaghan, T. V., et al. 2011a. Multiple effects of changes in Arctic snow cover. *Ambio* 40:32–45.
- Callaghan, T. V., M. Johansson, J. Key, T. Prowse, M. Ananicheva, and A. Klepikov. 2011b. Feedbacks and interactions: from the arctic cryosphere to the climate system. *Ambio* 40:75–86.
- Chapin, F. S., T. V. Callaghan, Y. Bergeron, M. Fukuda, J. F. Johnstone, G. Juday, and S. A. Zimov. 2004. Global change and the boreal forest: thresholds, shifting states or gradual change? *Ambio* 33:361.
- Compton, B., J. Rhymer, and M. McCollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. *Ecology* 83:833.
- Craiu, R. V., T. Duchesne, and D. Fortin. 2008. Inference methods for the conditional logistic regression model with longitudinal data. *Biometrical Journal* 50:97–109.
- Dailey, T. V., and N. T. Hobbs. 1989. Travel in alpine terrain: energy expenditures for locomotion by mountain goats and bighorn sheep. *Canadian Journal of Zoology* 67:2368–2375.
- Daly, C. 2006. Guidelines for assessing the suitability of spatial climate data sets. *International Journal of Climatology* 26:707–721.
- DeCesare, N. J., et al. 2012. Transcending scale dependence in identifying habitat with resource selection functions. *Ecology* 22:1068–1083.
- Deems, J. S., T. H. Painter, and D. C. Finnegan. 2013. Lidar measurement of snow depth: a review. *Journal of Glaciology* 59:467–479.
- Dickerson-Lange, S. E., R. F. Gersonde, J. A. Hubbard, T. E. Link, A. W. Nolin, G. H. Perry, T. R. Roth, N. E. Wayand, and J. D. Lundquist. 2017. Snow disappearance timing is dominated by forest effects on snow accumulation in warm winter climates of the Pacific Northwest, United States. *Hydrological Processes* 31:1846–1862.
- Eitel, J. U. H., et al. 2016. Beyond 3-D: the new spectrum of lidar applications for earth and ecological sciences. *Remote Sensing of Environment* 186:372–392.
- Fancy, S. G., and R. G. White. 1987. Energy expenditures for locomotion by barren-ground caribou. *Canadian Journal of Zoology* 65:122–128.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Frid, A. 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. *Animal Behaviour* 53:799–808.
- Geist, V. 1971. Mountain sheep: a study in behavior and evolution. University of Chicago Press, Chicago, Illinois, USA.
- Gelaro, R., et al. 2017. The modern-era retrospective analysis for research and applications, version 2 (MERRA-2). *Journal of Climate* 30:5419–5454.
- Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2014. Bayesian data analysis. Chapman & Hall, Boca Raton, Florida, USA.
- Geremia, C., P. J. White, J. A. Hoeting, R. L. Wallen, F. G. R. Watson, D. Blanton, and N. T. Hobbs. 2014. Integrating population- and individual-level information in a movement model of Yellowstone bison. *Ecological Applications* 24:346–362.
- Gilbert, S. L., K. J. Hundertmark, D. K. Person, M. S. Lindberg, and M. S. Boyce. 2017. Behavioral plasticity in a variable environment: snow depth and habitat interactions drive deer movement in winter. *Journal of Mammalogy* 98:246–259.
- Hall, D. K., and G. A. Riggs. 2007. Accuracy assessment of the MODIS snow products. *Hydrological Processes* 21:1534–1547.
- Hall, D. K., and G. A. Riggs. 2016. MODIS/Terra snow cover daily L3 global 500m grid, Version 6. [Indicate subset used]. NASA National Snow and Ice Data Center Distributed Active Archive Center, Boulder, Colorado, USA. doi: <https://doi.org/10.5067/MODIS/MOD10A1.006>
- Hall, D. K., G. A. Riggs, J. L. Foster, and S. V. Kumar. 2010. Development and evaluation of a cloud-gap-filled MODIS daily snow-cover product. *Remote Sensing of Environment* 114:496–503.
- Hansen, B. B., R. Aanes, I. Herfindal, J. Kohler, B. E. Sæther, and M. K. Oli. 2011. Climate, icing, and wild arctic reindeer: past relationships and future prospects. *Ecology* 92:1917–1923.
- Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* 86:2135–2144.
- Hedrick, A., H. P. Marshall, A. Winstral, K. Elder, S. Yueh, and D. Cline. 2015. Independent evaluation of the SNODAS snow depth product using regional-scale lidar-derived measurements. *Cryosphere* 9:13–23.
- Heilig, A., C. Mitterer, L. Schmid, N. Wever, J. Schweizer, H.-P. Marshall, and O. Eisen. 2015. Seasonal and diurnal cycles of liquid water in snow: measurements and modeling. *Journal of Geophysical Research: Earth Surface* 120:14452.
- Hepburn, R. L. 1978. A snow penetration gauge for studies of white-tailed deer and other northern animals. *Journal of Wildlife Management* 42:663–667.
- Hiemstra, C. A., G. E. Liston, and W. A. Reiners. 2006. Observing, modelling, and validating snow redistribution by wind in a Wyoming upper treeline landscape. *Ecological Modelling* 197:35–51.
- Hoefs, M. 1984. Productivity and carrying capacity of a subarctic sheep winter range. *Arctic* 37:141–147.
- Højlund, S., et al. 2016. Spatiotemporal characteristics of seasonal snow cover in Northeast Greenland from in situ observations. *Arctic, Antarctic, and Alpine Research* 48:653–671.
- Homer, C. G., J. A. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. D. Herold, J. D. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing* 81:345–354.
- Hosmer, D. W. J., S. L. Lemeshow, and R. X. Sturdivant. 2013. Applied logistic regression. John Wiley & Sons, Hoboken, New Jersey, USA.
- Jeong, D., and L. Sushama. 2017. Rain-on-snow events over North America based on two Canadian regional climate models. *Climate Dynamics* 50:303–316.
- Johnson, D. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002. Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology* 71:225–235.
- Kim, Y., J. S. Kimball, D. A. Robinson, and C. Derksen. 2015. New satellite climate data records indicate strong coupling between recent frozen season changes and snow cover over high northern latitudes. *Environmental Research Letters* 10:084004.
- Langlois, A., et al. 2017. Detection of rain-on-snow (ROS) events and ice layer formation using passive microwave radiometry: a context for Peary caribou habitat in the Canadian Arctic. *Remote Sensing of Environment* 189:84–95.
- Lemke, P., et al. 2007. Observations: changes in snow, ice and frozen ground. Pages 337–383 in S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Lendrum, P. E., J. M. Northrup, C. R. Anderson, G. E. Liston, C. L. Aldridge, K. R. Crooks, and G. Wittemyer. 2017. Predation risk across a dynamic landscape: effects of anthropogenic land

- use, natural landscape features, and prey distribution. *Landscape Ecology* 33:157–170.
- Li, H., X. Li, and P. Xiao. 2016. Impact of sensor zenith angle on MOD10A1 data reliability and modification of snow cover data for the Tarim River Basin. *Remote Sensing* 8:750.
- Liston, G. E. 2004. Representing subgrid snow cover heterogeneities in regional and global models. *Journal of Climate* 17:1381–1397.
- Liston, G. E., and K. Elder. 2006a. A distributed snow-evolution modeling system (SnowModel). *Journal of Hydrometeorology* 7:1259–1276.
- Liston, G. E., and K. Elder. 2006b. A meteorological distribution system for high-resolution terrestrial modeling (MicroMet). *Journal of Hydrometeorology* 7:217–234.
- Liston, G. E., R. B. Haehnel, M. Sturm, C. A. Hiemstra, S. Berzovskaya, and R. D. Tabler. 2007. Simulating complex snow distributions in windy environments using SnowTran-3D. *Journal of Glaciology* 53:241–256.
- Liston, G. E., and C. A. Hiemstra. 2008. A simple data assimilation system for complex snow distributions (SnowAssim). *Journal of Hydrometeorology* 9:989–1004.
- Liston, G. E., and C. A. Hiemstra. 2011. The changing cryosphere: Pan-Arctic snow trends (1979–2009). *Journal of Climate* 24:5691–5712.
- Liston, G. E., and S. H. Mernild. 2012. Greenland freshwater runoff. Part I: a runoff routing model for glaciated and non-glaciated landscapes (HydroFlow). *Journal of Climate* 25:5997–6014.
- Liston, G. E., C. J. Perham, R. T. Shideler, and A. N. Cheuvront. 2016. Modeling snowdrift habitat for polar bear dens. *Ecological Modelling* 320:114–134.
- Liston, G. E., J. G. Winther, O. Bruland, H. Elvehøy, K. Sand, and L. Karlöf. 2000. Snow and blue-ice distribution patterns on the coastal Antarctic Ice Sheet. *Antarctic Science* 12:69–79.
- Lundmark, C., and J. P. Ball. 2008. Living in snowy environments: quantifying the influence of snow on moose Behavior. *Arctic, Antarctic, and Alpine Research* 40:111–118.
- MacNearney, D. 2014. Investigation of winter habitat selection by woodland caribou in relation to forage abundance and snow accumulation. MS Thesis. Lakehead University, Thunder Bay, Ontario, Canada.
- Mallory, C. D., and M. S. Boyce. 2017. Observed and predicted effects of climate change on Arctic caribou and reindeer. *Environmental Reviews* 26:13–25.
- Manly, B. F. L., L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2007. *Resource selection by animals: statistical design and analysis for field studies*. Springer Science & Business Media, Berlin, Germany.
- Marshall, H. P., and G. Koh. 2008. FMCW radars for snow research. *Cold Regions Science and Technology* 52:118–131.
- Matthews, A., P. G. Spooner, D. Lunney, K. Green, and N. I. Klomp. 2010. The influences of snow cover, vegetation and topography on the upper range limit of common wombats *Vombatus ursinus* in the subalpine zone, Australia. *Diversity and Distributions* 16:277–287.
- Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. *Ecoscience* 16:238–247.
- McClintock, B. T., J. M. London, M. F. Cameron, and P. L. Boveng. 2017. Bridging the gaps in animal movement: hidden behaviors and ecological relationships revealed by integrated data streams. *Ecosphere* 8:e01751.
- McKinney, T., S. R. Boe, and J. C. deVos. 2003. GIS-based evaluation of escape terrain and desert bighorn sheep populations in Arizona. *Wildlife Society Bulletin* 31:1229–1236.
- Menard, S. 2002. *Applied logistic regression analysis*. Sage University Paper Series on Quantitative Applications in the Social Sciences. Second edition. Sage Publications, Thousand Oaks, California, USA.
- Messer, M., R. Garrott, S. Cherry, and P. White. 2008. Elk winter resource selection in a severe snow pack environment. *Terrestrial Ecology* 3:137–156.
- Mysterud, A., and G. Austrheim. 2014. Lasting effects of snow accumulation on summer performance of large herbivores in alpine ecosystems may not last. *Journal of Animal Ecology* 83:712–719.
- Mysterud, A., R. Langvatn, N. Yoccoz, and N. Stenseth. 2001. Plant phenology, migration and geographical variation in body weight of a large Herbivore: the effect of a variable topography. *Journal of Animal Ecology* 70:915–923.
- Mysterud, A., and B. E. Saether. 2011. Climate change and implications for the future distribution and management of ungulates in Europe. Pages 349–375 in R. Putnam, M. Apollonio, and R. Andersen, editors. *Ungulate management in Europe: problems and practices*. Cambridge University Press, Cambridge, UK.
- Nagler, T., and H. Rott. 2000. Retrieval of wet snow by means of multitemporal SAR data. *IEEE Transactions on Geoscience and Remote Sensing* 38:754–765.
- Naimi, B. 2015. usdm: uncertainty analysis for species distribution models. Version 1.1-15. R package. <https://cran.r-project.org/web/packages/usdm/>
- National Operational Hydrologic Remote Sensing Center. 2015. Snow Data Assimilation System (SNODAS) data products at NSIDC. National Snow and Ice Data Center, Boulder, Colorado, USA.
- Nichols, L. 1988. Simple methods of comparing winter snow conditions on alpine and subalpine ranges of Dall's sheep and mountain goats in Alaska. Pages 330–335 in W. M. Samuel, editor. *Proceedings of the 6th Biennial Symposium, North American Wild Sheep and Goat Council*. 11–15 April 1988, Banff, Alberta, Canada.
- Nichols, L., and F. Bunnell. 1999. Natural history of thinhorn sheep. Pages 23–77 in R. Valdez and P. R. Krausman, editors. *Mountain sheep of North America*. The University of Arizona Press, Tucson, Arizona, USA.
- NOHRSC. 2004. Snow Data Assimilation System (SNODAS) Data Products at NSIDC, Version 1. National Operational Hydrologic Remote Sensing Center, Boulder, Colorado, USA.
- Olsen, M. S., et al. 2011. The changing arctic cryosphere and likely consequences: an overview. *Ambio* 40:111–118.
- Painter, T. H., K. Rittger, C. McKenzie, P. Slaughter, R. E. Davis, and J. Dozier. 2009. Retrieval of subpixel snow covered area, grain size, and albedo from MODIS. *Remote Sensing of Environment* 113:868–879.
- Pan, W. 2001. Akaike's information criterion in generalized estimating equations. *Biometrics* 57:120–125.
- Parajka, J., and G. Blöschl. 2008. Spatio-temporal combination of MODIS images—potential for snow cover mapping. *Water Resources Research* 44:1–13.
- Parajka, J., N. Bezak, J. Burkhart, and L. Holko. 2017. Estimation of snow line elevation changes from MODIS snow cover data. *Conference Proceedings for the 19th EGU General Assembly*, 23–28 April, Vienna, Austria.
- Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. *Functional Ecology* 23:57–69.
- Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. *Journal of Wildlife Management* 48:474–488.
- Pauli, J. N., B. Zuckerberg, J. P. Whiteman, and W. Porter. 2013. The subnivium: a deteriorating seasonal refugium. *Frontiers in Ecology and the Environment* 11:260–267.
- Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology* 80:1322–1339.
- Post, E., et al. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325:1355–1358.
- Pozzanghera, C. B., K. J. Sivy, M. S. Lindberg, and L. R. Prugh. 2016. Variable effects of snow conditions across boreal mesocarnivore species. *Canadian Journal of Zoology* 94:697–705.
- Prima, M. C., T. Duchesne, and D. Fortin. 2017. Robust inference from conditional logistic regression applied to movement and habitat selection analysis. *PLoS ONE* 12:e0169779.

- Putkonen, J., T. C. Grenfell, K. Rennert, C. Bitz, P. Jacobson, and D. Russell. 2009. Rain on snow: little understood killer in the north. *Eos, Transactions American Geophysical Union* 90:221–222.
- R Core Development Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Rachlow, J., and R. Bowyer. 1991. Interannual variation in timing and synchrony of parturition in Dall's sheep. *Journal of Mammalogy* 72:487–492.
- Rachlow, J., and R. Bowyer. 1998. Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. *Journal of Zoology* 245:457–465.
- Reinking, A. K., K. T. Smith, K. L. Monteith, T. W. Mong, M. J. Read, and J. L. Beck. 2018. Intrinsic, environmental, and anthropogenic factors related to pronghorn summer mortality. *Journal of Wildlife Management* 82:608–617.
- Riley, S., S. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences* 5:23–27.
- Robinson, B. G., and E. H. Merrill. 2012. The influence of snow on the functional response of grazing ungulates. *Oikos* 121:28–34.
- Roffler, G. H., L. G. Adams, and M. Hebblewhite. 2017. Summer habitat selection by Dall's sheep in Wrangell-St. Elias National Park and Preserve, Alaska. *Journal of Mammalogy* 98:94–105.
- Rose, R. A., et al. 2015. Ten ways remote sensing can contribute to conservation. *Conservation Biology* 29:350–359.
- Sand, H., C. Wikenros, P. Wabakken, and O. Liberg. 2006. Effects of hunting group size, snow depth and age on the success of wolves hunting moose. *Animal Behaviour* 72:781–789.
- Sanecki, G. M., A. Cowling, K. Green, H. Wood, and D. Lindenmayer. 2006. Winter distribution of small mammals in relation to snow cover in the subalpine zones, Australia. *Journal of Zoology* 269:99–110.
- Sappington, J. M., K. M. Longshore, and D. B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *Journal of Wildlife Management* 71:1419–1426.
- Schaefer, J. A., and S. J. Mayor. 2007. Geostatistics reveal the scale of habitat selection. *Ecological Modelling* 209:401–406.
- Semmens, K. A., J. Ramage, A. Bartsch, and G. E. Liston. 2013. Early snowmelt events: detection, distribution, and significance in a major sub-arctic watershed. *Environmental Research Letters* 8:014020.
- Sheldon, J. W., R. L. Crabtree, C. S. Potter, D. J. Weiss, and B. Winkelman. 2007. Snow dynamics and mountain fox (*Vulpes vulpes macroura*) in Yellowstone: incorporating climate in species-habitat models. www.Yellowstoneresearch.org.
- Simmons, N. 1982. Seasonal ranges of Dall's sheep, Mackenzie Mountains, Northwest Territories. *Arctic* 35:512–518.
- Sivy, K. J., A. W. Nolin, C. Cosgrove, and L. Prugh. 2018. Critical snow density threshold for Dall sheep (*Ovis dalli dalli*). *Canadian Journal of Zoology*. <https://doi.org/10.1139/cjz-2017-0259>
- Sproles, E. A., A. W. Nolin, K. Rittger, and T. H. Painter. 2013. Climate change impacts on maritime mountain snowpack in the Oregon Cascades. *Hydrology and Earth System Sciences* 17:2581–2597.
- Stien, A., L. E. Loel, A. Mysterud, T. Severinsen, J. Kohler, and R. Langvatn. 2010. Icing events trigger range displacement in a high-Arctic ungulate. *Ecology* 91:915–920.
- Stoner, D. C., J. O. Sexton, J. Nagol, H. H. Bernales, T. C. Edwards, and C. Edwards. 2016. Ungulate reproductive parameters track satellite observations of plant phenology across latitude and climatological regimes. *PLoS ONE* 11:1–19.
- Telfer, E. S., and J. P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. *Ecology* 65:1828–1834.
- Therneau, T. 2015. A package for Survival Analysis in S. version 2.38. <https://cran.r-project.org/web/packages/survival/>
- Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. *Movement Ecology* 2:26.
- Verbyla, D., T. Hegel, A. Nolin, M. van de Kerk, and L. Prugh. 2017. Remote sensing of 2000–2016 alpine spring snowline elevation in Dall sheep mountain ranges of Alaska and western Canada. *Remote Sensing* 9:1157.
- Vihma, T., J. Screen, M. Tjernström, B. Newton, X. Zhang, V. Popova, C. Deser, M. Holland, and T. Prowse. 2016. The atmospheric role in the Arctic water cycle: a review on processes, past and future changes, and their impacts. *Journal of Geophysical Research: Biogeosciences* 121:586–620.
- Walker, A., and B. Goodison. 1993. Discrimination of a wet snow cover using passive microwave satellite data. *Annals of Glaciology* 17:307–311.
- Watson, F. G. R., T. N. Anderson, W. B. Newman, S. E. Alexander, and R. A. Garrott. 2006a. Optimal sampling schemes for estimating mean snow water equivalents in stratified heterogeneous landscapes. *Journal of Hydrology* 328:432–452.
- Watson, F. G. R., T. N. Anderson, W. B. Newman, S. S. Cornish and T. R. Thein. 2008. Chapter 6 modeling spatial snow pack dynamics. *Terrestrial Ecology* 3:85–112.
- Watson, F. G. R., W. B. Newman, J. C. Coughlan, and R. A. Garrott. 2006b. Testing a distributed snowpack simulation model against spatial observations. *Journal of Hydrology* 328:453–466.
- Wetherbee, G. A., and M. A. Mast. 2016. Annual variations in wet-deposition chemistry related to changes in climate. *Climate Dynamics* 47:3141–3155.
- Xin, Q., C. E. Woodcock, J. Liu, B. Tan, R. A. Melloh, and R. E. Davis. 2012. View angle effects on MODIS snow mapping in forests. *Remote Sensing of Environment* 118:50–59.
- Zhu, Z., and C. E. Woodcock. 2014. Automated cloud, cloud shadow, and snow detection in multitemporal Landsat data: an algorithm designed specifically for monitoring land cover change. *Remote Sensing of Environment* 152:217–234.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1773/full>

DATA AVAILABILITY

Data available from NASA's Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC): <https://doi.org/10.3334/ornl daac/1602>