

Research article

Defining the danger zone: critical snow properties for predator–prey interactions

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Oikos

2023: e09925

doi: [10.1111/oik.09925](https://doi.org/10.1111/oik.09925)

Subject Editor: Leif Egil Loe

Editor-in-Chief: Dries Bonte

Accepted 16 May 2023



Snowpack dynamics have a major influence on wildlife movement ecology and predator–prey interactions. Specific snow properties such as density, hardness, and depth determine how much an animal sinks into the snowpack, which in turn drives both the energetic cost of locomotion and predation risk. Here, we quantified the relationships between five field-measured snow variables and snow track sink depths for widely distributed predators (bobcats *Lynx rufus*, cougars *Puma concolor*, coyotes *Canis latrans*, wolves *C. lupus*) and sympatric ungulate prey (caribou *Rangifer tarandus*, white-tailed deer *Odocoileus virginianus*, mule deer *O. hemionus*, and moose *Alces alces*) in interior Alaska and northern Washington, USA. We first used generalized additive models to identify which snow metrics best predicted sink depths for each species and across all species. Next, we used breakpoint regression to identify thresholds of support for the best-performing predictor of sink depth for each species (i.e. values wherein tracks do not sink appreciably deeper into the snow). Finally, we identified ‘danger zones,’ wherein snow impedes the mobility of ungulates more than carnivores, by comparing sink depths relative to hind leg lengths among predator–prey pairs. Near-surface (0–20 cm) snow density was the strongest predictor of sink depth across species. Thresholds of support occurred at near-surface snow densities between 220–310 kg m⁻³ for predators and 300–410 kg m⁻³ for prey, and danger zones peaked at intermediate snow densities (200–300 kg m⁻³) for eight of the ten predator–prey pairs. These results can be used to link predator–prey relationships with spatially explicit snow modeling outputs and projected future changes in snow density. As climate change rapidly reshapes snowpack dynamics, these danger zones provide a useful framework to anticipate likely winners and losers of future winter conditions.

Keywords: canid, felid, movement ecology, predator–prey, snow ecology, ungulate

Introduction

Seasonal snow cover shapes a suite of ecological processes across nearly half of all land in the Northern Hemisphere (Robinson et al. 2014, Niittynen et al. 2018). The dynamic nature of snow throughout the landscape and throughout the year presents a challenge



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for evaluating wildlife–snow relationships (Reinking et al. 2022). Furthermore, climate change is rapidly altering seasonal snowpacks globally, with the greatest effects observed across northern Eurasia and North America (IPCC 2022). Snow cover duration (Brown and Mote 2009), autumn and spring extent (Derksen and Brown 2012, Thackeray et al. 2019), and overall snow mass (Pulliainen et al. 2020) are declining dramatically in the Northern Hemisphere. The rapid pace of these changes adds urgency to the outstanding need to understand wildlife-specific aspects of snow ecology (Mahoney et al. 2018, Boelman et al. 2019).

For large mammals inhabiting seasonally snowy regions, biological processes such as energy balance (Dailey and Hobbs 1989), access to winter forage (Hansen et al. 2011), recruitment of young (van de Kerk et al. 2018), daily movement rates (Pedersen et al. 2021), migration phenology (Gurarie et al. 2019), habitat selection (Mahoney et al. 2018, Ganz et al. 2022), and predator–prey interactions (Peers et al. 2020) are all mediated to some extent by snow. The impact of snow on many of these processes can be estimated with easily measured metrics. Snow depth, for example, is one of the most widely used snow metrics in wildlife ecology, with applications that include classifying winter severity (Nelson and Mech 1986), understanding predation success rates (Post et al. 1999, Horne et al. 2019), and modeling movement patterns (Droghini and Boutin 2018a). Satellite-derived variables such as snow cover phenology are well suited to explain broader trends in population dynamics (Rattenbury et al. 2018) and coarse-scale range shifts (Gurarie et al. 2019). Although these studies illustrate the value of including snow in ecological analyses, it is often difficult to establish a specific mechanistic link between snow properties and impacts on wildlife.

The sink depth of animal tracks offers one such linkage between theoretical and empirical snow ecology (Sivy et al. 2018) and is a key determinant of energetic costs of movement in snow-covered landscapes (Dailey and Hobbs 1989). Sink depth is a function of snowpack characteristics, animal gait, speed of travel, and species-specific foot loading (Parker et al. 1984, Mech and Peterson 2003), which is calculated by dividing an animal's body mass by the surface area of all four feet (Telfer and Kelsall 1984). Foot loads range widely among large mammals, but carnivores generally have foot loads that are 2–10 times lower than their ungulate prey (Telfer and Kelsall 1984, Murray and Boutin 1991, Murray and Larivière 2002, Mech and Peterson 2003). This difference in foot loading creates theoretical 'danger zones' for ungulates: locations and times where snow properties give an advantage to their predators during pursuit and capture.

Danger zones are defined by a combination of snow properties such as total depth, hardness, and density that together influence how deep an animal will sink into snow and therefore how impaired its mobility will be (Telfer and Kelsall 1984). Within a snowpack, snow is aggregated into horizontally arranged layers, each of which may have distinct physical properties that interact to modulate mass transfers across the entire snow column (Arons and Colbeck 1995, Pielmeier

and Schneebeli 2003). Thus, an animal will encounter multiple snow layers as it sinks until it reaches a layer sufficiently strong to support its body mass, until it penetrates through the entire snowpack, or until the underlying layers combine with snow compacted underfoot to support its body mass (Sivy et al. 2018). Each layer can be classified based on many snow properties that can be measured in the field (Fierz et al. 2009, Kinar and Pomeroy 2015) and that may contribute to whether that layer will support a given animal. Snow characteristics of the layers that support the animal's body mass without it sinking into the snow appreciably can be considered thresholds of support. Since ungulates have higher foot loads than predators (Telfer and Kelsall 1984), thresholds of support for ungulates should be higher than thresholds of support for predators. Absolute sink depths, as determined by these thresholds of support, can be scaled by leg lengths to facilitate comparisons of relative mobility impairment across species (Parker et al. 1984), thereby delineating danger zones for predator–prey pairs.

Approaches coupling snow science and wildlife biology have linked thresholds of support and more general animal movement with snow depth (Coady 1973, Nelson and Mech 1986), the presence of ice layers (Murie 1944, Stein et al. 2010, Leblond et al. 2016), density (Fancy and White 1987, Sivy et al. 2018), and hardness (Bunnell et al. 1990, Droghini and Boutin 2018b). However, all of these snow properties vary at multiple spatiotemporal scales, from individual snow crystal metamorphism to latitude-based spring solar melt (Fierz et al. 2009), and are linked in complex ways. For example, snow hardness (resistance to penetration) and density (mass per unit volume) are strongly correlated (Takeuchi et al. 1998, Riseth et al. 2011), but the relationship varies with snow grain shape. More mature crystal forms are much denser at the same hardness: the depth hoar common in a cold tundra snowpack averages nearly twice the density of newly fallen precipitation particles with the same layer hardness, and large uncertainties preclude deriving a similar relationship with wet (melted) snow grains (Geldsetzer and Jamieson 2000). As a result, the findings of studies conducted at a single study site or over a narrow time period may not be applicable across a broader geographic or temporal domain.

Globally, different combinations of climatic and landscape conditions create six snow classes: tundra, boreal forest, maritime, ephemeral, prairie, and montane forest (Sturm et al. 1995, Sturm and Liston 2021). Snow classes vary from deep and wet (maritime) to shallow and hard (tundra), depending on the prevailing physical environment (Sturm et al. 1995). Collectively, these six classes provide reasonable bounds for the wide range of snow properties an animal might encounter anywhere in the world (Sturm et al. 1995). For species whose geographic distribution spans multiple snow classes, a sample encompassing maximum variability is essential to develop robust estimates of snow support thresholds.

In this study, we analyzed the relationship between snow properties and animal track sink depths for eight large mammal species in Alaska and Washington, USA. By combining measurements from these two geographically distinct regions

across a variety of meteorological conditions and over multiple seasons, we surveyed a broad range of snow conditions. We sampled tracks from medium- and large-bodied carnivores and their ungulate prey. First, we evaluated the performance of five field-measured snow properties as predictors of track sink depth for each species. We hypothesized that snow density would best predict sink depth for larger-bodied species, as [Bunnell et al. \(1990\)](#) and [Sivy et al. \(2018\)](#) found, and surface penetrability would best predict sink depth for smaller-bodied carnivores ([Peers et al. 2020](#)). Second, we aggregated snow track data to identify the single top-performing snow metric across all sampled wildlife species. Because of the generally observed increase in mammal body size with latitude ([Thurber and Peterson 1991](#), [Ashton et al. 2000](#)), the large latitudinal gradient covered by our study sites, and spatial and temporal snow differences ([Sturm et al. 1995](#)), we assessed potential regional differences in these snow-sink depth relationships. We hypothesized that animals would sink deeper in the relatively wet snow of Washington than in the strongly bonded, wind-hardened snowpack of interior Alaska despite the typically larger body sizes of northern conspecifics ([Thurber and Peterson 1991](#), [Ashton et al. 2000](#), [Herfindal et al. 2006](#), [Meiri et al. 2007](#)). Third, we quantified critical thresholds of support for the best-performing snow metric. Finally, we scaled each species' snow-sink depth relationship by hind leg length to quantify relative mobility impairment, using these metrics to define danger zones where predators have a mobility advantage over prey. By coupling these sympatric carnivore–ungulate groupings, we delineated how snow influences predator–prey systems in rapidly changing northern regions.

Material and methods

Study area

We sampled large mammal snow tracks in Denali National Park and Preserve, Alaska (hereafter, Denali) and at two sites in Washington (Okanogan and northeast Washington; [Fig. 1](#)). Our study areas include portions of all six global snow classes per [Sturm and Liston \(2021\)](#): Denali is comprised of tundra and boreal forest, and our Washington sites contain primarily montane forest, with some prairie, ephemeral, and maritime areas. We conducted fieldwork in Washington during three consecutive winters (9 January–17 March 2021, 4 January–22 March 2022 and 4–21 January 2023), and during two winters (18 January–25 March 2022 and 27 January–14 March 2023) in Denali. In Washington, our study duration spanned the spring melt-freeze cycle, a sustained period of daytime temperatures above freezing ($>0^{\circ}\text{C}$) and nighttime temperatures below freezing (beginning approximately 20 February 2021 and 28 February 2022; USDA Natural Resources Conservation Service 2022). Our sampling in Denali included several sudden warming events accompanied by strong winds ('Chinooks') that further enhanced the effects of wind characteristic to regions

with a tundra snow class ([Sturm et al. 1995](#), [Bieniek et al. 2018](#)). Major Chinook wind events occurred in Denali on 23–25 January and 24–25 February 2022 (maximum wind speeds of 27 and 28.5 m s^{-1} , respectively; NEON 2022).

Focal species

We focused sampling on common ungulates and their main predators in our study areas. We sampled moose *Alces alces*, coyotes *Canis latrans*, and wolves *C. lupus* in both Alaska and Washington, whereas caribou *Rangifer tarandus* and Dall sheep *Ovis dalli* occurred only in our Alaska study area, and cougars *Puma concolor*, bobcats *Lynx rufus*, mule deer *Odocoileus hemionus*, and white-tailed deer *O. virginianus* occurred only in our Washington sites. Deer species could not be differentiated based on tracks alone, and thus the species of deer was recorded only when the animal making the snow track was observed. We traversed our study areas using snowmobiles, skis, dogsleds and snowshoes, following a semi-structured stratified sampling approach to disperse our observations over a wide variety of snow conditions, land-cover, and snow classes. We restricted sampling to tracks that appeared to have been made recently (usually < 24 h) when snow conditions were likely the same as the time of our survey. We estimated track freshness based on a variety of cues including comparisons of disturbed and undisturbed snow texture, presence or absence of melt-freeze crusts within the track, and hardness of snow track sidewalls ([Rezendes 1999](#), [Moskowitz 2010](#)). Once a set of fresh tracks was identified, we measured the sink depth and dimensions (width and length) of three consecutive footprints from one individual. For moose, we recorded age class, based either on visual confirmation of an individual creating snow tracks or based on track dimensions. Tracks of known juveniles (< 1 year old) averaged 10.4 cm wide by 10.6 cm long, whereas tracks of known adults (> 1 year old) averaged 12.8 cm wide by 15.3 cm long. We were less confident in our ability to differentiate age classes for smaller ungulates, so we did not specify age classes for deer, caribou, or sheep. We identified animal gait using a simple classification scheme (*sensu* [Rezendes 1999](#), [Moskowitz 2010](#)), and limited our observations to walking or trotting individuals.

Snow properties

To measure snow properties, we excavated a snow pit adjacent to each set of measured tracks, aligning the pit face parallel with the animal's direction of travel and set back 25–30 cm from the tracks to ensure that our 20 cm-long density cutter would not intercept animal-disturbed snow ([Fig. 2](#)). Because we sampled only very recent tracks, we assumed that snow conditions did not change significantly between when the tracks were made and when we conducted snow observations. Importantly, we selected only tracks where the animal was fully supported by the snow and disregarded all tracks that went through the entire snowpack and made contact with the ground. This approach was necessary to quantify thresholds

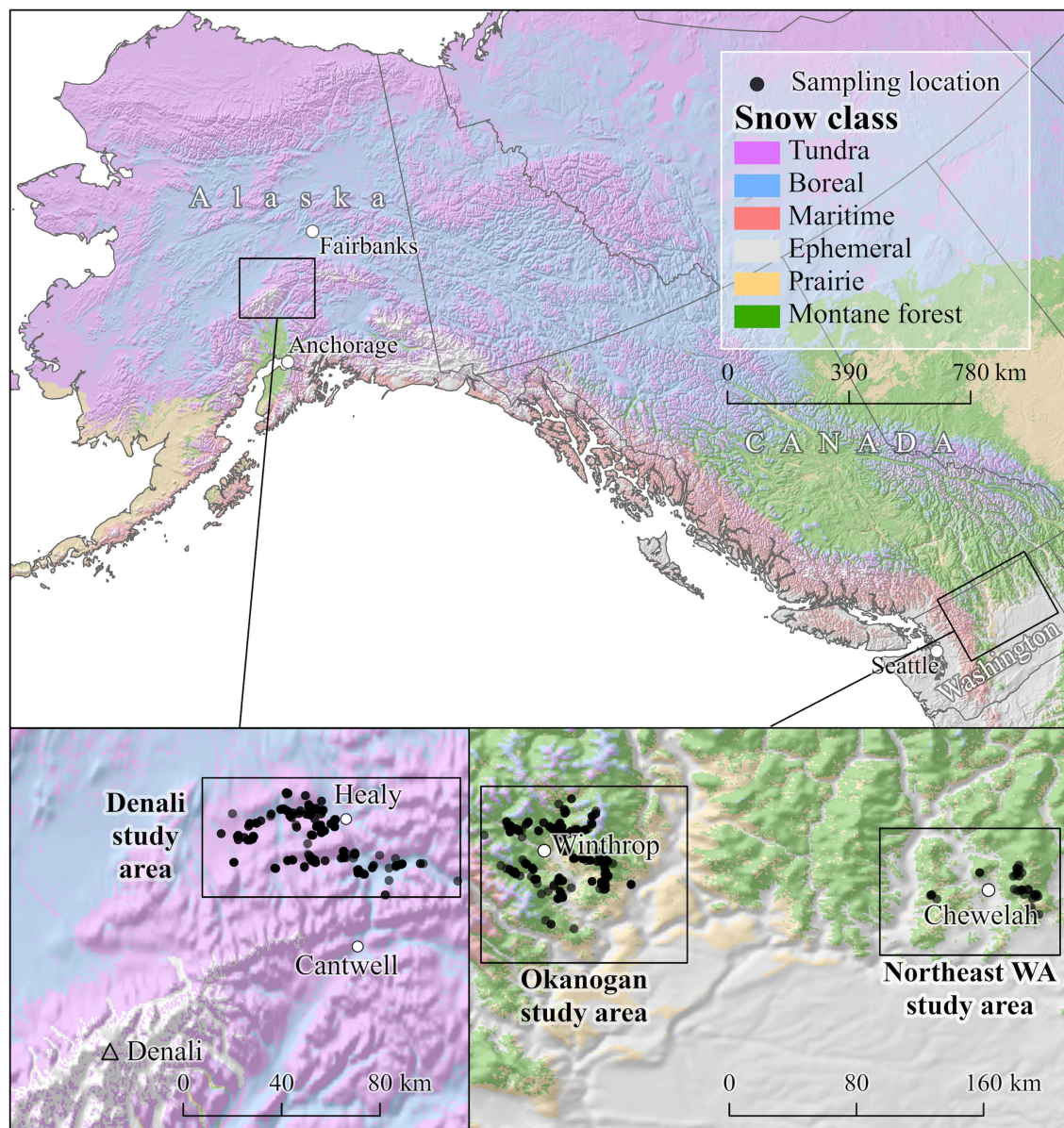


Figure 1. Study areas. The Denali study area in interior Alaska is comprised mostly of tundra and boreal snow. The Okanogan study area in Washington is diverse but is mostly comprised of montane forest. Other Okanogan snow classes are prairie and ephemeral, with some maritime on the western extremes and very limited boreal/tundra at the highest elevations. Northeast Washington contains montane forest, prairie, and ephemeral snow classes. Black points show locations of sampled snow tracks in each study area.

of snow strength (e.g. hardness or density) required to support the body mass of each species, but this sampling design precludes analyzing snow depth as a covariate of track sink depth.

We measured five snow properties at each site: snow density, penetrability, average hand-hardness, presence of ice layers, and total thickness of ice layers. Snow density is a central metric in snow science, with direct applications to calculating snow water equivalent (SWE), albedo, thermal balance, and wildlife movement cost (Bormann et al. 2013, Kinar and Pomeroy 2015, Sivy et al. 2018). Snow densities can range between 10 and 600 kg m⁻³ (Roebber et al. 2003) and vary

dramatically within a given snowpack profile based on depth, temperature gradient, new snowfall, snowmelt, wind compaction, and myriad climatological factors (Bormann et al. 2013). We used a 1000 cc steel density cutter (SnowMetrics RIP 1 Cutter) measuring 10 × 10 × 20 cm, and took two replicates at each of three depth classes: 0–10, 10–20 and 20–30 cm. We used the average value at each depth as our snow density metric *AvgDens*. Our average difference in replicate measurements was 15.2 kg m⁻³, so we rounded final density values to the nearest 10 kg m⁻³ when reporting results to account for measurement error. We limited sampling to the top 30 cm based on prior studies that indicated the



Figure 2. Illustration of field sampling protocol. We excavated a snow pit parallel to the animal's direction of travel and conducted observations, including measuring density of the top 30 cm (a; *AvgDens*), determining hand-hardness across the full pit's depth (*AvgHH*), quantifying thickness and depth of ice layers (*IceTop* and *TotalIce*), and measuring surface penetrability via tuna can drops (b; *AvgTuna*). The string under the tuna can measured 50 cm, the height at which the can was dropped from. Illustration by Sarah K. Glaser.

near-surface density is a better predictor of sink depth than overall density throughout the snow column (Bunnell et al. 1990, Sivy et al. 2018). However, we were concerned that 30 cm might be too shallow for predicting moose sink depth, so we therefore conducted full-depth snow density samples at 15 moose tracks. The relationship did not improve beyond the top 30 cm density (Supporting information), indicating

that our selected top-30 cm density sampling depth was sufficient.

To best capture snow hardness, we measured surface penetrability and hand-hardness throughout the snowpack. Penetrability (analogous to surface compaction, Fierz et al. 2009) was measured by dropping a 200 g cylindrical penetrometer (7 oz tuna can, Chicken of the Sea Chunk Light,

8.2 cm diameter \times 4.2 cm height) from a height of 50 cm above the snow surface and then measuring its sink depth (Fig. 2B). We conducted two tuna can drops at each site and averaged both to quantify penetrability *AvgTuna*. Similar simple and inexpensive methods have been used as a proxy for animal sink depth in prior wildlife studies (Murray and Boutin 1991, Kolbe et al. 2007, Pozzanghera et al. 2016, Droghini and Boutin 2018b, and Peers et al. 2020).

We also measured hand-hardness, a key component of a snowpack's stratigraphy (Kinar and Pomeroy 2015). The hand-hardness scale is widely used in avalanche forecasting to delineate layers of the snowpack that differ in their hardness (Fierz et al. 2009). Each layer is assigned a hardness based on whether a fist, four fingers, one finger, pencil, or knife can be pushed into the layer given a relatively constant force applied. We reclassified these on a numerical scale from 1 (fist-hardness; softest) to 5 (knife-hardness; hardest). For five depth horizons (top 10, 20, 30, 40 or 50 cm), we multiplied each hardness unit (1–5) by the total layer thickness (in cm), summed all measurements, and divided by depth to calculate thickness-weighted hand-hardness (*AvgHH*; sensu Sivy et al. 2018).

Our hand-hardness measurements formed the basis for delineating ice layers, which have been shown to significantly affect large mammal movements and foraging ability (Hansen et al. 2011). Ice, corresponding with knife-hardness, is typically formed through liquid water percolating into and refreezing on top of or within the snowpack (Fierz et al. 2009). We also observed extreme wind events tightly sintering snow grains into knife-hardness layers, which were also included as ice layers (Fierz et al. 2009). We determined the presence (1) or absence (0) of any knife-hardness layers within the top 10, 20, 30, 40 and 50 cm of the snowpack for the ice presence metric (*IceTop*), and summed the total knife-hardness layers' thickness to calculate total ice thickness (*IceTotal*) within the top 10, 20, 30, 40 and 50 cm of the snowpack. Because we collected stratigraphy data for the full snow column, we were able to calculate the 0–40 cm and 0–50 cm depth classes for *AvgHH*, *IceTop*, and *IceTotal* without having to conduct additional field measurements. Therefore, we included these depths although our density measurements terminated at 30 cm from snow surface.

Single-species modeling

We used generalized additive models (GAMs; Wood 2017) to determine the best predictors of sink depth for each species. GAMs use splines to create smoothed, non-linear relationships between predictors and the response variable (Wood 2017). Because track sink depth cannot be < 0 cm, we modeled sink depth using a gamma distribution (adding 0.00001 to all 0 cm track depths to satisfy the non-zero requirement of the gamma distribution).

Since density, hand-hardness, ice presence, and cumulative ice thickness included multiple depth classes that were highly correlated, we first determined which depth class for each of these variables performed best. We constructed all

models using one-term GAMs with penalized thin plate splines (Wood 2003) for continuous variables. We used a categorical fixed effect if ice was present in the top horizon of the snowpack (*IceTop*; 0=no ice; 1=ice). We used the percentage of null deviance explained (hereafter, pseudo- R^2 or pR^2) to determine the best overall predictor of sink depth (*AvgDens*, *AvgHH*, *IceTop*, *IceTotal* or *AvgTuna*) for each species (Wood 2017). We fit GAMs using the 'mgcv' package in R (Wood 2017, www.r-project.org).

Multi-taxa and regional comparison

In addition to species-specific predictors, we also aimed to determine which snow property best predicted track sink depth across multiple taxa in order to assess the influence of snow on predator–prey interactions. For this process, we followed a similar procedure to select the best depth class of the four depth-specific variables, again with a gamma-linked GAM with thin plate splines (Wood 2003). To choose a single snow variable that best predicted sink depth across all taxa, we constructed separate models for each snow covariate. Each model consisted of sink depth modelled in response to a 'by-variable' interaction between a given snow covariate (*AvgDens*, *AvgHH*, *IceTop*, *IceTotal* or *AvgTuna*) and species, which allowed each species to respond differently to snow properties. We selected the best single-term model for all species using deviance explained. We used this best overall model to test for regional differences in sink depth, to test for thresholds of support, and to delineate danger zones. In order to analyze regional differences in sink depth relationships, we added region to the best overall model as a by-variable interaction term and compared fitted models using Akaike information criterion corrected for small sample sizes (AIC_c), which accounts for goodness of fit while penalizing models with additional parameters to minimize overfitting (Anderson and Burnham 2002). We considered the model with the lowest AIC_c as the best fitting model if no other candidate model had AIC_c values within 2 ($\Delta AIC_c > 2$). If two or more candidate models were within 2 AIC_c of the leading model ($\Delta AIC_c < 2$), we considered those models to each have substantial support.

Thresholds of support

To identify support thresholds, we used linear piecewise regression to directly estimate inflection points. Piecewise regression, also known as 'broken-stick' or segmented regression, is used to determine thresholds (breakpoints) at which ecological relationships change (Toms and Lesperance 2003, Sivy et al. 2018). Because GAMs are designed to create a smoothed response, thresholds are more difficult to identify, whereas piecewise regression explicitly identifies potential abrupt thresholds (Toms and Lesperance 2003). We used the 'segmented' package in R (Muggeo 2017, www.r-project.org) to generate breakpoints, retrieve corrected AIC values (AIC_c ; Anderson and Burnham 2002), and calculate adjusted R^2 values.

We used AIC_c to determine whether adding a breakpoint improved model fit compared to a simple linear model. For each species, if either model was more than 2 AIC_c lower ($\Delta AIC_c > 2$) than the other, we selected the model with the lowest AIC_c value. If ΔAIC_c was < 2 , we considered these models as having equivalent support (Anderson and Burnham 2002) and therefore selected the segmented model, as our goal was to identify thresholds of support if present. To determine a threshold of support for species in which the linear regression outperformed the breakpoint regression (i.e. moose), we solved the linear regression equation for a sink depth equal to the average of the other species' breakpoints, adjusted by hind leg length.

Peak danger zones

A threshold of support is important for determining values of the critical snow property that support the animal's body mass without causing it to sink in the snow appreciably. However, the degree of movement impairment and energy expenditure for an animal sinking into the snowpack should vary considerably among species. For example, a 10 cm sink depth for deer may not result in a measurable impediment to locomotion (Parker et al. 1984), but this sink depth could substantially impair the mobility of a smaller species like coyote (Crête and Larivière 2003). The key factor in how much movement is altered is animal sink depth relative to size (Parker et al. 1984, Murray and Boutin 1991). Although there are many complex biomechanic and morphological metrics that link movement with size, hind leg length is a well-accepted analogue for movement ability, explaining 98% of variance in cost of locomotion across diverse vertebrate taxa (Pontzer 2007) and significantly predicting maximum speed in mammals (Garland and Janis 1993). Furthermore, hind leg length is a widely available measurement for diverse species (Garland and Janis 1993, Kilbourne and Hoffman 2013), facilitating comparisons for the eight species studied here.

We calculated relative sink depth for each species as its sink depth divided by hind leg length (Table 1), a morphologically

adjusted metric of cost of movement. First, we used our best single-term GAM to generate species-specific relative sink depth predictions across the measured range of snow densities. Next, we subtracted the predicted relative sink depths of predators from prey to calculate the difference in relative sink depths. Finally, we defined danger zones based on this difference in relative sink depth, providing a measure of peak disparity in relative sink depths. If the carnivore sank less than the ungulate at a given snow condition (difference in relative sink depth $> 0\%$), the carnivore would have a relative movement advantage, progressively leading to a danger zone. Conversely, if the ungulate sank less than the carnivore (difference in relative sink depth $\leq 0\%$), there would be no elevated danger to the ungulate and the carnivore may be at a relative disadvantage. The maximum difference in relative sink depth – denoted as peak danger – represented the snow properties where the predator's movement advantage was greatest. We considered only common predator–prey pairs: bobcat–deer, cougar–deer, cougar–juvenile moose, cougar–adult moose, coyote–deer, coyote–caribou, wolf–caribou, wolf–deer, wolf–juvenile moose and wolf–adult moose. Despite range overlap, we did not examine moose pairings with bobcats or coyotes, because bobcats and coyotes are too small to successfully kill moose (Newbury 2013, Benson et al. 2017).

Results

We measured a total of 707 sets of mammal tracks in Denali ($n=296$), northeast Washington ($n=35$), and Okanogan ($n=376$; Table 1). Across all species, track sink depth ranged from 0–88.3 cm ($\bar{x}=16.9$ cm). Species with higher foot loads sank deeper into the snow on average (deer = 16.6 cm; adult moose = 36.4 cm) than species with lower foot loads (coyotes = 7.7 cm; wolves = 9.7 cm). Most observed animal tracks were < 30 cm deep ($553/706=78\%$), supporting our decision to limit density measurements to the upper 30 cm. Due to few observations, we were unable to analyze snow

Table 1. Species track summary and distribution by study area. Due to low sample sizes, we did not analyze snow property–sink depth relationships for Dall sheep. Species included in these analyses are in bold. Due to large variations in morphology due to age class, gender, and region, hind limb length and foot loading values should be considered as general estimates rather than precise values. Sources: ^aKilbourne and Hoffman (2013); ^bGarland and Janis (1993); ^cLankester et al. (1993) (33-week-old moose calf); ^dTelfer and Kelsall (1984); ^eMurray and Larivière (2002).

Species	Average track width (cm)	Average track length (cm)	Average track sink depth (cm)	n Total	n Okanogan	n NE WA	n AK	Hind leg length (cm)	Foot loading ($g\ cm^{-2}$)
Bobcat	5.4	5.4	4.8	44	39	5	0	43.7 ^a	NA
Caribou	12.2	13.1	19.8	51	0	0	51	101.2 ^b	190 ^d
Cougar	9.8	9.5	12.4	39	38	1	0	71.1 ^a	NA
Coyote	6.0	7.0	7.7	185	122	8	55	44.0 ^a	160 ^e
Dall Sheep	5.2	7.2	6.4	6	0	0	6	NA	330 ^d
Deer	5.6	7.3	16.6	67	66	1	0	80.9 (<i>O. virginianus</i>) ^b ; 78.2 (<i>O. hemionus</i>) ^b	490 ^d
Moose (adult)	11.8	14.3	36.4	150	50	12	88	123.8 ^b	650 ^d
Moose (juvenile)	10.3	11.8	28.2	35	4	0	31	66.2 ^c	NA
Wolf	10.5	11.4	9.7	130	57	8	65	65.7 ^a	180 ^e

property-track relationships for Dall sheep ($n=6$). Snow properties varied widely (Table 2), with snow depth ranging from 11–235 cm, density varying from 21–577 kg m⁻³, tuna can sink depth ranging from 0–31.3 cm, and total ice thickness ranging from 0–31 cm in the top 50 cm of the snowpack. Snow density varied by snow class, with lightest densities in boreal forest, followed by tundra, and no significant differences between the other snow classes (Supporting information).

Single-species modeling

Snow density was the single best predictor for caribou (*AvgDens0-10*; $pR^2=0.77$), deer (*AvgDens0-30*; $pR^2=0.33$), juvenile moose (*AvgDens0-10*; $pR^2=0.85$), and adult moose (*AvgDens0-20*; $pR^2=0.57$). Across all species, ice layer metrics performed worse than density, tuna can penetrometer, and hand-hardness metrics (Table 2). For cougars and wolves, *AvgHH* was the best performing predictor, although pR^2 values were nearly identical between *AvgDens0-10* ($pR^2=0.438$) and *AvgHH0-10* ($pR^2=0.445$) for wolves. *AvgTuna* was the best performing predictor for bobcat ($pR^2=0.34$) and coyote ($pR^2=0.23$) sink depth, although no snow metric explained more than 23% of deviance for coyotes (Table 2). Across all species, the average tuna can sink depth was 5.8 cm, which was shallower than the average sink depth of all species except bobcats (4.8 cm; Table 1). Despite performing poorly for moose ($pR^2=0.16$), the tuna can was a surprisingly good predictor of sink depth across all species ($pR^2=0.50$). Hand-hardness

varied widely in its ability to predict sink depth, as the best predictor for cougars and wolves but performing poorly for coyotes and bobcats (maximum $pR^2=0.25$). Across all species and all variables, the 0–10 cm and 0–20 cm metrics nearest the surface ranked among the best predictors, whereas the 0–50 cm metrics consistently ranked last.

Multi-taxa and regional comparison

Across all species, *AvgDens0-20* was the best performing predictor ($pR^2=0.51$) for sink depth, followed closely by *AvgDens0-10* ($pR^2=0.51$) and *AvgTuna* ($pR^2=0.50$; Table 2). *AvgDens0-30* ($pR^2=0.49$), *AvgHH0-10* ($pR^2=0.47$) and *AvgHH0-20* ($pR^2=0.47$) also performed well. The relationship between sink depth and density varied by region for moose but not for coyotes or wolves (Supporting information). With some variation at low densities (<150 kg m⁻³), moose sank deeper for a given snow density in Washington compared to Alaska (Fig. 3, Supporting information). Coyote and wolf sink depths in Washington and Alaska were similar across all densities except lighter than 170 kg m⁻³, where Washington canids sank slightly deeper (Fig. 3, Supporting information).

Thresholds of support

Segmented linear models provided a similar representation of snow-sink depth relationships as the more flexible GAMs for all species (Fig. 4). The best performing model included

Table 2. Evaluation of snow variables as predictors of sink depths for seven mammal species. Pseudo- R^2 values (proportion of deviance explained) from univariate generalized additive models are shown. *AvgDens*=snow surface density as measured by a 10 × 10 cm 1000 cc density cutter; *IceTop*=presence of ice layers; *AvgHH*=thickness-weighted hand-hardness average using the five-point stratigraphy scale; *AvgTuna*=sink depth of cylindrical penetrometer (i.e. tuna can); *TotalIce*=cumulative ice thickness. We measured snow properties at multiple depth horizons for some variables. Each variable was measured in 10 cm increments from the surface and grouped into 3–5 depth horizons. The best performing depth class of each variable for each species is in bold, and the best overall predictor for each species is starred.

Variable	Range	Proportion of null deviance explained								
		Bobcat	Caribou	Cougar	Coyote	Deer	Moose (adult)	Moose (juvenile)	Wolf	All species
<i>AvgDens0-10</i>	23–502	0.30	0.77*	0.29	0.18	0.29	0.43	0.85*	0.44	0.51
<i>AvgDens0-20</i>	38–523	0.29	0.77	0.30	0.20	0.33	0.57*	0.80	0.35	0.51*
<i>AvgDens0-30</i>	60–516	0.27	0.77	0.33	0.17	0.33*	0.52	0.82	0.30	0.49
<i>IceTop10</i>	0–1	0.11	0.19	0.13	0.01	0.06	0.06	0.28	0.14	0.33
<i>IceTop20</i>	0–1	0.04	0.15	0.15	0.01	0.07	0.10	0.36	0.05	0.31
<i>IceTop30</i>	0–1	0.01	0.18	0.18	0.01	0.15	0.09	0.26	0.02	0.31
<i>IceTop40</i>	0–1	0.01	0.08	0.15	0.00	0.15	0.10	0.33	0.01	0.30
<i>IceTop50</i>	0–1	0.00	0.07	0.15	0.00	0.15	0.03	0.27	0.01	0.30
<i>AvgHH0-10</i>	1–5	0.24	0.64	0.34	0.13	0.28	0.20	0.58	0.44*	0.47
<i>AvgHH0-20</i>	1–4.95	0.19	0.70	0.37*	0.12	0.29	0.35	0.76	0.35	0.47
<i>AvgHH0-30</i>	1–4.97	0.18	0.67	0.25	0.06	0.24	0.34	0.57	0.26	0.43
<i>AvgHH0-40</i>	1–4.81	0.25	0.61	0.20	0.05	0.22	0.37	0.61	0.21	0.42
<i>AvgHH0-50</i>	1–4.81	0.23	0.47	0.17	0.05	0.18	0.36	0.59	0.20	0.40
<i>AvgTuna</i>	0–31.3	0.34*	0.62	0.28	0.23*	0.30	0.16	0.83	0.41	0.50
<i>TotalIce10</i>	0–10	0.17	0.21	0.21	0.02	0.07	0.13	0.54	0.14	0.35
<i>TotalIce20</i>	0–19	0.14	0.17	0.13	0.03	0.07	0.24	0.54	0.11	0.35
<i>TotalIce30</i>	0–29	0.05	0.19	0.16	0.03	0.10	0.22	0.54	0.10	0.34
<i>TotalIce40</i>	0–29	0.07	0.15	0.16	0.03	0.14	0.24	0.39	0.08	0.35
<i>TotalIce50</i>	0–31	0.05	0.14	0.16	0.05	0.14	0.18	0.39	0.05	0.34

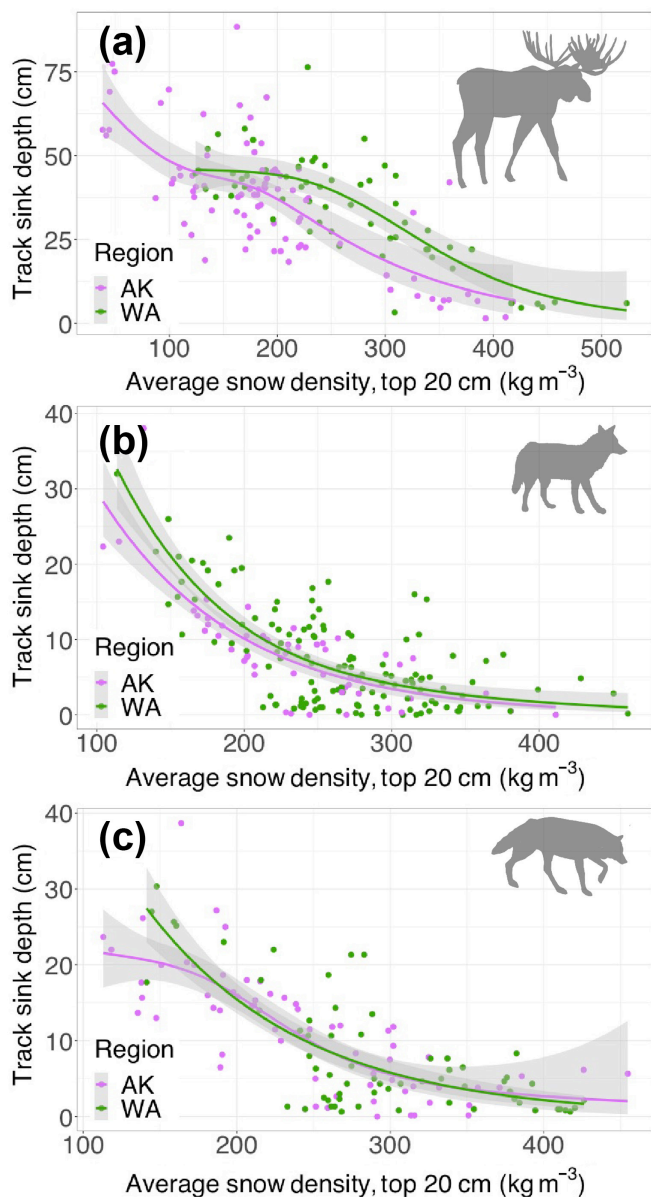


Figure 3. Regional differences in sink depth-snow density relationships for (a) moose, (b) coyotes, and (c) wolves. Fitted lines and 95% confidence intervals (grey bands) from generalized additive models with region as an interaction term (Alaska = purple; Washington = green) are shown. The relationship between sink depth and snow density (0–20 cm; *AvgDens0-20*) varied by region for moose but not did vary for coyotes or wolves. Full regional analysis results are shown in the Supporting information.

a breakpoint at 280 kg m^{-3} (95% CI: $240\text{--}330 \text{ kg m}^{-3}$) for bobcats, 310 kg m^{-3} (95% CI: $280\text{--}350 \text{ kg m}^{-3}$) for cougars, 220 kg m^{-3} (95% CI: $200\text{--}230 \text{ kg m}^{-3}$) for coyotes, and 270 kg m^{-3} (95% CI: $240\text{--}300 \text{ kg m}^{-3}$) for wolves (Table 3). At light snow densities ($<200 \text{ kg m}^{-3}$), predator sink depth changed rapidly until a breakpoint, after which the sink depth changed an insignificant amount. Ungulate sink depths followed a similar pattern, with breakpoints at 360 kg m^{-3} (95% CI: $280\text{--}430 \text{ kg m}^{-3}$) for caribou, 300 kg m^{-3}

(95% CI: $240\text{--}370 \text{ kg m}^{-3}$) for deer, and 360 kg m^{-3} (95% CI: $280\text{--}450 \text{ kg m}^{-3}$) for juvenile moose. Sink depths for adult moose were best predicted by an unmodified linear model of *AvgDens0-20* (Table 3). For species with sink depth best modeled by breakpoint regression, sink depths at the breakpoint ranged from 2–13 cm (5–16% of hind leg length) and did not appreciably change after the breakpoint (Fig. 4). The breakpoints can therefore be considered thresholds of support, critical snow densities above which the animal does not sink into the snow appreciably (Sivy et al. 2018). For adult moose, we used the fitted linear model to calculate a threshold of support analogous to those of the other species. We calculated the average sink depth across all other species as a proportion of hind leg length and used this value (9.2%) to estimate a comparable depth for adult moose (11 cm). This threshold of support for adult moose was 410 kg m^{-3} (95% CI: $380\text{--}450 \text{ kg m}^{-3}$), which corresponded to an inflection point in the GAM curve (Fig. 4G).

Peak danger zones

All ungulate species had identifiable danger zones (Fig. 5), defined as ranges of snow conditions where prey species sink deeper than predators relative to leg length. These danger zones peaked at intermediate snow densities: the density associated with maximum danger ranged from 190 kg m^{-3} (deer-wolf and juvenile moose-wolf) to 340 kg m^{-3} (deer-cougar; Table 4). Caribou had the lowest danger peaks, sinking only 6% deeper than wolves, in relative terms, at 200 kg m^{-3} (Fig. 5). In contrast, all sampled snow densities ($110\text{--}460 \text{ kg m}^{-3}$) represent deer-wolf danger zones, and deer had a relative mobility disadvantage compared to all predators at densities above 210 kg m^{-3} . Adult moose had broad danger zones for cougars ($200\text{--}450 \text{ kg m}^{-3}$) and wolves ($140\text{--}460 \text{ kg m}^{-3}$). Most sampled snow densities represented danger zones for juvenile moose (Table 4), although at narrow, moderate-density ranges juvenile moose gained a slight movement advantage over cougars ($300\text{--}390 \text{ kg m}^{-3}$) and wolves ($340\text{--}380 \text{ kg m}^{-3}$). Juvenile moose had the greatest relative mobility disadvantage of all ungulates studied, sinking 18% less than cougars at 200 kg m^{-3} and 31% less than wolves at 190 kg m^{-3} (Table 4).

Discussion

Snow is a critical yet understudied component of winter ecology for large mammals across the Northern Hemisphere, as even subtle changes in snow conditions may favor some species over others (Boelman et al. 2019, Peers et al. 2020). Our study delineates the characteristics in near-surface snow properties that correlate with shifts in wildlife sink depth, a close proxy for energy expenditure and overall vulnerability to predation or conversely, hunting success (Fancy and White 1987, Dailey and Hobbs 1989, Crête and Larivière 2003). Thresholds of support varied among species largely as expected based on foot loading, with surprisingly similar relationships across our

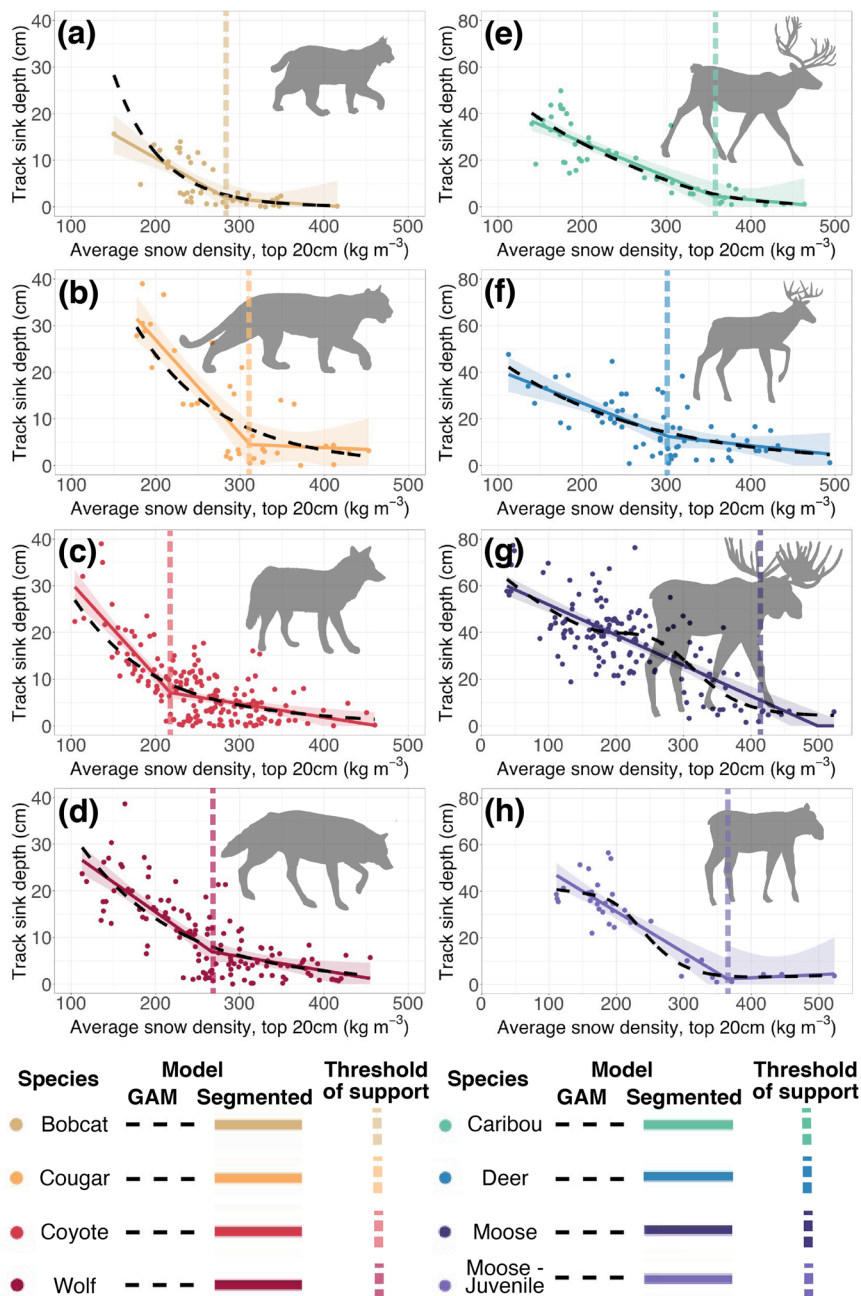


Figure 4. Comparison of segmented linear regression (solid lines), generalized additive models (dashed lines), and thresholds of support (vertical dashed lines) for sink depth-snow density relationships for (a) bobcats, (b) cougars, (c) coyotes, (d) wolves, (e) caribou, (f) deer, (g) adult moose and (h) juvenile moose. A one-breakpoint segmented regression best fit all species except adult moose. Shading shows 95% confidence intervals for the breakpoint regressions, which fit separate linear regressions for each segment.

study regions. Despite major differences in body sizes and foot loading among focal species, ‘danger zones’ peaked at intermediate near-surface snow density values of 200–300 kg m⁻³ for eight of the ten ungulate–carnivore pairs. As the climate continues to change and alter snow properties, our findings indicate that shifts in the distribution and abundance of snow within this density range will be most consequential in tipping the balance in favor of predators or prey.

Predator strategy has a major role in determining whether snow helps or hinders hunting success. Although predation strategy may be more of a spectrum than a binary classification (Gittleman 1985, Scharf et al. 2006), cursorial predators such as wolves and coyotes typically travel long distances to locate prey before engaging in a chase (Wilmers et al. 2007). In contrast, stalking predators such as bobcats and cougars make localized search movements (Bailey et al.

Table 3. Model selection for breakpoint regression model predicting animal sink depths using average near-surface (0–20 cm) snow density. We determined support for model type (i.e. linear vs segmented) based on ΔAIC_c . For each species, we used AIC_c to determine whether adding a breakpoint would be more informative compared with a simpler standard linear model. If either the segmented or the linear model was more than 2 AIC_c lower ($\Delta AIC_c > 2$) than the other, we selected that as the best fitting model. If the change in AIC_c was < 2 between the segmented and linear models ($\Delta AIC_c < 2$), we determined that there was equivalent support for both models and therefore selected the segmented model, as our goal was to identify thresholds of support if present. For species with a segmented best fit, the slope of the final segment was not significantly different than zero, indicating that the breakpoint corresponds with a threshold of support.

Species	Linear model				Segmented linear model				Best-fitting model			
	Log likelihood	AIC_c	Adjusted R^2	Log likelihood	AIC_c	Adjusted R^2	Model shape	Threshold of support (95% CI; kg m ⁻³)	Intercept (cm)	Coefficient(s)		
Caribou	-176.602	359.7	0.71	-175.113	361.6	0.71	Segmented	360 (280–430)	57.6 ± 8.8	-0.15 ± 0.04; -0.03 ± 0.14		
Deer	-240.043	486.5	0.43	-237.249	485.5	0.46	Segmented	300 (240–370)	54.8 ± 13.2	-0.14 ± 0.06; -0.04 ± 0.08		
Moose (adult)	-576.098	1158.4	0.52	-575.123	1160.7	0.52	Non-segmented	410 (380–450)	64.8 ± 4.9	-0.13 ± 0.02		
Moose (juvenile)	-125.939	258.7	0.68	-122.078	256.2	0.73	Segmented	360 (280–450)	66.3 ± 9.7	-0.18 ± 0.05; 0.01 ± 0.16		
Bobcat	-115.206	237	0.45	-112.103	235.8	0.50	Segmented	280 (240–330)	31.0 ± 10.5	-0.10 ± 0.04; -0.01 ± 0.07		
Cougar	-132.649	272	0.58	-124.508	260.8	0.71	Segmented	310 (280–350)	67.1 ± 14.4	-0.20 ± 0.06; -0.01 ± 0.09		
Coyote	-566.648	1139.4	0.43	-535.904	1082.1	0.58	Segmented	220 (200–230)	50.6 ± 8.0	-0.20 ± 0.04; -0.03 ± 0.05		
Wolf	-399.47	805.1	0.53	-387.693	785.9	0.60	Segmented	270 (240–300)	41.0 ± 6.0	-0.13 ± 0.03; -0.03 ± 0.04		

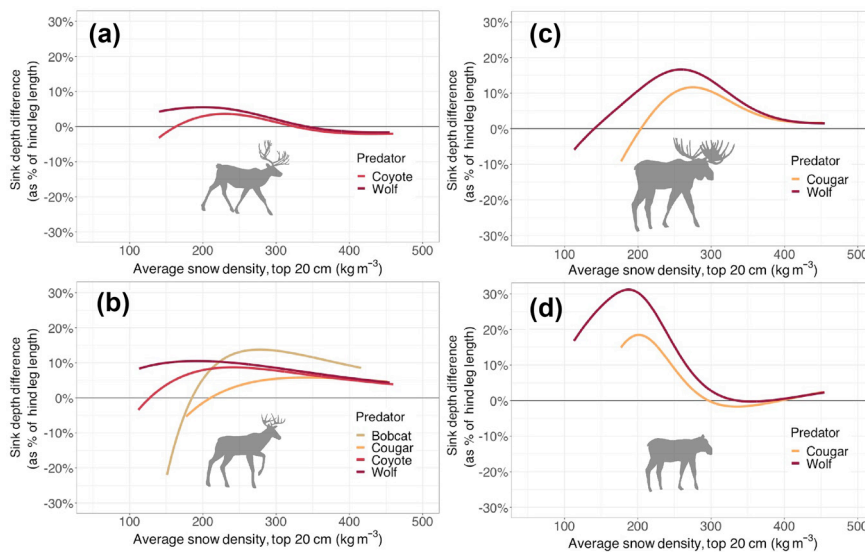


Figure 5. Peak danger zones for (a) caribou, (b) deer, (c) adult moose, and (d) juvenile moose relative to sympatric predators. The y-axis represents the difference between prey and predator sinking depth, calculated relative to hind leg length (Table 1). Positive values represent snow densities where prey sink to deeper relative depths than predators, defining ‘danger zones,’ wherein predators have comparative movement advantage. Negative values represent densities where the ungulate has a relative movement advantage.

2013, Makin et al. 2017) and use land cover or terrain features to stalk prey until close enough for a sudden attack (Wilmers et al. 2007, Bailey et al. 2013, Makin et al. 2017). The increased distances covered by cursorial predators may lead to higher energetic expenditures than more sessile stalking and ambush predators, especially when deep, low-density snow is present (Crête and Larivière 2003, Scharf et al. 2006). However, this cost may be offset by impaired escape abilities of prey in deep snow, especially when conditions result in a movement advantage for predators relative to ungulate prey (i.e. danger zones). Such locomotion advantages may manifest as greater hunting success (Huggard 1993), more frequent kill rates (Nelson and Mech 1986, Huggard 1993, Jędrzejewski et al. 2002), and greater opportunities to kill larger individuals or species compared with snow-free hunting (Peterson et al. 1984, Post et al. 1999, Smith et al. 2003). Because snow conditions and prey escape capability more strongly shape predation success for coursers than stalkers (Husseman et al. 2003), cursorial predators may benefit more than stalking predators from exploiting danger zones. In our system, cougars also had narrower danger zones and lower peaks than wolves for both deer and moose, indicating that wolves may have a relative hunting advantage over a wider range of snow densities because of their morphology (longer legs and lower foot loading) compared to cougars. Thus, hunting mode and morphology can both affect the importance of snow density for the hunting success of carnivores, which may subsequently influence how strongly predation rates vary with snow conditions.

As snow-adapted species with the lowest foot-load of ungulates we studied, caribou had the lowest peak danger (Fig. 5, Table 4). Deer, in contrast, had compromised movement relative to predators at nearly all snow conditions sampled, and the effect of snow density on their vulnerability varied

substantially among predators. For example, wolves had a mobility advantage of 5–10% across the full range of sampled snow densities, whereas cougars did not have a mobility advantage until snow density exceeded 200 kg m^{-3} . Both moose and juvenile moose had high peak danger compared with other predator–prey pairs, with cougars and wolves having a relative mobility advantage in most snow conditions (Fig. 5, Table 4). Thus, climate-induced changes to snow density may have relatively large and predictable impacts on moose–predator interactions, relatively minor impacts on caribou, and impacts on deer that may depend on carnivore community composition. Given that large mammals are known to select for terrain and fine-scale features that reduce their sinking depth (Murray and Boutin 1991, Lingle 2002, Kolbe et al. 2007, Droghini and Boutin 2018a), the specific snow properties defining each predator–prey danger zone peak can inform multi-species models of habitat selection and species interactions.

Our assessment of five snow metrics across multiple depth classes can help ecologists prioritize measuring the more effective metrics (Kinar and Pomeroy 2015). Of particular note was the effectiveness of the simple tuna can (cylindrical penetrometer). The average surface penetration of the tuna can captured the majority of overall variability in sink depth by species (Table 2), was the second-best overall predictor, and can be used as a proxy for our best predictor (*AvgDens0-20*; Supporting information). The tuna can especially excelled at quantifying conditions for smaller-bodied species: the relationship between tuna can sink depth and animal sink depth was nearly 1:1 for both coyotes and bobcats, suggesting the tuna can’s force of impact and surface area are similar to the force exerted by smaller predators. Furthermore, this inexpensive instrument is lightweight, easy to carry in the field, and quick to deploy, all of which are key considerations

Table 4. Danger zones for caribou, deer and moose. Danger zones are defined as near-surface (0–20 cm) snow densities where the predator sinks less than sympatric prey, relative to hind leg length. Peak danger is the maximum difference in relative sink depth between predator and prey, quantified by dividing sink depth by hind leg length. If the predator never sinks less than the prey, there is no elevated danger to the prey species and therefore no danger zone.

Prey species	Bobcat			Cougar			Coyote			Wolf		
	Danger zone range (kg m ⁻³)	Peak danger (95% CI); density (kg m ⁻³)	Peak danger (95% CI); density (kg m ⁻³)	Danger zone range (kg m ⁻³)	Peak danger (95% CI); density (kg m ⁻³)	Peak danger (95% CI); density (kg m ⁻³)	Danger zone range (kg m ⁻³)	Peak danger (95% CI); density (kg m ⁻³)	Peak danger (95% CI); density (kg m ⁻³)	Danger zone range (kg m ⁻³)	Peak danger (95% CI); density (kg m ⁻³)	
Caribou	NA	NA	NA	NA	NA	NA	160–330	4% (–3 to 11%); 230	6% (–3 to 14%); 200	140–340	6% (–3 to 14%); 200	
Deer	190–420	14% (9–18%); 280	6% (1–10%); 340	210–450	12% (4–19%); 280	18% (–5 to 39%); 200	130–460	9% (3–15%); 240	11% (0–22%); 190	110–460	11% (0–22%); 190	
Moose (adult)	NA	NA	12% (4–19%); 280	200–450	18% (–5 to 39%); 200	NA	NA	NA	17% (11–22%); 260	140–460	17% (11–22%); 260	
Moose (juvenile)	NA	NA	18% (–5 to 39%); 200	180–300; 390–450	NA	NA	NA	NA	31% (18–45%); 190	110–340; 380–460	31% (18–45%); 190	

in an extended field campaign. We join a number of other studies finding similar penetrometers effective for wildlife applications (Murray and Boutin 1991, Kolbe et al. 2007, Pozzanghera et al. 2016, Sivy et al. 2018, Peers et al. 2020) and encourage future researchers to consider this easily accessible snow measurement tool.

Although near-surface density was the strongest predictor of wildlife sink depth, sink depth is a function of multiple interacting physical properties, of which density is only one component. The influential role of unaccounted-for snow properties may explain some of the variability among species in how well our measured snow properties explained sink depths. Because our sampling was widely distributed both temporally and spatially, we likely included samples with wide ranges of these unaccounted-for snow properties. For example, several centimeters of light new snow on top of a dense wind slab would be averaged into a single moderate value in our 0–10 cm density measurement, but this snowpack would affect sink depth differently than a homogenous layer of the same moderate density. This unaccounted-for heterogeneity may have affected smaller-bodied species like coyotes, which had the lowest deviance explained in sink depths. Although we found that near-surface snow density was consistently the best predictor of wildlife sink depth, sampling with a finer-resolution density cutter to measure snow density at sub-10 cm increments could help refine sink depth relationships.

We did not examine the role of snow depth, one of the most widely used proxies of snow's impact on large mammals (Nelson and Mech 1986, Murray and Boutin 1991, Pedersen et al. 2021, Borg and Schirokauer 2022). Because our goal was to quantify thresholds of support, we surveyed only tracks where animals were supported above the bottom of the snowpack, biasing our site selection towards areas with deeper snow. An extensive body of literature suggests that total snow depth is a major driver of habitat selection, movement, and predator–prey interactions (Nelson and Mech 1986, Mahoney et al. 2018, Horne et al. 2019, Cunningham et al. 2022). Compared to snow depth, snow density has received far less than attention as a driver of wildlife dynamics, but our findings highlight the importance of near-surface density for movement efficiency and predator–prey interactions. We expect that snow depth should have the greatest impact on energetics of movement where snow densities fall below the thresholds of support we identified, and hunting success should be most affected by snow depth in areas where snow densities fall within danger zones. Coupling near-surface snow density with snow depth measurements should greatly enhance our ability to determine how snow affects wildlife movement and predator–prey dynamics.

The broad geographic scope of our study allowed us to analyze whether the relationship between snow properties and animal sink depth changed by region. We did not observe regional differences in sink depth–snow density relationships for coyotes or wolves, but we found that moose sank deeper in Washington than in Alaska for intermediate snow densities (Fig. 2). Furthermore, we found that track dimensions for coyotes, moose, and wolves were larger in Alaska than

in Washington (Supporting information), and other studies indicate that all three of these species have larger body sizes in northern regions than further south (Ashton et al. 2000, Herfindal et al. 2006, Meiri et al. 2007). This pattern may indicate that the larger foot surface areas we observed for all species in Alaska compared to Washington (Supporting information) more than compensate for the effect of a larger body size in terms of determining foot loading and subsequent sink depth. However, the regional differences we observed were relatively minor, indicating that the relationships and thresholds we quantified here should apply broadly across other regions, populations, and snow classes.

Our analyses across ten predator–prey pairs offer a community-based framework to assess the biological impact of snow. By integrating our results with animal location data and spatially and temporally explicit snow models (Liston and Elder 2006), future efforts can determine what role snow support thresholds have in determining habitat selection. By modeling the geographic distribution of danger zones across the landscape, our work can predict the areas where prey are most at risk, or where predators may find it increasingly difficult to hunt. Winter kill site investigations offer an opportunity to explicitly consider the role of snow in predation events, and quantifying snow properties along the chase and kill sequences would further enhance our understanding of danger zones. Climate change may already be reducing danger zones, as major observed impacts on snowpack include lower overall snow-water equivalent values (Kapnick and Hall 2012), increased mid-winter melting (Musselman et al. 2021), decreased spatial coverage (Pulliainen et al. 2020), and shorter winters (Derksen and Brown 2012). These changes may collectively shift snow to denser, more ungulate-favorable conditions, as well as give predators fewer days and less snowy terrain to exploit their advantage. Understanding when and where danger zones occur remains an outstanding, urgent need for resource managers to anticipate and proactively adapt to changing snow conditions.

Acknowledgements – We recognize the Indigenous stewards of the lands and wildlife that inspired our research. Denali is the traditional homeland of the Tanana and Koyukon peoples of the larger Dene (Athabaskan) Nation. Our Washington sites are part of the traditional homeland of the Nlaka'pamux Nation, Syilx (Okanagan) Nation, and the Confederated Tribes of the Colville Reservation. Expert trackers C. Phelan, J. Gaposchkin and C. Hoffman were critical to our field efforts. S. K. Glaser contributed to fieldwork and created the illustrations included here. Our field crew included A. Machowicz, C. Vanbianchi, J. Childs-Walker, R. Mower, R. Windell, K. Cronin, I. Rohan and D. Gordon. We acknowledge key contributors at Denali National Park and Preserve, including B. Borg, D. Schirokauer, K. Klauder, D. Olson, as well as the Denali National Park Sled Dog Kennels staff and dogsled teams, led by D. Tomeo, J. Reppert and Prusik. Wildlife insight from B. Kertson and spatial data enabled by P. Whelan, both at the Washington Department of Fish and Game, greatly helped with our efforts. We thank J. Rohrer at the USFS for his help and guidance. Staff at the National Ecological Observatory Network (NEON) provided access to their site in Denali and to the data collected by their observational network. Finally, comments by K. Shively, K.

Breen, Y. Hentati, M. Procko, T. Ganz, S. Kreling, T. Nuñez and E. Reese greatly improved this manuscript.

Funding – BKS, CXC, JDL, and LRP were supported by NASA Interdisciplinary Sciences grant no. 80NSSC20K1291. Denali National Park and Preserve supported our research through the use of key NPS-owned equipment, including snowmachines, a trailer, and miscellaneous winter travel equipment.

Author contributions

Benjamin K. Sullender: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (supporting); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Calum X. Cunningham:** Formal analysis (equal); Investigation (supporting); Methodology (equal); Visualization (supporting); Writing – review and editing (supporting). **Jessica D. Lundquist:** Conceptualization (supporting); Funding acquisition (supporting); Methodology (supporting); Writing – review and editing (supporting). **Laura R. Prugh:** Conceptualization (lead); Formal analysis (supporting); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC): <https://doi.org/10.3334/ORNLDAAC/2188> (Sullender et al. 2023). All R code used in this analysis is available at <https://github.com/bsullender/SnowTracks>.

Supporting information

The Supporting information associated with this article is available with the online version.

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