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NOTE

Critical snow density threshold for Dall's sheep (*Ovis dalli dalli*)

Kelly J. Sivy, Anne W. Nolin, Christopher L. Cosgrove, and Laura R. Prugh

Abstract: Snow cover can significantly impact animal movement and energetics, yet few studies have investigated the link between physical properties of snow and energetic costs. Quantification of thresholds in snow properties that influence animal movement are needed to help address this knowledge gap. Recent population declines of Dall's sheep (*Ovis dalli dalli* Nelson, 1884) could be due in part to changing snow conditions. We examined the effect of snow density, snow depth, and snow hardness on sinking depths of Dall's sheep tracks encountered in Wrangell–St. Elias National Park and Preserve, Alaska. Snow depth was a poor predictor of sinking depths of sheep tracks ($R^2 = 0.02$, $p = 0.38$), as was mean weighted hardness ($R^2 = 0.09$, $p = 0.07$). Across competing models, top layer snow density (0–10 cm) and sheep age class were the best predictors of track sink depths ($R^2 = 0.58$). Track sink depth decreased with increasing snow density, and the snowpack supported the mass of a sheep above a density threshold of 329 ± 18 kg/m³ (mean ± SE). This threshold could aid interpretation of winter movement and energetic costs by animals, thus improving our ability to predict consequences of changing snowpack conditions on wildlife.

Key words: climate change, Dall's sheep, energetics, *Ovis dalli dalli*, snow.

Résumé : Si le manteau neigeux peut avoir une incidence significative sur les déplacements et l'énergétique des animaux, peu d'études ont examiné le lien entre les propriétés physiques de la neige et les coûts énergétiques. Une quantification des seuils de propriétés de la neige qui influencent les déplacements des animaux est nécessaire pour combler ce manque de connaissances. Des baisses récentes de populations de mouflons de Dall (*Ovis dalli dalli* Nelson, 1884) pourraient être en partie dues à des conditions de neige changeantes. Nous avons examiné l'effet de la densité, de l'épaisseur et de la dureté de la neige sur la profondeur d'enfoncement d'empreintes de mouflons de Dall observées dans le parc national et la réserve de Wrangell–St. Elias (Alaska). L'épaisseur de la neige est un piètre prédicteur de la profondeur d'enfoncement des empreintes de mouflon (R^2 = 0,02, p = 0,38), tout comme la dureté pondérée moyenne (R^2 = 0,09, p = 0,07). Pour différents modèles concurrents, la densité de la couche supérieure (0–10 cm) de neige et la classe d'âge des mouflons s'avèrent les meilleurs prédicteurs de la profondeur d'enfoncement des empreintes (R^2 = 0,58). Cette dernière diminue inversement à la densité de la neige et, au-delà d'un seuil de densité de 329 ± 18 kg/m³ (moyenne ± ÉT), le manteau neigeux supporte la masse d'un mouflon. Ce seuil pourrait faciliter l'interprétation des déplacements et coûts énergétiques hivernaux des animaux, améliorant ainsi la capacité de prédire les conséquences de changements des conditions du manteau neigeux sur les animaux sauvages. [Traduit par la Rédaction]

Mots-clés : changement climatique, mouflon de Dall, énergétique, *Ovis dalli dalli*, neige.

Introduction

Snow cover is a complex and dynamic attribute of animal environments that covers high latitudes and elevations in more than half of the Northern Hemisphere (Groisman and Davies 2001). Seasonal snow cover can strongly affect the viability of animal populations by impacting movement and foraging, especially for ungulates (Cederlund et al. 1991; Goodson et al. 1991; Mech et al. 2001; Delgiudice et al. 2002; Christianson and Creel 2007). The effect of snow on wildlife is often represented by a single index (e.g., percent cover, depth), and there remains a need for rigorous investigation of the link between physical snow properties and energetic costs incurred by animals. Identifying the thresholds of physical snow properties that influence animal movement, and thus energetic cost, will be a considerable step forward in refining our understanding of habitat selection patterns and population viability.

Snow depth and snow density are relevant to animal movement because they can strongly influence energy expenditure by ungulates travelling in snow (Parker et al. 1984). Snow depth is the vertical accumulation of snow and ice crystals measured from ground level (Fierz et al. 2009). Snow density is the mass per unit volume of snow; the denser the snow, the firmer the snowpack. Snow hardness is a third snow property that could also influence animal energetics and is a measure of resistance against penetration of an object into the snow (Fierz et al. 2009). Snow hardness is influenced by cohesion among snow grains and strength of individual grains. Within a snowpack, there can be numerous layers of different snow hardness, each representing a unique snowfall event (Pomeroy and Brun 2001). Wind, precipitation, melt–freeze events, and gradients of temperature and water vapor strongly influence these snowpack properties, and they contribute to the formation and burial of surface crusts, ice lenses, and layers of varying hardness that can further impede or facilitate animal grazing and travel (Bunnell et al. 1990; Armstrong and Brun 2008; Lundmark and Ball 2008).

The relationship between energy expenditure by animals and snow depth, density, and hardness depends on an animal's foot loading. Foot loading is the force per unit area resulting from an animal's body mass, divided by the surface area of all four feet

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(Telfer and Kelsall 1979), and is also influenced by the type of movement (e.g., standing, walking, running). Differences in snow density and hardness on the ease of travel could explain why snow depth has inconsistent effects on ungulate movement (Telfer and Kelsall 1979, 1984; Bunnell et al. 1990). Dense, hard-packed, or crusted snow could make travel easier irrespective of snow depth if the mass of the animal is supported, whereas weaknesses in the snowpack in relation to an animal's mass could cause it to sink into the snow. Snow depth may not matter if snow density exceeds the threshold needed to support an animal's foot loading. Likewise, we expect that the effect of snow density on energetics to not be linear if animals do not sink into the snow above a critical density threshold, given that animal tracks will not sink into the snow above species-specific density thresholds.

Here, we examine the effects of snow depth, density, and hardness on snow track sink depths of Dall's sheep (*Ovis dalli dalli* Nelson, 1884) in the Wrangell Mountains of Alaska. Dall's sheep are endemic to alpine ecosystems at northern latitudes that remain snow-covered throughout much of the year. During winter months, sheep move from steep escape terrain to meadows where they forage for grasses and lichens beneath the snow (Hoefs and Cowan 1979). Many of these high elevation areas are wind-exposed, causing formation of wind-packed crusts interspersed with deep snow drifts. Snowpack in high latitude tundra regions has historically been characterized as cold and dry, with few melt features (e.g., ice layers), and may persist for up to 10 months seasonally (Sturm et al. 1995).

Although Dall's sheep are adapted to snowy environments, climate change is already affecting winter conditions at northern latitudes (Olsen et al. 2011; Serreze and Barry 2011). Recent declines in Dall's sheep populations throughout their range may be due in part to extreme weather events and changing snow conditions, but few quantitative analyses have been done (Loehr et al. 2010; Alaska Department of Fish and Game 2011). While snow depth appears to be consistently declining in the Arctic (Brown et al. 2010; Derksen and Brown 2012), higher temperatures and increases in winter precipitation are expected to contribute to episodic melting and more rain-on-snow events, which alters the structural properties of snow that affect animal mobility and access to forage (Post et al. 2009; Callaghan et al. 2011; Hansen et al. 2014). Variations in snow cover extent and snow depth are also expected to affect animal mobility and forage access (Callaghan et al. 2011; Olsen et al. 2011; Derksen and Brown 2012; Hansen et al. 2014).

We measured track sink depths of Dall's sheep in relation to snow characteristics to (*i*) determine which snow properties impose the greatest energetic cost to sheep and (*ii*) identify the thresholds of snow properties that support the body mass of Dall's sheep. The sink depth of tracks in the snow is closely correlated with energetic cost in ungulates and is therefore a reliable index for evaluating energy expenditure (Parker et al. 1984; Fancy and White 1987; Dailey and Hobbs 1989). We hypothesized that track sink depth would be nonlinearly related to snow properties whereby sink depth would increase with snow depth and decrease with snow density until a critical density threshold is reached where the snow would support the body mass of the animal and sink depths would be constant and near zero. We also assessed the relationship between snow depth and depth of the snow column directly underneath a track (hereafter, depth of snow underfoot) to evaluate whether snow depth underfoot could provide some level of structural support to the mass of a sheep in deeper snow. As snow depth increases, if snow underfoot is structurally supportive, then we would expect a positive relationship where the depth underfoot increases with increasing snow depth. If the snow depth underfoot was not supportive, then we would expect the depth underfoot to be unrelated to snow depth. We further hypothesized that snowpacks featuring more hard-packed snow layers would be more supportive of tracks, compared with snowpacks with fewer hard-packed layers but of similar snow density.

Materials and methods

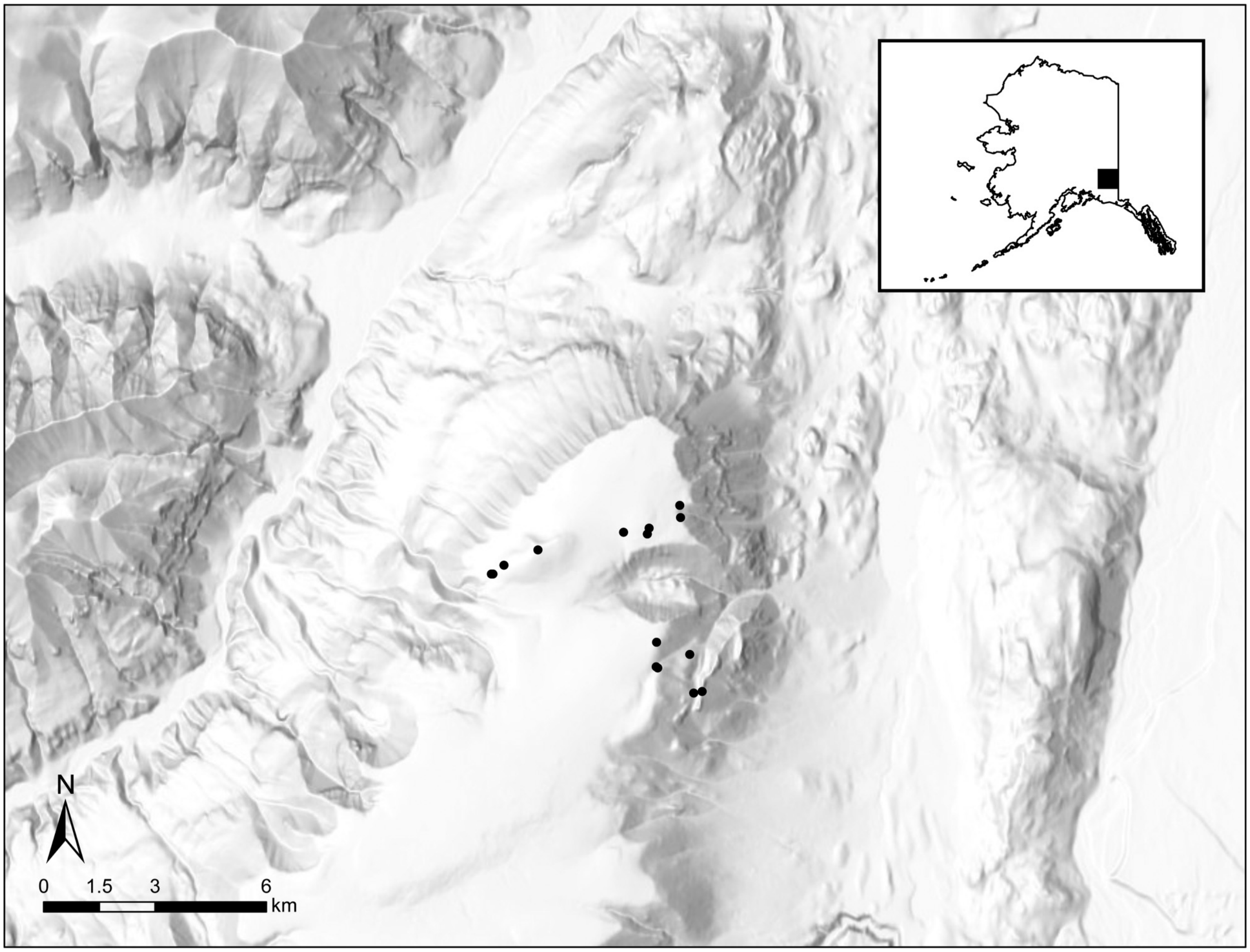
Data on sheep track sink depths and snow properties were collected between 17 and 26 March 2017 at Jaeger Mesa (62°16′N, 143°02′W) in Wrangell–St. Elias National Park and Preserve, Alaska (Fig. 1). Approximately 20% of the world's Dall's sheep population resides in Wrangell–St. Elias National Park and Preserve, yet populations have declined by 30% since the 1990s (Strickland et al 1993; National Park Service 2013). Jaeger Mesa is a remote alpine mesa at ~2000 m elevation, above the tree line, and characterized by alpine tundra and exposed, steep rocky slopes. The snowpack characteristics are consistent with "tundra" snow cover class: a generally thin (10–75 cm in depth), cold, wind-blown snowpack with depth hoar forming the base layer, multiple wind slabs, and patterned by surface sastrugi (Sturm et al. 1995). Mean winter temperatures range from –20 to –5 °C.

Data were collected at fresh sheep trails (<48 h old) encountered while skiing or snowshoeing. Each sheep trail was considered a single track site, from which we selected a set of 4–10 individual, consecutive hoofprints for measurement. Each individual hoofprint was thus considered a subsample from each track site. The criteria for selecting tracks was that they were on a consistent slope, did not penetrate through to bare ground, and were not obscured by windblown snow or stepped in by other sheep.

At each track site, we estimated the age class of the animal that created the trail by comparing the length and width of the hoofprint to published lengths and widths of hoofprints for Dall's sheep adults and lambs (Elbroch 2003). Hoofprints ≥4.5 cm wide and 5 cm long were classified as adults, whereas hoofprints <4.5 cm wide and 5 cm long were classified as lambs. We measured the sink depth of each hoofprint to the nearest half centimetre, and depths of hoofprints were averaged at each track site. A single snow pit was excavated adjacent to each track site, parallel to the track direction to measure snow density and assess the hardness and thickness of layers in the snow profile. Snow pits between 1 and 2 m wide were excavated to expose a shear vertical face extending from the snow surface to the ground. We used brushes to expose and identify individual layers along the snow pit face and used craft sticks to mark the top and bottom of each recognizable layer. Total snow depth of the snow pit face and thickness of each snow layer were measured to the nearest centimetre. Hardness of each layer was rated on a scale from one to five using the hand hardness test, a widely used field index for classifying snow hardness that corresponds to the amount of resistance experienced by an object pushed into the snow (American Avalanche Association 2004; Fierz et al. 2009; Höller and Fromm 2010). The hand hardness values from softest to hardest were as follows: fist (1), four fingers (2), one finger (3), blunt end of pencil (4), and knife blade (5). For each layer, we multiplied the hardness rating (i.e., 1–5) by its layer thickness. Mean weighted hardness for each snow pit was then calculated as the sum of thickness × hardness of layers in each pit, divided by the total snow depth.

We measured snow density of the top 10 cm of the snowpack (i.e., 0–10 cm depth from snow surface; hereafter referred to as top horizon) using a Snowmetrics 1000 cc (1000 cm^3) stainless steel cutter inserted perpendicular to the snow pit face and level with the snow surface (Fig. 2). Each sample was weighed using a digital scale (ACCULAB VI-4 kg) to provide a direct measure of snow density. Where snow depths permitted, we measured snow density of as many subsequent 10 cm horizons as possible using the same procedure. Replicate snow density samples (N = 2) for each horizon were averaged. Snow density values for all horizons were then averaged to represent snow density for the entire snow column (AvgDensity).

Fig. 1. Study area showing locations of Dall's sheep (*Ovis dalli dalli*) track sites evaluated in March 2017 on Jaeger Mesa, Wrangell–St. Elias National Park and Preserve, Alaska.



Data were inspected for normality using visualization plots and the Shapiro–Wilk test (Shapiro and Wilk 1965). To address our first objective, we used linear regression to model the effect of sheep age class (adults versus lambs), snow density, snow depth, and weighted hardness on the mean sheep track sink depths at each track site, and the relationship between overall snow depth and depth of the snow underfoot. Predictors were considered significant at $\alpha = 0.05$. Because the number of horizons for snow density varied by track site (as a function of snow depth), and hardness data were not collected at nine track sites, data were subset for analyses to ensure that comparisons among predictors were made using competing models with the same data set. For models constructed with the full data set ($N = 45$), we used model selection to identify the top-ranking model accounting for the greatest amount of variability in sinking depth of tracks (Burnham and Anderson 2002). We based model comparisons on values of Akaike's information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). For models constructed using less than the full data set, we compared R^2 values to determine the amount of variability in track sink depth accounted for by each predictor. All analyses were performed in program R (R Core Team 2014).

To identify a density threshold that would support the mass of a sheep, we used piecewise regression implemented with the R package "segmented" (Muggeo 2008). Piecewise regression provides a means for estimating the tipping point or transition zone at which a relationship between predictor and response variable changes (Toms and Lesperance 2003). Starting values for breakpoints in the piecewise regression were provided based on visual inspection of scatter plots between predictor and response variables (Muggeo 2008).

Results

We collected measurements from 204 individual tracks at 45 sheep trails (adults = 36, lambs = 9). Tracks classified as adults were, on average, 5 cm wide by 5.9 cm long; tracks classified as lambs were, on average, 4.1 cm wide by 4.9 long. Track sink depths varied from 0.5 to 24 cm (8.71 ± 5.61 cm, mean ± SD). Snow depth ranged from 12 to 56 cm (24.03 ± 10.6 cm, mean ± SD). Snow density ranged from 216 to 380 kg/m³ (280 ± 38.8 kg/m³, mean ± SD).

Snow density in the top horizon (0–10 cm) had a significant effect on the sinking depth of sheep tracks ($R^2 = 0.54$, $p < 0.001$). Top horizon snow density and age class accounted for the greatest amount of variation in track sink depth of all the models evaluated ($R^2 = 0.58$; Density1: $p < 0.001$; Age class: $p = 0.06$; Fig. 3). Track sink depths for both adults and lambs decreased with increasing snow density in the top horizon, yet a model of the interaction between age and top horizon density did not indicate a significant difference in the slope for adults and lambs (Density1 × Age: $p = 0.57$).

The two best models among our candidate set were the model with sheep age and top horizon snow density ($AIC_c = 241.01$) and the model with only top horizon snow density ($AIC_c = 242.51$).

Fig. 2. K.J. Sivy collects data on snowpack characteristics and track sink depths at a Dall's sheep (*Ovis dalli dalli*) track site in March 2017 on Jaeger Mesa, Wrangell–St. Elias National Park and Preserve, Alaska. Color version online.

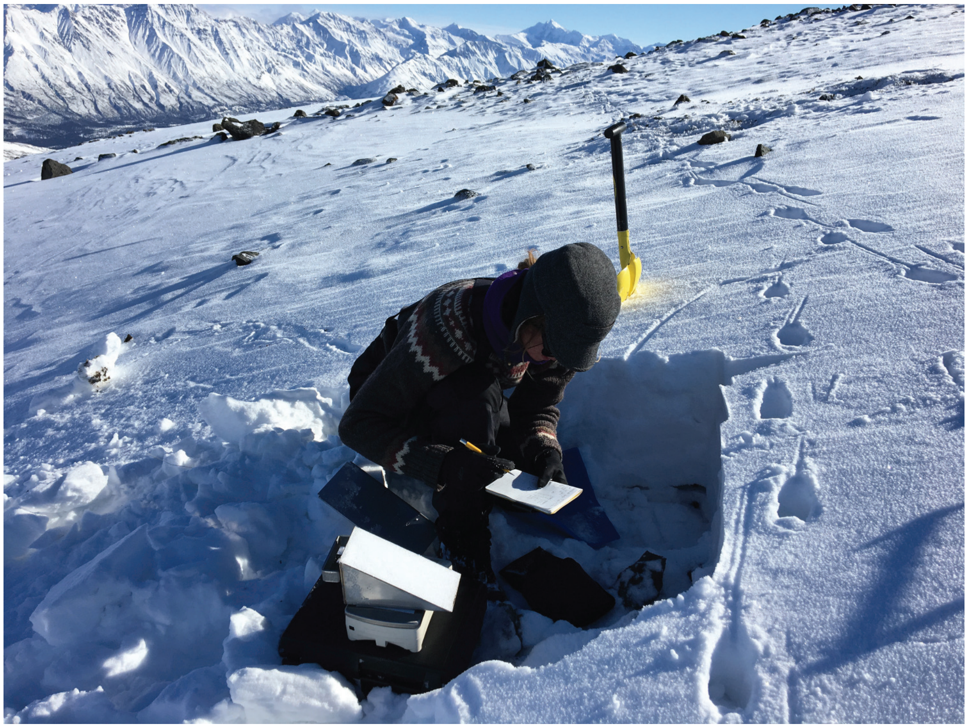
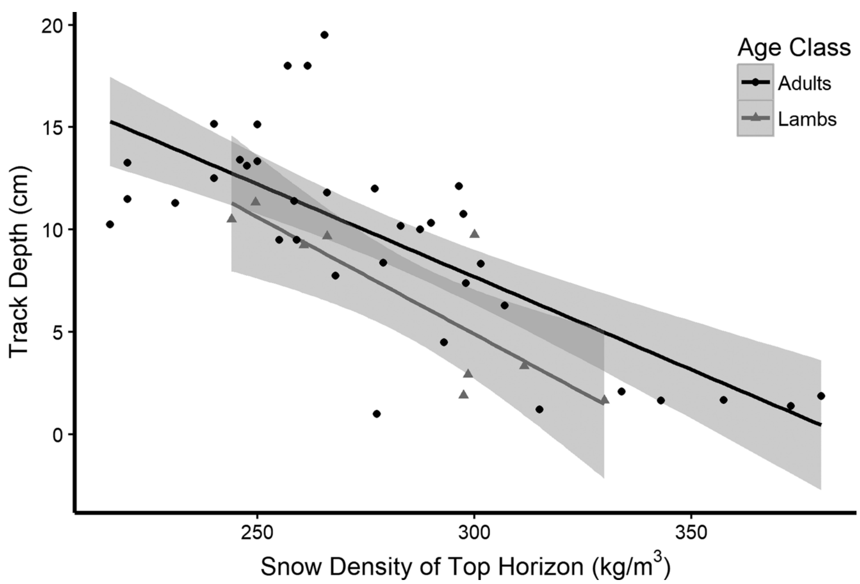


Fig. 3. Linear regression showing the top-ranking model ($R^2 = 0.58$) describing the effect of top horizon (0–10 cm) snow density on mean sink depths of adult and lamb Dall's sheep (*Ovis dalli dalli*) tracks. Shading indicates 95% confidence interval.



Together these two models accounted for 80% of AIC_c weight (Table 1). The interaction model Density1 × Age accounted for an additional 18% AIC_c weight and differed from the top-ranking model by just over 2.18 AIC_c units. All remaining models had AIC_c differences of ≥6.5 AIC_c units from the two top-ranking models, indicating little support. The regression model with snow density only in the top horizon had greater AIC_c support than the model with snow density averaged over the entire snow column (AIC_c = 250.21).

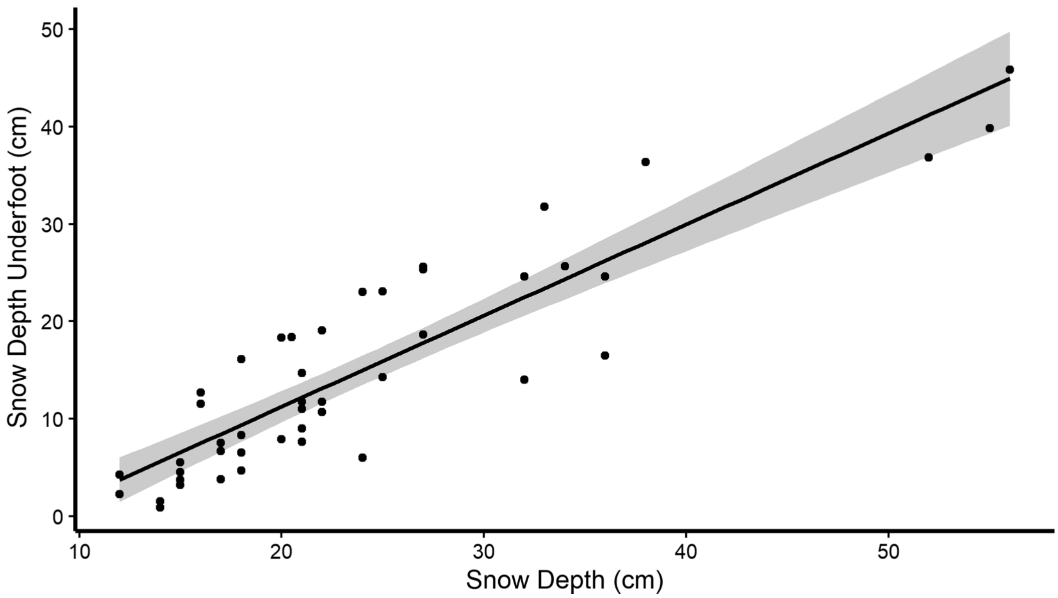
Track sink depth did not appear to be affected by snow density of the second (10–20 cm) horizon; however, there were few density measurements between 10 and 20 cm due to generally shallow snowpack ($N = 15$, $R^2_{[13]} = 0.08$, $p < 0.307$). Track sink depth was not affected by total snow depth ($N = 45$, $R^2_{[43]} = 0.02$, $p = 0.38$). Depth of snow underfoot, however, was strongly affected by total snow depth ($N = 45$, $R^2_{[43]} = 0.80$, $p < 0.001$; Fig. 4) and was a significant but weak predictor of sink depth ($N = 45$, $R^2_{[43]} = 0.1$, $p = 0.0317$). Weighted hardness was moderately correlated with mean snow density ($N = 36$, Pearson's $r = 0.46$). Weighted hardness accounted for little variability and was not a significant predictor of track sink depth ($N = 36$, $R^2_{[34]} = 0.09$, $p = 0.07$,). The interaction between total snow depth and snow density on track sink depth explained less variability in track depth ($R^2 = 0.38$) than the model with snow

Table 1. Model selection rankings for the effect of snow density, snow depth, and age class on Dall's sheep (*Ovis dalli dalli*) track sink depth in Wrangell–St. Elias National Park and Preserve, Alaska.

Model description	K	AIC_c	ΔAIC_c	AIC_c weight	Cumulative weight	Log likelihood
Density1 + Age	4	241.01	0.00	0.54	0.54	–116.01
Density1	3	242.51	1.50	0.26	0.80	–117.96
Density1 × Age	5	243.19	2.18	0.18	0.98	–115.83
AvgDensity × SnowDepth + Age	6	249.07	8.06	0.01	0.99	–117.43
AvgDensity	3	250.21	9.20	0.01	1.00	–121.81
AvgDensity × SnowDepth	5	250.46	9.45	0.00	1.00	–119.46
DepthUnderfoot	3	272.84	31.83	0.00	1.00	–133.13
SnowDepth	3	276.89	35.88	0.00	1.00	–135.15
SnowDepth + Age	4	277.19	36.18	0.00	1.00	–134.10

Note: K, number of parameters; AIC_c, Akaike's information criterion corrected for small sample size.

Fig. 4. Linear regression illustrating the increase in snow beneath Dall's sheep (*Ovis dalli dalli*) tracks with the increase in total snow depth (R^2 = 0.80). Shading indicates 95% confidence interval.



density alone (R^2 = 0.54); no predictors in the interaction model were significant (AvgDensity: p = 0.35; Hardness: p = 0.92; AvgDensity × Hardness: p = 0.91).

Piecewise regression estimated two thresholds in snow densities that influenced track sink depths (Fig. 5). Track sink depths increased slightly until snow density approached 257 ± 9 kg/m³ (mean ± SE), and sink depths then decreased with snow density and appeared to stabilize at snow densities >329 ± 18 kg/m³ (mean ± SE). Considering only adults, these snow density thresholds were 251 ± 9 and 337 ± 26 kg/m³ (mean ± SE), respectively. The sample size of lamb tracks was too small (N = 9) to identify a separate threshold for lambs.

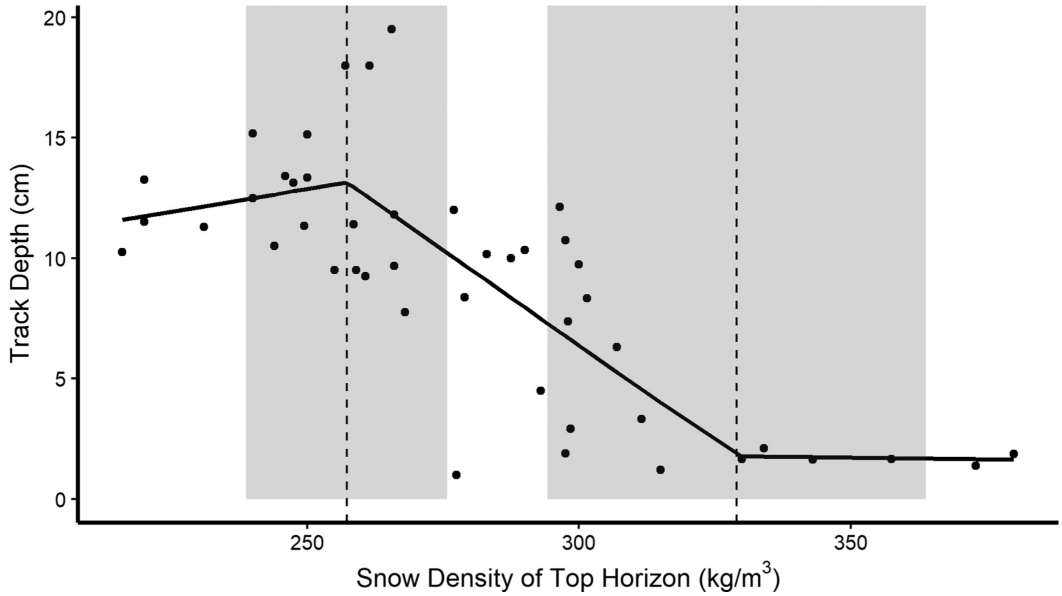
Discussion

We present the first evaluation of the effect of snow properties on track sink depths of Dall's sheep, an iconic ungulate species endemic to boreal alpine ecosystems and susceptible to changes in snowpack resulting from climate change. We detected a snow density threshold in our field observations, whereby the snowpack supported the mass of Dall's sheep and their tracks remained on the snow surface. Track sink depths are an indicator of energetic cost (Parker et al. 1984; Dailey and Hobbs 1989; Bunnell et al. 1990), and this work further highlights the relevance of accounting for snow density in studies of ungulate winter movement. In areas where winter severity is expected to adversely affect movement, snow density measurements could refine animal movement population models by providing a mechanistic link between observed habitat selection patterns and larger scale population trends of interest.

Of the snow properties that we measured, snow density accounted for the greatest amount (nearly 60%) of variation in track sink depths. Visual inspection of the regression curve indicates that track sink depths were reduced at higher snow densities. We estimated a threshold indicating that sheep tracks stabilized at their minimum sinking depths where snow density was ≥327 kg/m³. Across all classes of snow, snow density can vary as much as 7%–23% within 10 m or less (Jonas et al. 2009; López-Moreno et al. 2013). Compared with other classes of snow, the density of tundra-class snowpack has considerable variability despite little variation in depth (Sturm et al. 2010). This is likely because two of its major components, depth hoar and windslab, covers the full range of density for dry snow (Benson and Sturm 1993). Reported mean values for tundra-class snow range from 278 to 380 kg/m³ (Sturm et al. 1995, 2010), with the higher end of that range exceeding our observed threshold for supporting the mass of sheep. This spatial variability of dry, tundra-class snow might facilitate Dall's sheep using areas of low snow density for forage and areas of high snow density for travel in a high elevation tundra area like the Wrangel Mountains.

In addition to having high spatial variability, snow density also changes over time. Freshly fallen snow is generally within the range of 30–150 kg/m³ (i.e., unsupportive of sheep tracks), with

Fig. 5. Piecewise regression indicating the thresholds in snow density and corresponding changes in sink depths of Dall's sheep (*Ovis dalli dalli*) tracks in the snow. Vertical broken lines show estimated breakpoints and shaded areas indicate ±1.96 SE.



the lowest values occurring in cold dry climates, typical of northern latitudes, whereas higher densities are characteristic of warmer, wetter regions (Armstrong and Brun 2008). Wind, precipitation, temperature, and moisture gradients strongly affect densification processes and can double or triple the density of freshly fallen snow within 24 h (Armstrong and Brun 2008), rapidly contributing to conditions that could become supportive of sheep. Density of wet snow can exceed 400 kg/m^3, and seasonal snowpacks (snow that has accumulated and settled within one season) may approach 400–600 kg/m^3, which should exceed the supportive range for sheep (McClung and Shaerer 1993; Armstrong and Brun 2008). These densities would likely be in the range to support other ungulates; however, we are unaware of snow density thresholds reported for other species.

Dall's sheep track sink depths appeared to stabilize in response to higher snow density at ~4 cm sinking depth, whereas sinking depths at lower snow densities averaged ~10 cm. Variability in snow density at the patch level could have a substantial effect on an animal's net energy expenditure and movement patterns (Droghini and Boutin 2018). Energy expended by cervids is reported to increase exponentially with track sink depth (Parker et al. 1984; Fancy and White 1987). A study of mountain goats (*Oreamnos americanus* (Blainville, 1816)) and bighorn sheep (*Ovis canadensis* Shaw, 1804) similarly showed an exponential relationship between track sink depth and energetic cost (adjusted for snow density); however, once track sink depths exceeded 1.2–2.0 times the chest height, energetic cost appeared to level off (Dailey and Hobbs 1989). To our knowledge, the relationship between track sink depth and energy cost for Dall's sheep has not been determined. Because Dall's sheep have similar chest height and foot loading as bighorn sheep (Telfer and Kelsall 1984), we would expect energetic cost to also increase with track sink depths until sinking depths exceed chest height. Once snow depths exceed chest height, the advantages of denser snow may diminish rapidly given the energetic cost of wading through, as opposed to stepping into, the snow (Parker et al. 1984).

We expected snow depth to influence track sink depth, but we observed no effect. Mean snow depths sampled were less than 50% of estimated mean chest height reported for Dall's sheep (mean = 54 cm, N = 29; Telfer and Kelsall 1984). Track sink depths in this study (<20% of chest height) were well below the asymptote reported for bighorn sheep (Dailey and Hobbs 1989). Dall's sheep could have been using areas with shallow snow depths and higher snow density (i.e., wind-swept areas). This broad-scale habitat selection could explain the lack of effect of total snow depth on sink depth in our range of observations and further suggests that snow conditions sampled for this study could have been at the low range of energetic cost required for travel.

Although total snow depth was not a significant predictor of track sink depths, the strong positive relationship between total snow depth and snow depth underfoot suggests that deeper snow could interact with snow density to minimize track sink depths. We did not observe a significant interaction between snow density and snow depth on track sink depth, but the positive relationship between total snow depth and snow depth underfoot suggests compaction of snow underfoot provided some level of structural support, otherwise tracks should have sunk farther into the snow. We did not have sufficient range in track sink depths and snow depths to identify a critical minimum snow depth, which would indicate the minimum snow depth for structural support (Lundmark and Ball 2008). Hardness of snow layers also had a weak effect on sinking depth of tracks. The index that we developed (mean weighted hardness) may not have captured additional variability not already accounted for by snow density (because hardness increases with snow density). Alternatively, the gradient in hardness and thickness between snow layers may not have been strong enough to affect track sink depth.

Climate change predictions for northern latitudes indicate a transition from cold dry winters to warmer wetter winters, with increased likelihood of mixed rain and snow and rain on snow events (Olsen et al. 2011; Hansen et al. 2014). Because temperature and moisture gradients are primary drivers of densification processes, these predicted weather pattern changes could influence the density of freshly fallen snow and rate of densification. Denser snow may be more efficient for travel, but this would likely come at the expense of foraging efficiency. Like many other ungulate grazers, Dall's sheep must nose or dig through the snow ("cratering") to access winter forage (Hoefs and Cowan 1979), which requires more effort in deep or dense snow and reduces forage intake rates (Robinson and Merrill 2012). Caribou (*Rangifer tarandus* (Linnaeus, 1758)) expended nearly twice as much energy when cratering for lichens beneath dense (280–500 kg/m^3) crusted snow compared with fluffy (180 kg/m^3) uncrusted snow (Fancy and White 1985). The tendency for various ungulate species to change their cratering tactics in response to increased snow depth and density (Seip and Bunnell 1985; Schaefer 1996; Johnson et al. 2001; Fortin et al. 2005) suggests thresholds for energetic costs of foraging could contrast with thresholds related to locomotion.

Climate change is also expected to alter predator–prey interactions by influencing snow conditions that influence pursuit and capture (Penczykowski et al. 2017). Ungulates tend to have higher foot loadings and lower snow coping abilities than their predators (Telfer and Kelsall 1984; Buskirk et al. 2000), indicating that predators have the advantage when pursuing ungulate prey in deep snow (Fuller 1991; Mech et al. 1998; Sand et al. 2006). Deep snow years could favor predators and strengthen top-down cascades, whereas low snow years could favor ungulate prey and weaken top-down cascades (Penczykowski et al. 2017). The influence of snow density on predator–prey interactions, however, appears to be unknown and could provide important additional insights for determining snow depth thresholds between predators and their ungulate prey. Wolves (*Canis lupus* Linnaeus, 1758) and coyotes (*Canis latrans* Say, 1823) are the main mammalian predators of Dall's sheep in Alaska (Hoefs and Cowan 1979; Arthur and Prugh 2010). Wolves and coyotes prefer areas of shallow compact snow (Pozzanghera et al. 2016; Droghini and Boutin 2018). Determining snow density thresholds for wolves and coyotes in comparison with those identified here for Dall's sheep could help to identify the danger zone in snow density that enhances vulnerability to predation.

This study occurred in one location, for one snowpack, and at one time of year. Snowpacks are highly variable, as there are numerous physical processes that contribute to snow metamorphosis over time (Pomeroy and Brun 2001). Measurements throughout the season could yield additional insights as to how snow density, depth, and hardness might interact to support or collapse under pressure from an animal's body mass. Many approaches and indices have been used to estimate snow hardness and compaction, therefore we also suggest the importance of refining and standardizing the methodology for measuring snow property thresholds relative to animal energetics, so that measurements across studies are comparable. A smaller density cutter depth than the 10 cm cutter used in this study could allow finer scale evaluation of snow density within different snow layers, especially for shallow snowpacks. Use of snow micropenetrometers (SMP; Schneebeli et al. 1999) could provide a more quantitatively consistent measure of resistive strength of the snow. Pielmeier and Schneebeli (2003) showed a significant statistical correlation between SMP-measured snow hardness and hand-measured snow hardness. SMP could be evaluated for assessing track sinking depths in relation to snow hardness, especially where stratigraphy is likely to have significant variability within sites.

In conclusion, we documented a snow density threshold for Dall's sheep, which could aid interpretation of movement and habitat selection given the relationship between track sinking depth and energetic cost determined in other ungulate species. This work addresses a critical gap as to the mechanisms by which various snow properties influence energetics of Dall's sheep, which could be extended to other ungulates especially in ecosystems where snow conditions are expected to transition as a result of climate change. Assessing snow properties requires intensive field efforts; however, recent advancements in remote sensing technology and snow modeling could provide snow density maps at spatial scales relevant to animal movement (Sturm et al. 2010; Rasmus et al. 2014; Liston et al. 2016). Incorporating snow properties into models of animal energetics and movement could significantly advance our understanding of how a dynamic environmental variable influences movement over daily, seasonal, and yearly time periods.

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References

Alaska Department of Fish and Game. 2011. Dall sheep management report of survey-inventory activities 1 July 2007 – 30 June 2010. *Edited by* P. Harper. Alaska Department of Fish and Game, Juneau.

American Avalanche Association. 2004. Snow, weather, and avalanches: observational guidelines for avalanche programs in the United States. American Avalanche Association, Pagosa Springs, Colo.

Armstrong, R.L., and Brun, E. 2008. Snow and climate: physical processes, surface energy exchange and modeling. Cambridge University Press, Cambridge.

Arthur, S.M., and Prugh, L.R. 2010. Predator-mediated indirect effects of snowshoe hares on Dall's sheep in Alaska. J. Wildl. Manage. **74**(8): 1709–1721. doi:10.2193/2009-322.

Benson, C.S., and Sturm, M. 1993. Structure and wind transport of seasonal snow on the Arctic slope of Alaska. Ann. Glaciol. **18**: 261–267. doi:10.3189/S0260305500011629.

Brown, R., Derksen, C., and Wang, L. 2010. A multi-data set analysis of variability and change in Arctic spring snow cover extent, 1967–2008. J. Geophys. Res. Atmos. **115**(16). doi:10.1029/2010JD013975.

Bunnell, F.L., Parker, K.L., McNay, R.S., and Hovey, F.W. 1990. Sinking depths of black-tailed deer in snow, and their indices. Can. J. Zool. **68**(5): 917–922. doi:10.1139/z90-132.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Springer, New York.

Buskirk, S.W., Ruggiero, L.F., and Krebs, C.J. 2000. Habitat fragmentation and interspecific competition: implications for lynx conservation. *In* Ecology and conservation of lynx in the United States. *Edited by* L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires. University Press of Colorado, Boulder. pp. 83–100.

Callaghan, T.V., Johansson, M., Brown, R.D., Groisman, P.Y., Labba, N., Radionov, V., Barry, R.G., Bulygina, O.N., Essery, R.L.H., Frolov, D.M., Golubev, V.N., Grenfell, T.C., Petrushina, M.N., Razuvaev, V.N., Robinson, D.A., Romanov, P., Shindell, D., Shmakin, A.B., Sokratov, S.A., Warren, S., and Yang, D. 2011. The changing face of Arctic snow cover: a synthesis of observed and projected changes. Ambio, **40**: 17–31. doi:10.1007/s13280-011-0212-y.

Cederlund, G.G.N., Sand, H., and Pehrson, A. 1991. Body mass dynamics of moose calves in relation to winter severity. J. Wildl. Manage. **55**(4): 675–681. doi:10.2307/3809517.

Christianson, D., and Creel, S. 2007. A review of environmental factors affecting elk winter diets. J. Wildl. Manage. **71**(1): 164–176. doi:10.2193/2005-575.

Dailey, T.V., and Hobbs, N.T. 1989. Travel in alpine terrain: energy expenditures for locomotion by mountain goats and bighorn sheep. Can. J. Zool. **67**(10): 2368–2375. doi:10.1139/z89-335.

Delgiudice, G.D., Riggs, M.R., Joly, P., and Pan, W. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. J. Wildl. Manage. **66**(3): 698–717. doi:10.2307/3803136.

Derksen, C., and Brown, R. 2012. Spring snow cover extent reductions in the 2008–2012 period exceeding climate model projections. Geophys. Res. Lett. **39**(19): 1–6. doi:10.1029/2012GL053387.

Droghini, A., and Boutin, S. 2018. Snow conditions influence grey wolf (*Canis lupus*) travel paths: the effect of human-created linear features. Can. J. Zool. **96**(1): 39–47. doi:10.1139/cjz-2017-0041.

Elbroch, L.M. 2003. Mammal tracks and sign: a guide to North American species. Stackpole Books, Mechanicsburg, Pa.

Fancy, S.G., and White, R.G. 1985. Energy expenditures by caribou while cratering in snow. J. Wildl. Manage. **49**(4): 987–993. doi:10.2307/3801384.

Fancy, S.G., and White, R.G. 1987. Energy expenditures for locomotion by barren-ground caribou. Can. J. Zool. **65**(1): 122–128. doi:10.1139/z87-018.

Fierz, C., Armstrong, R.L., Durand, Y., Etchevers, P., Greene, E., McClung, D.M., Nishimura, K., Satyawali, P.K., and Sokratov, S.A. 2009. The international classification for seasonal snow on the ground. IHP-VII Tech. Doc. Hydrol. **83**(1): 90. Available from http://www.cosis.net/abstracts/EGU05/09775/EGU05-J-09775.pdf.

Fortin, D., Morales, J.M., and Boyce, M.S. 2005. Elk winter foraging at fine scale in Yellowstone National Park. Oecologia, **145**(2): 335–343. doi:10.1007/s00442-005-0122-4. PMID:15965755.

Fuller, T. 1991. Effect of snow depth on wolf activity and prey selection in north central Minnesota. Can. J. Zool. **69**(2): 283–287. doi:10.1139/z91-044.

Goodson, N.J., Stevens, D.R., and Bailey, J.A. 1991. Effects of snow on foraging ecology and nutrition of bighorn sheep. J. Wildl. Manage. **55**(2): 214–222. doi:10.2307/3809142.

Groisman, P.Y., and Davies, T.D. 2001. Snow cover and the climate system. *In* Snow ecology: an interdisciplinary examination of snow-covered ecosystems.

Edited by G.H. Jones, J. Pomeroy, D. Walker, and R. Hoham. Cambridge University Press, Cambridge. pp. 1–44.

Hansen, B.B., Isaksen, K., Benestad, R.E., Kohler, J., Pedersen, Å.Ø., Loe, L.E., Coulson, S.J., Larsen, J.O., and Varpe, Ø. 2014. Warmer and wetter winters: characteristics and implications of an extreme weather event in the high Arctic. Environ. Res. Lett. **9**(11). doi:10.1088/1748-9326/9/11/114021.

Hoefs, M., and Cowan, I. 1979. Ecological investigations of a population of Dall sheep (*Ovis dalli dalli* Nelson). British Columbia Provincial Museum, Victoria.

Höller, P., and Fromm, R. 2010. Quantification of the hand hardness test. Ann. Glaciol. **51**(54): 39–44. doi:10.3189/172756410791386454.

Johnson, C.J., Parker, K.L., and Heard, D.C. 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia, **127**(4): 590–602. doi:10.1007/s004420000573. PMID: 28547497.

Jonas, T., Marty, C., and Magnusson, J. 2009. Estimating the snow water equivalent from snow depth measurements in the Swiss Alps. J. Hydrol. **378**(1–2): 161–167. doi:10.1016/j.jhydrol.2009.09.021.

Liston, G.E., Perham, C.J., Shideler, R.T., and Cheuvront, A.N. 2016. Modeling snowdrift habitat for polar bear dens. Ecol. Modell. **320**: 114–134. doi:10.1016/j.ecolmodel.2015.09.010.

Loehr, J., Carey, J., O'Hara, R.B., and Hik, D.S. 2010. The role of phenotypic plasticity in responses of hunted thinhorn sheep ram horn growth to changing climate conditions. J. Evol. Biol. **23**(4): 783–790. doi:10.1111/j.1420-9101.2010.01948.x. PMID:20163506.

López-Moreno, J.I., Fassnacht, S.R., Heath, J.T., Musselman, K.N., Revuelto, J., Latron, J., Morán-Tejeda, E., and Jonas, T. 2013. Small scale spatial variability of snow density and depth over complex alpine terrain: implications for estimating snow water equivalent. Adv. Water Resour. **55**: 40–52. doi:10.1016/j.advwatres.2012.08.010.

Lundmark, C., and Ball, J.P. 2008. Living in snowy environments: quantifying the influence of snow on moose behavior. Arctic Antarct. Alp. Res. **40**(1): 111–118. doi:10.1657/1523-0430(06-103)[LUNDMARK]2.0.CO;2.

McClung, D.M., and Shaerer, P. 1993. The avalanche handbook. The Mountaineers Books, Seattle, Wash.

Mech, L., Adams, L., Meier, T., Burch, J., and Dale, B. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis.

Mech, L.D., Smith, D.W., Murphy, K.M., and Macnulty, D.R. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. J. Wildl. Manage. **65**(4): 998–1003. doi:10.2307/3803048.

Muggeo, V.M.R. 2008. Segmented: an R package to fit regression models with broken-line relationships. R News, **8**(May): 20–25. doi:10.1159/000323281.

National Park Service. 2013. Monitoring Dall's sheep in the Central Alaska Network. Available from National Park Service Integrated Resource Management Applications (https://irma.nps.gov/Portal/). Ref. No. 2197712.

Olsen, M.S., Callaghan, T.V., Reist, J.D., Reiersen, L.O., Dahl-Jensen, D., Granskog, M.A., Goodison, B., Hovelsrud, G.K., Johansson, M., Kallenborn, R., Key, J., Klepikov, A., Meier, W., Overland, J.E., Prowse, T.D., Sharp, M., Vincent, W.F., and Walsh, J. 2011. The changing Arctic cryosphere and likely consequences: an overview. Ambio, **40**(Suppl. 1): 111–118. doi:10.1007/s13280-011-0220-y.

Parker, K.L., Robbins, C.T., and Hanley, T.A. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. **48**(2): 474–488. doi:10.2307/3801180.

Penczykowski, R.M., Connolly, B.M., and Barton, B.T. 2017. Winter is changing: trophic interactions under altered snow regimes. Food Webs, **13**: 80–91. doi:10.1016/j.fooweb.2017.02.006.

Pielmeier, C., and Schneebeli, M. 2003. Stratigraphy and changes in hardness of snow measured by hand, ramsonde and snow micro penetrometer: a comparison with planar sections. Cold Reg. Sci. Technol. **37**(3): 393–405. doi:10.1016/S0165-232X(03)00079-X.

Pomeroy, J., and Brun, E. 2001. Physical properties of snow. *In* Snow ecology: an interdisciplinary examination of snow-covered ecosystems. *Edited by* H.G. Jones, J.W. Pomeroy, D.A. Walker, and R.W. Hoham. Cambridge University Press, Cambridge. pp. 485–527.

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M., and Aastrup, P. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science, **325**(5946): 1355–1358. doi:10.1126/science.1173113. PMID:19745143.

Pozzanghera, C.B., Sivy, K.J., Lindberg, M.S., and Prugh, L.R. 2016. Variable effects of snow conditions across boreal mesocarnivore species. Can. J. Zool. **94**(10): 697–705. doi:10.1139/cjz-2016-0050.

Rasmus, S., Kumpula, J., and Siitari, J. 2014. Can a snow structure model estimate snow characteristics relevant to reindeer husbandry? Rangifer, **34**(1): 37–56. doi:10.7557/2.34.1.2675.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Robinson, B.G., and Merrill, E.H. 2012. The influence of snow on the functional response of grazing ungulates. Oikos, **121**(1): 28–34. doi:10.1111/j.1600-0706.2011.19408.x.

Sand, H., Wikenros, C., Wabakken, P., and Liberg, O. 2006. Effects of hunting group size, snow depth and age on the success of wolves hunting moose. Anim. Behav. **72**(4): 781–789. doi:10.1016/j.anbehav.2005.11.030.

Schaefer, J.A. 1996. Canopy, snow, and lichens on woodland caribou range in southeastern Manitoba. Rangifer, **16**(4): 239–244. doi:10.7557/2.16.4.1249.

Schneebeli, M., Pielmeier, C., and Johnson, J.B. 1999. Measuring snow microstructure and hardness using a high resolution penetrometer. Cold Reg. Sci. Technol. **30**(1–3): 101–114. doi:10.1016/S0165-232X(99)00030-0.

Seip, D., and Bunnell, F. 1985. Foraging behaviour and food habits of Stone's sheep. Can. J. Zool. **63**(7): 1638–1646. doi:10.1139/z85-243.

Serreze, M.C., and Barry, R.G. 2011. Processes and impacts of Arctic amplification: a research synthesis. Glob. Planet. Change, **77**(1–2): 85–96. doi:10.1016/j.gloplacha.2011.03.004.

Shapiro, S.S., and Wilk, M.B. 1965. An analysis of variance test for normality (complete samples). Biometrika, **52**(3/4): 591–611. doi:10.2307/2333709.

Strickland, D., McDonald, L.L., Taylor, D., Jenkins, K., and Kern, J. 1993. Estimation of the number of Dall sheep in Wrangell–St. Elias National Park and Preserve. Bienn. Symp. North. Wild Sheep and Goat Counc. **8**: 237–255. Available from http://www.nwsgc.org/contents/1992contents.html.

Sturm, M., Holmgren, J., and Liston, G. 1995. A seasonal snow cover classification system for local to global applications. J. Clim. **8**(5): 1261–1283. doi:10.1175/1520-0442(1995)008<1261:ASSCCS>2.0.CO;2.

Sturm, M., Taras, B., Liston, G., Derksen, C., Jonas, T., and Lea, J. 2010. Estimating snow water equivalent using snow depth data and climate classes. J. Hydrometeorol. **11**(6): 1380–1394. doi:10.1175/2010JHM1202.1.

Telfer, E.S., and Kelsall, J.P. 1979. Studies of morphological parameters affecting ungulate locomotion in snow. Can. J. Zool. **57**(11): 2153–2159. doi:10.1139/z79-283.

Telfer, E.S., and Kelsall, J.P. 1984. Adaptation of some large North American mammals for survival in snow. Ecology, **65**(6): 1828–1834. doi:10.2307/1937779.

Toms, J.D., and Lesperance, M.L. 2003. Piecewise regressions: a tool for identifying ecological thresholds. Ecology, **84**(8): 2034–2041. doi:10.1890/02-0472.