Living on Winter's Edge: Snow Ecology of Large Mammals in Northern Ecosystems

Benjamin Knight Sullender

A dissertation
submitted in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

University of Washington
2025

Reading Committee:
Laura Prugh, Chair
Joshua Lawler
Jessica Lundquist

Program Authorized to Offer Degree:
School of Environmental and Forest Sciences

University of Washington

Abstract

Living on Winter’s Edge: Snow Ecology of Large Mammals in Northern Ecosystems

Benjamin Knight Sullender

Chair of the Supervisory Committee:
Laura Prugh
School of Environmental and Forest Sciences

Climate change is rapidly reshaping snowpacks around the world, with dramatic impacts on wildlife. My dissertation explored the role of snow in shaping predator–prey relationships and movement ecology, focusing on large mammals in the northern United States of America and Canada. Chapter 2 used winter fieldwork to quantify how specific snow properties influence the sink depths of tracks made by predators (bobcats, cougars, coyotes, and wolves) and their sympatric ungulate prey (caribou, deer, moose). Using generalized additive models, breakpoint regression, and animal morphology, I found that near-surface snow density is the most significant predictor of sink depth, with different thresholds for predators and prey. I identified "danger zones" where snow conditions impede ungulates’ movement more than predators, providing a framework to predict the impacts of climate-driven snow changes on predator–prey

dynamics. Chapter 3 applied an entirely different methodological approach to investigate whether these danger zones factor into apex predator habitat selection. Using GPS collar data for cougars, wolves, mule deer, and white-tailed deer, I found that snow depth and density significantly affect predator movement, with predators selecting for areas with either shallow or with deep, dense snow. Kill-site investigations for cougar-killed deer indicated similar snow preferences. In Chapter 4, I examined winter movements from an ungulate perspective, using GPS collared data from five moose populations across their entire latitudinal range. I found that, even in winter, high temperatures cause moose to adjust behavioral patterns and alter habitat selection, potentially forgoing foraging opportunities in favor of thermal refuge. These changes were most dramatic in southern moose and may be a contributing factor to recent moose range contraction along their southern margins. Finally, Chapter 5 integrated physically based snow modeling with climate projections to predict how changing snowpacks will alter predator–prey interactions. I focused on two apex predators, cougars and wolves, and their primary prey, mule deer and white-tailed deer, under two mid-century climate change scenarios (SSP2-4.5 and SSP5-8.5). My results showed significant declines in snow-mediated advantages for predators, with a reduction in both the duration and extent of snowpack conditions that favor predator movement (as identified in Chapter 3). These changes are expected to have disproportionate impacts on apex predators, potentially leading to shifts in predator home ranges, prey densities, and ecosystem dynamics. Collectively, these chapters underscore the profound effects of climate-driven changes in snowpack dynamics on large carnivore and ungulate behavior, with potential for significant shifts in predator–prey interactions across the Northern Hemisphere.

TABLE OF CONTENTS

LIST OF FIGURES

Figures in Chapter 2

Figures in Chapter 3

Figures in Chapter 4

Figures in Chapter 5

LIST OF TABLES

Tables in Chapter 2

Tables in Chapter 3

Tables in Chapter 4

Tables in Chapter 5

ACKNOWLEDGEMENTS

My dissertation was made possible through a combination of generous people, funders, and partnerships. First and foremost, I thank my committee – my advisor Laura Prugh, Jessica Lundquist, Briana Abrahms, Sarah Converse, and Josh Lawler – for guiding my academic journey. I leaned on the smart and dedicated folks at the Prugh lab, especially Calum Cunningham (patiently teaching GAMs, helping make sense of my disorganized scientific reasoning, and skiing volcanoes) and Taylor Ganz (patiently teaching SSFs, helping make sense of my disorganized field plans, and wrangling a work-life balance). I want to thank Sam Kreling, Yasmine Hentati, Katie Breen, Christine Phelan, and Kayla Dreher for support and friendship through the many up-and-down eras of grad student life. Even though we overlapped less, Jiangyue Wang, Ellie Reese, and Michael Procko all helped shape my work, and, along with the folks in Briana Abrahms' lab – Anna Nisi, Leigh West, Erik Johansson, and Kasim Rafiq – listened to many terrible drafts of these chapters and improved these ideas. Folks in Jessica Lundquist's Mountain Hydrology Group – namely, Ross Mower and Clinton Alden – provided critical snow physics (and ski-based) support, and Ross and Jiangyue corralled high-performance computers to produce and organize many terabytes of snow data despite my total ignorance.

Numerous folks on the field team made the snow-sampling project actually happen. Christine Phelan and Carmen Vanbianchi patiently taught me all I know about snow tracking, Jake Gaposchkin and Clara Hoffman helped keep priorities in place (safety first, fun second, data third), Julian Childs-Walker stepped up on some of the most arduous days out there (recovering snowmachines and a double-flat-tire trailer from a completely snowed-in shed down a half-mile of impassable road), Anna Machowicz and Becca Windell went out of their way to ensure successful field seasons, and Iona Rohan, Daniel Gordon, and Kelsey Cronin collected key data.

Funding for my dissertation was provided by a University of Washington School of Environmental and Forest Sciences Fellowship, National Aeronautics and Space Administration (NASA) Interdisciplinary Sciences grant no. 80NSSC20K1291ASA, the University of Washington Program on Climate Change Graubard Fellowship, and NASA Future Investigators in NASA Earth and Space Science and Technology (FINESST) award no. 80NSSC24K1582.

I was fortunate to step into productive, already-established partnerships, allowing me to hit the ground running. The Washington Predator-Prey Project started in 2016 and provided the foundation of my ecological study systems in the Pacific Northwest. Although many more people contributed to the project over the years, key people include UW faculty Laura Prugh, Aaron Wirsing, and Beth Gardner, grad students Taylor Ganz, Lauren Satterfield, Becca Windell, and Sarah Bassing, and Washington Department of Fish & Wildlife researchers Brian Kertson and Melia DeVivo. In Denali National Park and Preserve, Bridget Borg was essential for making my project possible, organizing permits, protocols, and logistics over multiple field seasons and a changing cast of people. Dave Schirokauer and Kaija Klauder helped ensure everything ran smoothly in Denali, with John Rohrer (USFS) going above and beyond to make our Washington work actually work. From the Denali National Park Kennels, David Tomeo, Jason Reppert, and sled dogs including Prusik, Steward, and Throne helped lead us out into remote areas and organized overnight sampling campaigns based at backcountry cabins.

Finally, and most importantly, my wonderful wife Sarah K. Glaser and my perfect doggo Prusik provided all kinds of critical support throughout the entire PhD process, from much-needed escapes to recharge in the mountains, to working (or napping, as the case may be) by my side through late nights, early mornings, and long days, to boundless patience as we navigated living in both Alaska and Washington at the same time. Here’s to Yolo and our growing pack.

CHAPTER 1: INTRODUCTION

1.1 Background

Snow shapes ecosystems across the planet in ways that are only beginning to be understood. Beyond directly feeding hydrological systems and indirectly influencing vegetation communities (Gergel et al. 2017), a diverse community of animals have evolved to exploit specific snow conditions (Penczykowski et al. 2017). However, snow is spatially heterogeneous, physically diverse, and dynamic, and subtle changes in snow conditions can have dramatic impacts on wildlife. Depending on physical properties, snow can provide a life-saving boost to thermoregulatory processes as insulation for subnivean mammals (Durner et al. 2003, Wilson and Durner 2020, Poirier et al. 2023) or can prove to be a lethal energy sink for ungulates attempting to move between habitats (Parker et al. 1984, Horne et al. 2019). Snow can inflict mass mortality as herbivores starve on inaccessible, iced pastures (Stien et al. 2010, Hansen et al. 2011), and these sudden influxes of carrion can also catalyze population booms in scavengers and other carnivores (Mech et al. 1987, Post et al. 1999, Hansen et al. 2013). Various aspects of snow have been linked with altering mammal behavior (Murray and Boutin 1991, Cunningham et al. 2022, Ortega et al. 2024, Prugh et al. 2024), habitat suitability (Glass et al. 2021, Pedersen et al. 2021), and a wide range of demographic parameters from survival (van de Kerk et al. 2018, Horne et al. 2019, Van de Kerk et al. 2020) to fecundity (Post et al. 1999, Borg and Schirokauer 2022).

These profound ecological impacts occur across a massive geographic area, as 48% of the world's land area is at least periodically snow-covered (Johnston et al. 2023). In northern ecosystems, snow cover typically lasts nine months of the year (Boelman et al. 2019), and, even in areas that receive only intermittent snow or no snow at all, the gradually melting snow from mountainous regions – the "world's water towers" – provide critical water resources to 1.9 billion people (Barnett et al. 2005, Immerzeel et al. 2020). Despite its global importance, the complex and dynamic nature of snow precludes easy integration into typical wildlife research (Reinking et al. 2022). Accurately quantifying snow properties at wildlife-relevant scales – both temporally and spatially – remains a central challenge in snow ecology (Mahoney et al. 2018, Reinking et al. 2022).

The rapid pace of climate change has added urgency to this challenge. Northern high-latitude ecosystems are warming at the fastest rates on Earth (Rantanen et al. 2022), with total precipitation, precipitation intensity, and mid-winter melt all expected to increase as the climate warms (Thackeray et al. 2019, Scaff et al. 2024). Together, greater snowmelt and the reductions in the fraction of precipitation falling as snow are projected to globally result in shorter snow cover duration, less snow cover extent, and less overall snow mass (Derksen and Brown 2012, Thackeray et al. 2019, Pulliainen et al. 2020, Musselman et al. 2021). These dramatic geophysical changes will alter many components of life for winter-adapted wildlife. As species adjust behavior, habitat use, and overall distribution, species interactions will shift accordingly, with ecosystem-wide repercussions (Blois et al. 2013, Pecl et al. 2017, Penczykowski et al. 2017).

1.2 Goals

In this dissertation, I dig into the intersection of snow science and wildlife biology. My second chapter, entitled "Defining the danger zone: Critical snow properties for predator-prey interactions," used intensive winter fieldwork in Denali National Park, Alaska, and in two regions of Washington state to delineate the specific snow properties that matter most to a suite of eight species of large mammals. I focused on a principal metric of energy expenditure – sink depth, defined as how much an animal sinks into the snowpack with each step. This mechanistic link between morphology and physical properties of snow allows me to extrapolate how different types of snow tip the balance in predator-prey relationships. I conclude the second chapter by defining "danger zones," the specific ranges of snow density wherein predators (wolves [*Canis lupus*], coyotes [*C. latrans*], bobcats [*Lynx rufus*], and cougars [*Puma concolor*]) gain a movement advantage in comparison to ungulate prey (caribou [*Rangifer tarandus*], moose [*Alces alces*], mule deer [*Odocoileus hemionus*], and white-tailed deer [*O. virginianus*]).

My third chapter, "Apex predators exploit advantageous snow conditions across hunting modes," used movement ecology, physically-based snow modeling, and a ground-breaking GPS collar dataset from the Washington Predator-Prey Project to investigate how these theoretical danger zones play out on the landscape. I analyzed locations from five years of simultaneously collared cougars, wolves, mule deer, and white-tailed deer in two regions of Washington state, the Okanogan and Northeast study areas. Thanks to support from snow-savvy collaborators, I extracted daily, fine-resolution snow conditions and combined these with landscape covariates within a step-selection framework to compare the relative influence of each of these variables on predator movement. I found that the movements of both cougars and wolves are strongly shaped by snow, counter to prevailing wisdom that wolves are far more associated with snow due to their typical hunting mode of long-distance chases over open terrain. This robust statistical analysis underscores the role of danger zones as one of the more important factors driving predator distribution – certain snow conditions provide such a strong advantage that predators may temporarily disregard typical hunting preferences.

Next, I explore how mid-winter conditions shape specific aspects of large mammal movement ecology in my fourth chapter, entitled “Warm winters, hot moose: temperature drives activity and habitat trade-offs across a cold-adapted species’ range.” Because snow affects ungulate behavior as well as that of their predators, I dove into two main components of moose responses to environmental conditions in winter: behavioral and habitat-mediated thermoregulation. I used GPS collar data from five populations of moose across their latitudinal range, from Colorado to the Yukon Territory, Canada. With these data, I used hidden Markov models to delineate how temperature and snow influence moose activity changes, then used these results to analyze how temperature alters diurnal activity patterns and habitat selection via step-selection functions. I found that, when faced with unusually warm winter temperatures, moose across their range are more likely to remain sedentary, become more nocturnal and less diurnal, and forgo preferred foraging habitat for potential thermal refuge. These findings indicate that moose may already be at or near their thermal limit in southern populations, with minimal remaining adaptive capacity to respond to warming winters.

Finally, my fifth chapter – “Climate change diminishes snow-mediated movement advantage for apex predators” – explores the impact climate-change projections on danger zone across the same two study regions of Washington state (Okanogan and Northeast). Again through the guidance of snow- and supercomputer-experts, I generated five years of detailed physical snowpack data for two scenarios of climate change and compared these with five baseline years by extracting relevant snow properties across the study areas and within GPS-collared predator home ranges. I found that the extent and duration of snow conditions that provide predators an advantage over ungulate prey – “danger zones” – will dramatically decline, with the most pronounced declines in current predator home ranges. As species respond to changing snow conditions, my results indicate that ungulates stand to significantly benefit from future snowpacks, and, unless otherwise mitigated by range shifts or compensated by dramatically increased prey density, predators will suffer from the underlying geophysical changes in snow.

1.3 Implications

My dissertation has applications to a wide range of ecological theory and scientific frontiers. My overarching conclusion that snow conditions alter predator-prey interactions extends our understanding of how environmental factors mediate Lotka-Volterra models of predator-prey dynamics (Post et al. 1999) and are implicated in trophic cascades (McLaren and Peterson 1994). More specifically, I show that snow provides a hunting advantage that, in some conditions, outweighs other landscape characteristics for predators. Second, although diminishing snowpacks may have other benefits for herbivores related to improving forage opportunities, large ungulates may have limited capacity to respond to additional increases in temperature and thus face a thermoregulatory bottleneck. Thus, more frequent and severe midwinter warm spells (Tuel and Martius 2024) might render Bergmann's rule maladaptive (Ashton et al. 2000, Hoy et al. 2018), as larger-bodied mammals must contend with abrupt warm conditions amidst typically cold northern climates. Third, climate change may fundamentally reconfigure predator–prey relationships in snowy ecosystems. As hydrologists, wildlife biologists, natural resource managers, decision-makers, and winter enthusiasts alike grapple with our changing snowpacks, my dissertation outlines several key advances in our understanding of how snow shapes our world.

1.4 References

Ashton, K. G., Tracy, M. C. and de Quieroz, A. 2000. Is Bergmann's Rule Valid for Mammals? - The American Naturalist 156: 26.

Barnett, T. P., Adam, J. C. and Lettenmaier, D. P. 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. - Nature 438: 303–309.

Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C. and Finnegan, S. 2013. Climate Change and the Past, Present, and Future of Biotic Interactions. - Science 341: 499–504.

Boelman, N. T., Liston, G. E., Gurarie, E., Meddens, A. J. H., Mahoney, P. J., Kirchner, P. B., Bohrer, G., Brinkman, T. J., Cosgrove, C. L., Eitel, J. U. H., Hebblewhite, M., Kimball, J. S., LaPoint, S., Nolin, A. W., Pedersen, S. H., Prugh, L. R., Reinking, A. K. and Vierling, L. A. 2019. Integrating snow science and wildlife ecology in Arctic-boreal North America. - Environ. Res. Lett. 14: 010401.

Borg, B. L. and Schirokauer, D. W. 2022. The Role of Weather and Long-Term Prey Dynamics as Drivers of Wolf Population Dynamics in a Multi-Prey System. - Front. Ecol. Evol. 10: 791161.

Cunningham, C. X., Liston, G. E., Reinking, A. K., Boelman, N. T., Brinkman, T. J., Joly, K., Hebblewhite, M., Boutin, S., Czetwertynski, S., Sielecki, L. E. and Prugh, L. R. 2022. Human and animal movements combine with snow to increase moose-vehicle collisions in winter. - Environ. Res. Lett. 17: 125007.

Derksen, C. and Brown, R. 2012. Spring snow cover extent reductions in the 2008-2012 period exceeding climate model projections: SPRING SNOW COVER EXTENT REDUCTIONS. - Geophys. Res. Lett. 39: n/a-n/a.

Durner, G. M., Amstrup, S. C. and Fischbach, A. S. 2003. Habitat Characteristics of Polar Bear Terrestrial Maternal Den Sites in Northern Alaska. - ARCTIC 56: 55–62.

Gergel, D. R., Nijssen, B., Abatzoglou, J. T., Lettenmaier, D. P. and Stumbaugh, M. R. 2017. Effects of climate change on snowpack and fire potential in the western USA. - Climatic Change 141: 287–299.

Glass, T. W., Breed, G. A., Liston, G. E., Reinking, A. K., Robards, M. D. and Kielland, K. 2021. Spatiotemporally variable snow properties drive habitat use of an Arctic mesopredator. - Oecologia 195: 887–899.

Hansen, B. B., Aanes, R., Herfindal, I., Kohler, J. and Sæther, B.-E. 2011. Climate, icing, and wild arctic reindeer: past relationships and future prospects. - Ecology 92: 1917–1923.

Hansen, B. B., Grøtan, V., Aanes, R., Sæther, B.-E., Stien, A., Fuglei, E., Ims, R. A., Yoccoz, N. G. and Pedersen, Å. Ø. 2013. Climate Events Synchronize the Dynamics of a Resident Vertebrate Community in the High Arctic. - Science 339: 313–315.

Horne, J. S., Hurley, M. A., White, C. G. and Rachael, J. 2019. Effects of wolf pack size and winter conditions on elk mortality. - Jour. Wild. Mgmt. 83: 1103–1116.

Hoy, S. R., Peterson, R. O. and Vucetich, J. A. 2018. Climate warming is associated with smaller body size and shorter lifespans in moose near their southern range limit. - Global Change Biology 24: 2488–2497.

Immerzeel, W. W., Lutz, A. F., Andrade, M., Bahl, A., Biemans, H., Bolch, T., Hyde, S., Brumby, S., Davies, B. J., Elmore, A. C., Emmer, A., Feng, M., Fernández, A., Haritashya, U., Kargel, J. S., Koppes, M., Kraaijenbrink, P. D. A., Kulkarni, A. V., Mayewski, P. A., Nepal, S., Pacheco, P., Painter, T. H., Pellicciotti, F., Rajaram, H., Rupper, S., Sinisalo, A., Shrestha, A. B., Viviroli, D., Wada, Y., Xiao, C., Yao, T. and Baillie, J. E. M. 2020. Importance and vulnerability of the world's water towers. - Nature 577: 364–369.

Johnston, J., Jacobs, J. M. and Cho, E. 2023. Global Snow Seasonality Regimes from Satellite Records of Snow Cover. - Journal of Hydrometeorology in press.

Mahoney, P. J., Liston, G. E., LaPoint, S., Gurarie, E., Mangipane, B., Wells, A. G., Brinkman, T. J., Eitel, J. U. H., Hebblewhite, M., Nolin, A. W., Boelman, N. and Prugh, L. R. 2018. Navigating snowscapes: scale-dependent responses of mountain sheep to snowpack properties. - Ecol Appl 28: 1715–1729.

McLaren, B. E. and Peterson, R. O. 1994. Wolves, Moose, and Tree Rings on Isle Royale. - Science 266: 1555–1558.

Mech, L. D., McRoberts, R. E., Peterson, R. O. and Page, R. E. 1987. Relationship of Deer and Moose Populations to Previous Winters' Snow. - The Journal of Animal Ecology 56: 615.

Murray, D. L. and Boutin, S. 1991. The influence of snow on lynx and coyote movements: does morphology affect behavior? - Oecologia 88: 463–469.

Musselman, K. N., Addor, N., Vano, J. A. and Molotch, N. P. 2021. Winter melt trends portend widespread declines in snow water resources. - Nat. Clim. Chang. 11: 418–424.

Ortega, A. C., Merkle, J. A., Sawyer, H., Monteith, K. L., Lionberger, P., Valdez, M. and Kauffman, M. J. 2024. A test of the frost wave hypothesis in a temperate ungulate. - Ecology: e4238.

Parker, K. L., Robbins, C. T. and Hanley, T. A. 1984. Energy Expenditures for Locomotion by Mule Deer and Elk. - The Journal of Wildlife Management 48: 474.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia,

R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., Lenoir, J., Linnetved, H. I., Martin, V. Y., McCormack, P. C., McDonald, J., Mitchell, N. J., Mustonen, T., Pandolfi, J. M., Pettorelli, N., Popova, E., Robinson, S. A., Scheffers, B. R., Shaw, J. D., Sorte, C. J. B., Strugnell, J. M., Sunday, J. M., Tuanmu, M.-N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E. and Williams, S. E. 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. - Science 355: eaai9214.

Pedersen, S. H., Bentzen, T. W., Reinking, A. K., Liston, G. E., Elder, K., Lenart, E. A., Prichard, A. K. and Welker, J. M. 2021. Quantifying effects of snow depth on caribou winter range selection and movement in Arctic Alaska. - Mov Ecol 9: 48.

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.

Poirier, M., Gauthier, G., Domine, F. and Fauteux, D. 2023. Lemming winter habitat: the quest for warm and soft snow. - Oecologia 202: 211–225.

Post, E., Peterson, R. O., Stenseth, N. Chr. and McLaren, B. E. 1999. Ecosystem consequences of wolf behavioural response to climate. - Nature 401: 905–907.

Prugh, L. R., Lundquist, J. D., Sullender, B. K., Cunningham, C. X., Dechow, J., Borg, B. L., Sousanes, P. J., Stehn, S. and Durand, M. T. 2024. Landscape heterogeneity buffers the impact of an extreme weather event on wildlife. - Commun Biol 7: 1515.

Pulliainen, J., Luojus, K., Derksen, C., Mudryk, L., Lemmetyinen, J., Salminen, M., Ikonen, J., Takala, M., Cohen, J., Smolander, T. and Norberg, J. 2020. Patterns and trends of Northern Hemisphere snow mass from 1980 to 2018. - Nature 581: 294–298.

Rantanen, M., Karpechko, A. Yu., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T. and Laaksonen, A. 2022. The Arctic has warmed nearly four times faster than the globe since 1979. - Commun Earth Environ 3: 168.

Reinking, A. K., Højlund Pedersen, S., Elder, K., Boelman, N. T., Glass, T. W., Oates, B. A., Bergen, S., Roberts, S., Prugh, L. R., Brinkman, T. J., Coughenour, M. B., Feltner, J. A., Barker, K. J., Bentzen, T. W., Pedersen, Å. Ø., Schmidt, N. M. and Liston, G. E. 2022. Collaborative wildlife–snow science: Integrating wildlife and snow expertise to improve research and management. - Ecosphere in press.

Scaff, L., Krogh, S. A., Musselman, K., Harpold, A., Li, Y., Lillo-Saavedra, M., Oyarzún, R. and Rasmussen, R. 2024. The Impacts of Changing Winter Warm Spells on Snow Ablation Over Western North America. - Water Resources Research 60: e2023WR034492.

Stien, A., Loe, L. E., Mysterud, A., Severinsen, T., Kohler, J. and Langvatn, R. 2010. Icing events trigger range displacement in a high-arctic ungulate. - Ecology 91: 915–920.

Thackeray, C. W., Derksen, C., Fletcher, C. G. and Hall, A. 2019. Snow and Climate: Feedbacks, Drivers, and Indices of Change. - Curr Clim Change Rep 5: 322–333.

Tuel, A. and Martius, O. 2024. Persistent warm and cold spells in the Northern Hemisphere extratropics: regionalisation, synoptic-scale dynamics and temperature budget. - Weather Clim. Dynam. 5: 263–292.

van de Kerk, M., Verbyla, D., Nolin, A. W., Sivy, K. J. and Prugh, L. R. 2018. Range-wide variation in the effect of spring snow phenology on Dall sheep population dynamics. - Environ. Res. Lett. 13: 075008.

Van de Kerk, M., Arthur, S., Bertram, M., Borg, B., Herriges, J., Lawler, J., Mangipane, B., Lambert Koizumi, C., Wendling, B. and Prugh, L. 2020. Environmental Influences on Dall's Sheep Survival. - Jour. Wild. Mgmt. 84: 1127–1138.

Wilson, R. R. and Durner, G. M. 2020. Seismic Survey Design and Effects on Maternal Polar Bear Dens. - Jour. Wild. Mgmt. 84: 201–212.

CHAPTER 2: DEFINING THE DANGER ZONE: CRITICAL SNOW PROPERTIES FOR PREDATOR-PREY INTERACTIONS

Publication history: A version of this chapter was previously published in *Oikos*. The full citation for this publication is:

> Sullender B.K., C.X. Cunningham, J.D. Lundquist, and L.R. Prugh. 2023. Defining the danger zone: critical snow properties for predator–prey interactions. *Oikos* 2023:e09925. https://doi.org/10.1111/oik.09925.

2.1 Abstract

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.

2.2 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 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 2019). Snow cover duration (Brown & Mote 2009), autumn and spring extent (Derksen & 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 & 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), 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 & Mech 1986), understanding predation success rates (Post et al. 1999; Horne et al. 2019), and modeling movement patterns (Droghini & 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 & 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 & Peterson 2003), which is calculated by dividing an animal's body mass by the surface area of all four feet (Telfer & 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 & Kelsall 1984; Murray & Boutin 1991; Murray & Lariviere 2002; Mech & 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 & 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 & Colbeck 1995; Pielmeier & 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 & 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 & 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 1974; Nelson & Mech 1986), the presence of ice layers (Murie 1944; Stein et al. 2010; Leblond et al. 2016), density (Fancy & White 1987; Sivy et al. 2018), and hardness (Bunnell et al. 1990; Droghini & 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 (Riseth et al. 2011; Takeuchi et al. 1998), 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 & 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 & 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 Sivy et al. (2018) and Bunnell et al. (1990) found, and surface penetrability would best predict sink depth for the 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 & 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 & 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.

2.3 Methods

2.3.1 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; Figure 2.1). Our study areas include portions of all six global snow classes per Sturm & 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°C) and nighttime temperatures below freezing (beginning approximately Feb 20, 2021 and Feb 28, 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 Jan 23-25 and Feb 24-25, 2022 (maximum wind speeds of 27 and 28.5 m/s, respectively; NEON 2022).

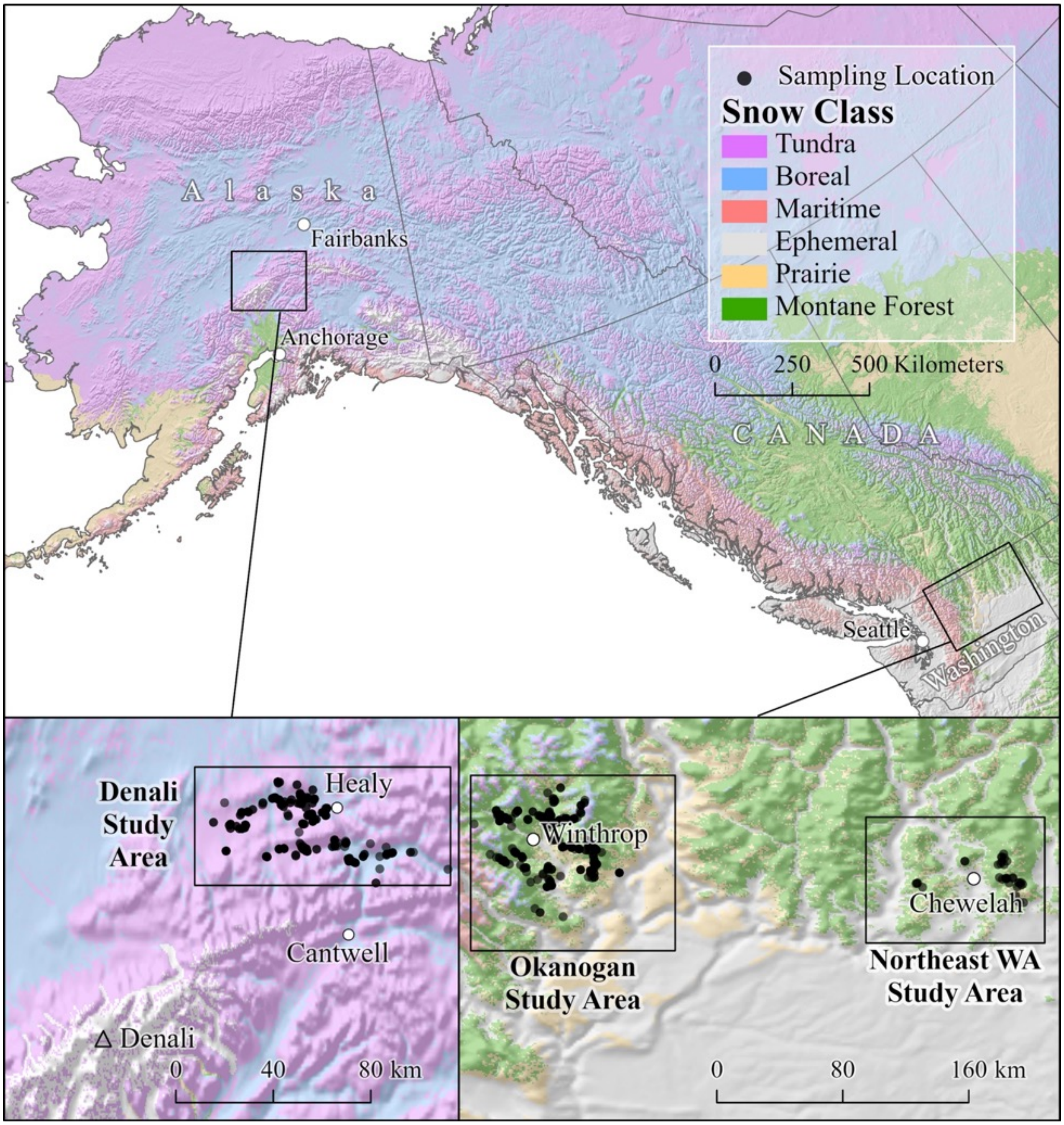

Figure 2.1. Study areas. The Denali study area in interior Alaska is comprised mostly of tundra and boreal snow. The Okanogan study area in Washington is diverse but is mostly comprised of montane forest. Other Okanogan snow classes are prairie and ephemeral, with some maritime on the western extremes 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.

2.3.2 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, landcover, 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 (less than one year old) averaged 10.4 cm wide by 10.6 cm long, whereas tracks of known adults (greater than one 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.

2.3.3 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 (Figure 2.2). 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 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 & 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 cm x 10 cm x 20 cm, and took two replicates at each of three depth classes: 0-10 cm, 10-20 cm, 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 near-surface density is a better predictor of sink depth than overall density throughout the snow column (Bunnell at el. 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 (Appendix A), 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 x 4.2 cm height) from a height of 50 cm above the snow surface and then measuring its sink depth (Figure 2.2B). 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 & Boutin 1991, Kolbe et al. 2007, Pozzanghera et al. 2016, Droghini & Boutin 2018b, and Peers et al. 2020).

We also measured hand-hardness, a key component of a snowpack's stratigraphy (Kinar & 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, 4 fingers, 1 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 50cm 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.

Figure 2.2. 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.

2.3.4 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 less than 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; R Core Team 2022).

2.3.5 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 & 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.

2.3.6 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 & 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 & Lesperance 2003). We used the *segmented* package in R (Muggeo 2017; R Core Team 2022) to generate breakpoints, retrieve corrected AIC values (AIC_c; Anderson & 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 less than 2, we considered these models as having equivalent support (Anderson & 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.

2.3.7 Peak Danger Zones

A threshold of support is important for determining the critical snow property that supports 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 a coyote (Crête & Larivière 2003). The key factor in how much movement is altered is how deep the animal sinks relative to its size (Parker et al. 1984; Murray & 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 & Janis 1991). Furthermore, hind leg length is a widely available measurement for diverse species (Garland & Janis 1991; Kilbourne & 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 2.1), 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 ≤ 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).

2.4 Results

We measured a total of 707 sets of mammal tracks in Denali (*n* = 296), Northeast Washington (*n* = 35), and Okanogan (*n* = 376; Table 2.1). 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; moose = 36.4 cm) than species with lower foot loads (coyotes = 7.7 cm; wolves = 9.7 cm). Most observed animal tracks were less than 30cm deep (553/706 = 78%), supporting our decision to limit density measurements to the upper 30cm. Due to few observations, we were unable to analyze snow property-track relationships for Dall sheep (*n* = 6). Snow properties varied widely (Table 2.2), 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 (Appendix A).

2.4.1 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 2.2). 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 2.2). 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 (4.8cm; Table 2.1). 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.

2.4.2 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 2.2).

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 (Appendix A). With some variation at low densities (<150 kg/m^3), moose sank deeper for a given snow density in Washington compared to Alaska (Figure 2.3; Appendix A). 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 (Figure 2.3; Appendix A).

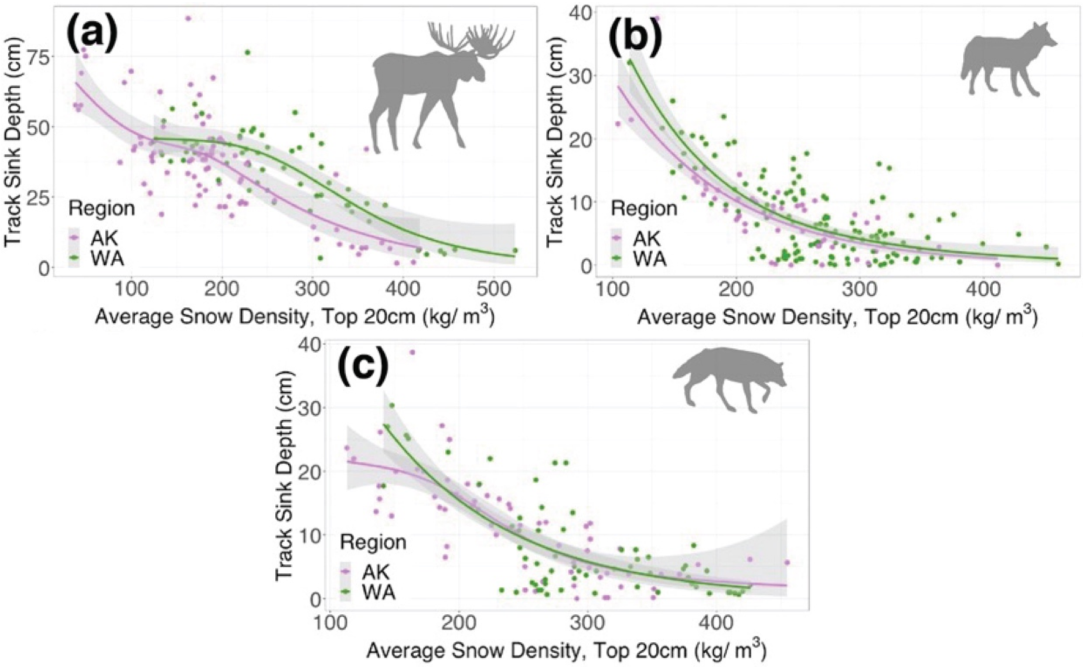

Figure 2.3. Regional differences in sink depth-snow density relationships for (a) moose, (b) coyotes, and (c) wolves. Fitted lines and 95% confidence intervals (grey bands) from generalized additive models with region as an interaction term (Alaska = purple; Washington = green) are shown. The relationship between sink depth and snow density (0-20cm; *AvgDens0-20*) varied by region for moose but not did vary for coyotes or wolves. Full regional analysis results are shown in Appendix A.

2.4.3 Thresholds of Support

Segmented linear models provided a similar representation of snow-sink depth relationships as the more flexible GAMs for all species (Figure 2.4). The best performing model included a breakpoint at 280 kg/m^3 (95% CI: 240-330 kg/m^3) for bobcats, 310 kg/m^3 (95% CI: 280-350 kg/m^3) for cougars, 220 kg/m^3 (95% CI: 200-230 kg/m^3) for coyotes, and 270 kg/m^3 (95% CI: 240-300 kg/m^3) for wolves (Table 2.3). At light snow densities (<200 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: 280-430 kg/m^3) for caribou, 300 kg/m^3 (95% CI: 240-370 kg/m^3) for deer, and 360 kg/m^3 (95% CI: 280-450 kg/m^3) for juvenile moose. Sink depths for adult moose were best predicted by an unmodified linear model of *AvgDens0-20* (Table 2.3). 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 (Figure 2.4). 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: 380-450 kg/m^3), which corresponded to an inflection point in the GAM curve (Figure 2.4G).

Table 2.1. 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: [a] Kilbourne & Hoffman (2013); [b] Garland & Janis (1993); [c] Lankester et al. (1993) (33-week-old moose calf); [d] Telfer & Kelsall (1984); [e] Murray & Lariviere (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 (*O. virginianus*)[b]; 78.2 (*O. hemionus*)[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]

Table 2.2. Evaluation of snow variables as predictors of sink depths for seven mammal species. Pseudo-R2 values (proportion of deviance explained) from univariate generalized additive models are shown. *AvgDens* = snow surface density; *IceTop* = presence of ice layers; *AvgHH* = thickness-weighted hand-hardness average; *AvgTuna* = sink depth of cylindrical penetrometer; *TotalIce* = cumulative ice thickness. We measured snow properties at multiple depth horizons (in 10cm increments) for some variables. 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	Bobcat	Caribou	Cougar	Coyote	Deer	Moose-Adult	Moose-Juvenile	Wolf	All Species
AvgDens0-10	23-502	**0.30**	**0.77***	0.29	0.18	0.29	0.43	**0.85***	**0.44**	0.51
AvgDens0-20	38-523	0.29	0.77	0.30	**0.20**	0.33	**0.57***	0.80	0.35	**0.51***
AvgDens0-30	60-516	0.27	0.77	**0.33**	0.17	**0.33***	0.52	0.82	0.30	0.49
IceTop10	0-1	**0.11**	**0.19**	0.13	0.01	0.06	0.06	0.28	**0.14**	**0.33**
IceTop20	0-1	0.04	0.15	0.15	0.01	0.07	**0.10**	**0.36**	0.05	0.31
IceTop30	0-1	0.01	0.18	**0.18**	**0.01**	**0.15**	0.09	0.26	0.02	0.31
IceTop40	0-1	0.01	0.08	0.15	0.00	**0.15**	0.10	0.33	0.01	0.30
IceTop50	0-1	0.00	0.07	0.15	0.00	**0.15**	0.03	0.27	0.01	0.30
AvgHH0-10	1-5	0.24	0.64	0.34	**0.13**	0.28	0.20	0.58	**0.44***	**0.47**
AvgHH0-20	1-4.95	0.19	**0.70**	**0.37***	0.12	**0.29**	0.35	**0.76**	0.35	0.47
AvgHH0-30	1-4.97	0.18	0.67	0.25	0.06	0.24	0.34	0.57	0.26	0.43
AvgHH0-40	1-4.81	**0.25**	0.61	0.20	0.05	0.22	**0.37**	0.61	0.21	0.42
AvgHH0-50	1-4.81	0.23	0.47	0.17	0.05	0.18	0.36	0.59	0.20	0.40
AvgTuna	0-31.3	0.34*	0.62	0.28	0.23*	0.30	0.16	0.83	0.41	0.50
TotalIce10	0-10	**0.17**	**0.21**	**0.21**	0.02	0.07	0.13	**0.54**	**0.14**	**0.35**
TotalIce20	0-19	0.14	0.17	0.13	0.03	0.07	0.24	0.54	0.11	0.35
TotalIce30	0-29	0.05	0.19	0.16	0.03	0.10	0.22	0.54	0.10	0.34
TotalIce40	0-29	0.07	0.15	0.16	0.03	**0.14**	**0.24**	0.39	0.08	0.35
TotalIce50	0-31	0.05	0.14	0.16	**0.05**	0.14	0.18	0.39	0.05	0.34

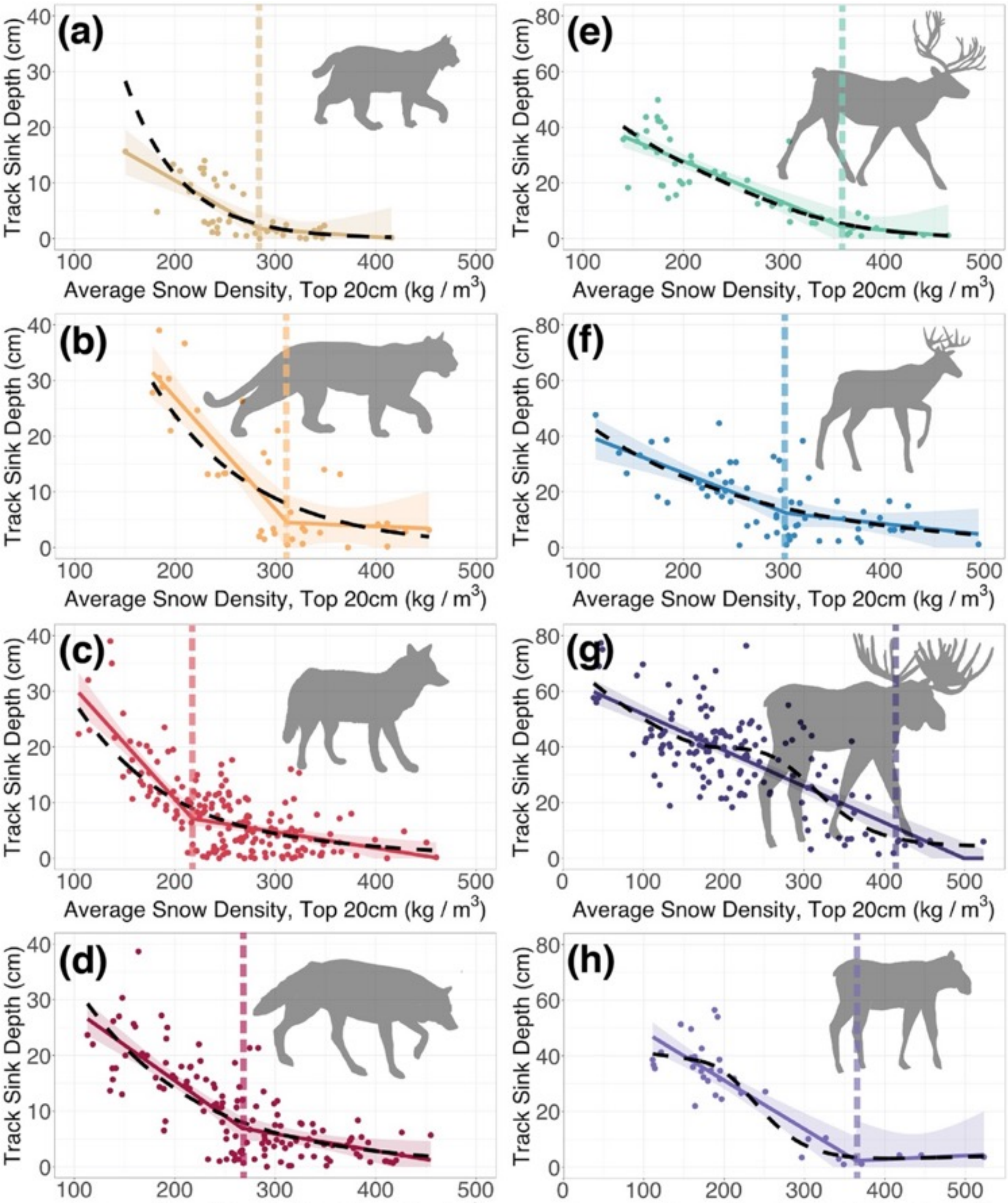

Figure 2.4. Comparison of segmented linear regression (solid lines), generalized additive models (dashed lines), and thresholds of support (vertical dashed lines) for sink depth-snow density relationships for (a) bobcats, (b) cougars, (c) coyotes, (d) wolves, (e) caribou, (f) deer, (g) adult

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.

2.4.4 Peak Danger Zones

All ungulate species had identifiable danger zones (Figure 2.5), 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 2.4). Caribou had the lowest danger peaks, sinking only 6% deeper than wolves, in relative terms, at 200 kg/m^3 (Figure 2.5). In contrast, all sampled snow densities (110-460 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 (200-450 kg/m^3) and wolves (140-460 kg/m^3). Most sampled snow densities represented danger zones for juvenile moose (Table 2.4), although at narrow, moderate-density ranges juvenile moose gained a slight movement advantage over cougars (300-390 kg/m^3) and wolves (340-380 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 2.4).

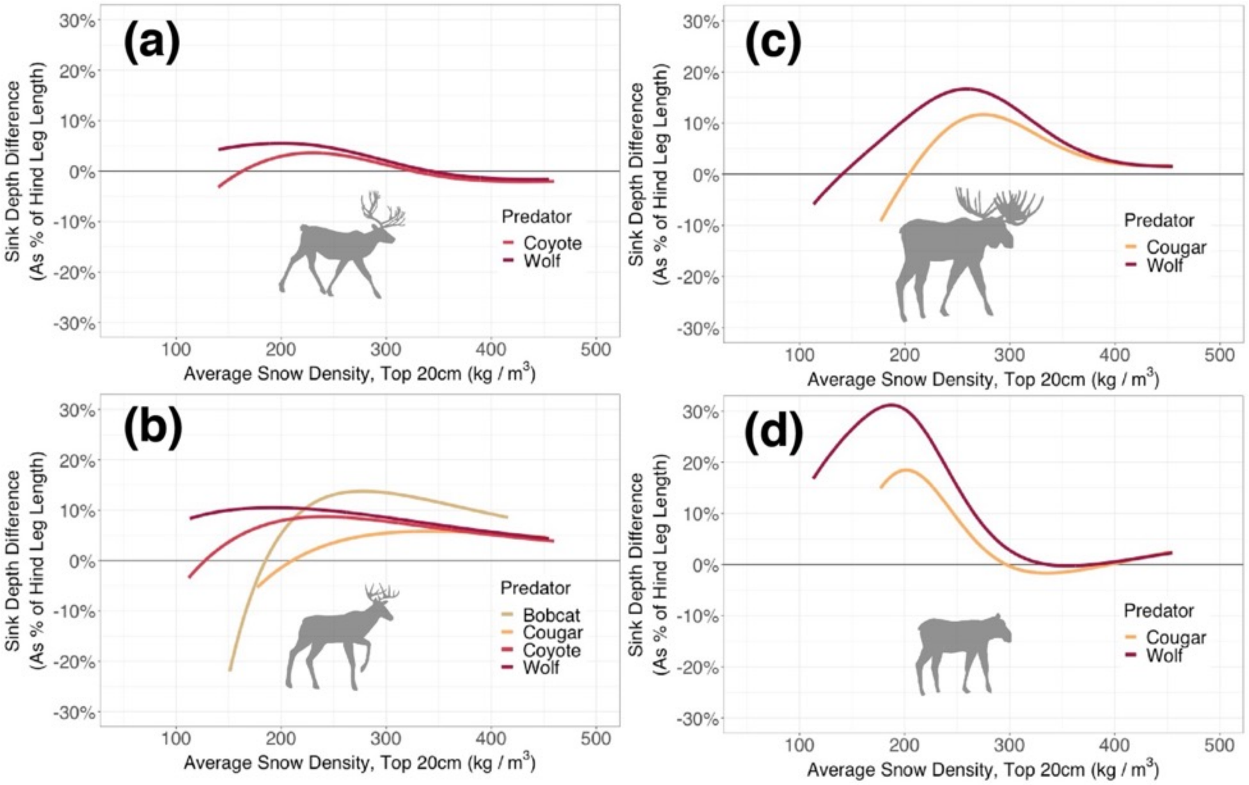

Figure 2.5. Peak danger zones for (a) caribou, (b) deer, (c) adult moose, and (d) juvenile moose relative to sympatric predators. The y-axis represents the difference between prey and predator sinking depth, calculated relative to hind leg length (see Table 2.1). Positive values represent snow densities 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.

Table 2.3. Model selection for breakpoint regression model predicting animal sink depths using average near-surface (0-20cm) snow density. We determined support for model type (ie, 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 ($\Delta \text{AIC}_c > 2$) than the other, we selected that as the best fitting model. If the change in AIC_c was less than 2 between the segmented and linear models ($\Delta \text{AIC}_c < 2$), 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

Table 2.3. Continued.

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)
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

Table 2.4. Danger zones for caribou, deer, and moose. Danger zones are defined as near-surface (0-20cm) 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.

	Bobcat		**Cougar**		**Coyote**		**Wolf**	
Prey Species	Danger Zone Range (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)	Danger Zone Range (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	160-330	4% (-3-11%); 230	140-340	6% (-3-14%); 200
Deer	190-420	14% (9-18%); 280	210-450	6% (1-10%); 340	130-460	9% (3-15%); 240	110-460	11% (0-22%); 190
Moose-Adult	NA	NA	200-450	12% (4-19%); 280	NA	NA	140-460	17% (11-22%); 260
Moose-Juvenile	NA	NA	180-300; 390-450	18% (-5-39%); 200	NA	NA	110-340; 380-460	31% (18-45%); 190

2.5 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 (Dailey & Hobbs 1989; Fancy & White 1987; Crête & Larivière 2003). Thresholds of support varied among species largely as expected based on foot loading, with surprisingly similar relationships across our 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. 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

& 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 & 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 ambushers (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 (Figure 2.5; Table 2.4). 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 densities, whereas cougars did not have a mobility advantage until 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 (Figure 2.5; Table 2.4). 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 & Boutin 1991; Lingle 2002; Kolbe et al. 2007; Droghini & Boutin 2017), 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 & 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 2.2), was the second-best overall predictor, and can be used as a proxy for our best predictor (*AvgDens0-20*; Appendix A). 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 in an extended field campaign. We join a number of other studies finding similar penetrometers effective for wildlife applications (Murray & 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 & Mech 1986; Murray & Boutin 1991; Pedersen et al. 2021; Borg & 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 & 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 Alaska for intermediate snow densities (Figure 2.2). Furthermore, we found that track dimensions for coyotes, moose, and wolves were larger in Alaska than in Washington (Appendix A), 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 (Appendix A) 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 & 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 & Hall 2012), increased mid-winter melting (Musselman et al. 2021), decreased spatial coverage (Pulliainen et al. 2020), and shorter winters (Derksen & 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.

2.6 References

Anderson, D. R. and Burnham, K. P. 2002. Avoiding Pitfalls When Using Information-Theoretic Methods. - J. Wildl. Manage. 66: 912.

Arons, E. M. and Colbeck, S. C. 1995. Geometry of heat and mass transfer in dry snow: A review of theory and experiment. - Rev. Geophys. 33: 463.

Ashton, K. G., Tracy, M. C. and de Quieroz, A. 2000. Is Bergmann's Rule Valid for Mammals? - Am. Nat. 156: 26.

Bailey, I. Myatt, J. P. and Wilson, A. M. 2013. Group hunting within the Carnivora: physiological, cognitive and environmental influences on strategy and cooperation. - Behav. Ecol. Sociobiol. 67: 1–17.

Benson, J. F., Loveless, K. M., Rutledge, L. Y. and Patterson, B. R. 2017. Ungulate predation and ecological roles of wolves and coyotes in eastern North America. - Ecol. Appl. 27: 718–733.

Bergman, E. J., Garrott, R. A., Creel, S., Borkowksi, J. J., Jaffe, R. and Watson, F. G. R. 2006. Assessment Of Prey Vulnerability Through Analysis Of Wolf Movements And Kill Sites. - Ecol. Appl. 16: 273–284.

Bieniek, P. A., Bhatt, U. S., Wlash, J. E., Lader, R., Griffith, B., Roach, J. K. and Thoman, R. L. 2018. Assessment of Alaska Rain-on-Snow Events Using Dynamical Downscaling. – J. Appl. Meteorol. Climatol. 57: 1847–1863.

Boelman, N. T., Liston, G. E., Gurarie, E., Meddens, A. J. H., Mahoney, P. J., Kirchner, P. B., Bohrer, G., Brinkman, T. J., Cosgrove, C. L., Eitel, J. U. H., Hebblewhite, M., Kimball, J. S., LaPoint, S., Nolin, A. W., Pedersen, S. H., Prugh, L. R., Reinking, A. K. and Vierling, L. A. 2019. Integrating snow science and wildlife ecology in Arctic-boreal North America. - Environ. Res. Lett. 14: 010401.

Borg, B. L. and Schirokauer, D. W. 2022. The Role of Weather and Long-Term Prey Dynamics as Drivers of Wolf Population Dynamics in a Multi-Prey System. - Front. Ecol. Evol. 10: 791161.

Bormann, K. J., Westra, S., Evans, J. P. and McCabe, M. F. 2013. Spatial and temporal variability in seasonal snow density. – J. Hydrol. 484: 63–73.

Brown, R. D. and Mote, P. W. 2009. The Response of Northern Hemisphere Snow Cover to a Changing Climate. - J. Climate 22: 2124–2145.

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: 917–922.

Coady, J. W. 1973. Influence of snow on behavior of moose. - Proc. Intl. Sym. Moose Ecol. 101: 417–436.

Crête, M. and Larivière, S. 2003. Estimating the costs of locomotion in snow for coyotes. - Can. J. Zool. 81: 1808–1814.

Cunningham, C. X., Liston, G. E., Reinking, A. K., Boelman, N. T., Brinkman, T. J., Joly, K., Hebblewhite, M., Boutin, S., Czetwertynski, S., Sielecki, L .E and Prugh, L. R. 2022. Human and animal movements combine with snow to increase moose-vehicle collisions in winter. - Environ. Res. Lett. 17: 125007.

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: 2368–2375.

Dellinger, J. A., Shores, C. R., Craig, A., Heithaus, M. R., Ripple, W. J. and Wirsing A. J. 2019. Habitat use of sympatric prey suggests divergent anti-predator responses to recolonizing gray wolves. - Oecologia 189: 487–500.

Derksen, C. and Brown, R. 2012. Spring snow cover extent reductions in the 2008-2012 period exceeding climate model projections. - Geophys. Res. Lett. 39: L19504.

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

Droghini, A. and Boutin, S. 2018b. The calm during the storm: Snowfall events decrease the movement rates of grey wolves (*Canis lupus*) - PLoS ONE 13: e0205742.

Fancy, S. G. and White, R. G. 1987. Energy expenditures for locomotion by barren-ground caribou. - Can. J. Zool. 65: 122–128.

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 Technical Documents in Hydrology N°83, IACS Contribution N°1, UNESCO-IHP, Paris.

Ganz, T. R., DeVivo, M. T., Kertson, B. N., Roussin, T., Satterfield, L., Wirsing, A. J. and Prugh, L. R. 2022. Interactive effects of wildfires, season and predator activity shape mule deer movements. - J. Anim. Ecol. 91: 2273–2288.

Garland, T. and Janis, C. M. 1993. Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? - J. Zool. 229: 133–151.

Geldsetzer, T. and Jamieson, J. B. 2000. Estimating dry snow density from grain form and hand hardness. - Proc. Intl. Snow Sci. Workshop 1: 121-127.

Gergel, D. R., Nijssen, B., Abatzoglou, J. T., Lettenmaier, D. P. and Stumbaugh, M. R. 2017. Effects of climate change on snowpack and fire potential in the western USA. - Climatic Change 141: 287–299.

Gittleman, J. L. 1985. Carnivore body size: Ecological and taxonomic correlates. - Oecologia 67: 540–554.

Gurarie, E., Hebblewhite, M., Joly, K., Kelly, A. P., Adamczewski, J., Davidson, S. C., Davison, T., Gunn, A., Suitor, M. J., Fagan, W. F. and Boelman, N. 2019. Tactical departures and strategic arrivals: Divergent effects of climate and weather on caribou spring migrations. - Ecosphere 10: e02971.

Hansen, B. B., Aanes, R., Herfindal, I., Kohler, J. and Saether, B. 2011. Climate, icing, and wild arctic reindeer: past relationships and future prospects. - Ecology 92: 1917–1923.

Herfindal, I., Solberg, E. J., Saether, B., Høgda, K. A. and Andersen R. 2006. Environmental phenology and geographical gradients in moose body mass. - Oecologia 150: 213–224.

Horne, J. S., Hurley, M. A., White, C. G. and Rachael, J. 2019. Effects of wolf pack size and winter conditions on elk mortality. – J. Wildl. Manage. 83: 1103–1116.

IPCC 2022. The Ocean and Cryosphere in a Changing Climate: Special Report of the Intergovernmental Panel on Climate Change. - Cambridge University Press.

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B., Selva, N., Zub, K. and Szymura, L. 2002. Kill rates and predation by wolves on ungulate populations in Bialowieza Primeval Forest (Poland). - Ecology 83: 1341–1356.

Kilbourne, B. M. and Hoffman, L. C. 2013. Scale Effects between Body Size and Limb Design in Quadrupedal Mammals. - PLoS ONE 8: e78392.

Kinar, N. J. and Pomeroy, J. W. 2015. Measurement of the physical properties of the snowpack: Measurement of snowpack. - Rev. Geophys. 53: 481–544.

Kolbe, J. A., Squires, J. R., Pletscher, D. H. and Ruggiero, L. F. 2007. The Effect of Snowmobile Trails on Coyote Movements Within Lynx Home Ranges. - J. Wildl. Manage. 71: 1409–1418.

Lankester, M. W., Wheeler-Smith, T. and Dudzinski, S. 1993. Care, growth and cost of captive moose calves. - Alces 29:249-262.

Leblond, M., St-Laurent, M. and Côté, S. D. 2016. Caribou, water, and ice – fine-scale movements of a migratory arctic ungulate in the context of climate change. - Mov. Ecol. 4: 14.

Lingle, S. 2002. Coyote predation and habitat segregation of white-tailed deer and mule deer. - Ecology 83: 2037–2048.

Liston, G. E. and Elder, K. 2006. A Distributed Snow-Evolution Modeling System (SnowModel). – J. Hydromet. 7: 1259–1276.

Mahoney, P. J., Liston, G. E., LaPoint, S., Gurarie, E., Mangipane, B., Wells, A. G., Brinkman, T. J., Eitel, J. U. H., Hebblewhite, M., Nolin, A. W., Boelman, N. and Prugh, L. R. 2018. Navigating snowscapes: scale-dependent responses of mountain sheep to snowpack properties. – Ecol. Appl. 28: 1715–1729.

Makin, D. F., Chamaillé-Jammes, S. and Shrader, A. M. 2017. Herbivores employ a suite of antipredator behaviours to minimize risk from ambush and cursorial predators. - Anim. Behav. 127: 225–231.

Mech, L. D. and Peterson, R. O. 2003. Wolf-Prey Relations. - In: Mech, L. D. and Boitani, L. (eds), Wolves: Behavior, Ecology, and Conservation. Univ. Chicago Press, pp.131-161.

Meiri, S. et al. 2007. What determines conformity to Bergmann's rule? - Global Ecol. Biogeogr. 16: 788–794.

Moskowitz, D. 2010. *Wildlife of the Pacific Northwest*. - Timber Press.

Muggeo, V. M. R. 2017. Interval estimation for the breakpoint in segmented regression: a smoothed score-based approach. - Aust. N. Z. J. Stat. 59: 311–322.

Murie, A. 1944. *The Wolves of Mount McKinley*. - US Govt. Printing Office.

Murray, D. L. and Boutin, S. 1991. The influence of snow on lynx and coyote movements: does morphology affect behavior? - Oecologia 88: 463–469.

Murray, D. L. and Larivière, S. 2002. The relationship between foot size of wild canids and regional snow conditions: evidence for selection against a high footload? – J. Zool. 256: 289–299.

Musselman, K. N., Addor, N., Vano, J. A. and Molotch, N. P. 2021. Winter melt trends portend widespread declines in snow water resources. - Nat. Clim. Change 11: 418–424.

Nelson, M. E. and Mech, L. D. 1986. Relationship between Snow Depth and Gray Wolf Predation on White-Tailed Deer. - J. Wildl. Manage. 50: 471.

Newbury, R. K. 2013. Behavioral ecology of the bobcat in a region with deep winter snows. - PhD thesis, University of British Columbia (Okanagan), Canada.

Niittynen, P., Heikkinen, R. and Luoto, M. 2018. Snow cover is a neglected driver of Arctic biodiversity loss. - Nat. Clim. Change 8: 997–1001.

Nolin, A. W. and Daly, C. 2006. Mapping "At Risk" Snow in the Pacific Northwest. – J. Hydromet. 7: 1164–1171.

Pan, C. G., Kirchner, P. B., Kimball, J. S., Kim, Y. and Du, J. 2018. Rain-on-snow events in Alaska, their frequency and distribution from satellite observations. - Environ. Res. Lett. 13: 075004.

Parker, K. L., Robbins, C. T. and Hanley, T. A.1984. Energy Expenditures for Locomotion by Mule Deer and Elk. - J. Wild. Manage. 48: 474.

Pedersen, S. H., Bentzen, T. W., Reinking, A. K., Liston, G. E., Elder, K., Lenart, E. A., Prichard, A. K. and Welker, J. M. 2021. Quantifying effects of snow depth on caribou winter range selection and movement in Arctic Alaska. - Mov. Ecol. 9: 48.

Peers, M. J. L., Majchrzak, Y. N., Menzies, A. K., Studd, E. K., Bastille-Rousseau, G., Boonstra, R., Humphries, M., Jung, T. S., Kenney, A. J., Krebs, C. J., Murray, D. L. and Boutin, S. 2020. Climate change increases predation risk for a keystone species of the boreal forest. - Nat. Clim. Change. 10: 1149–1153.

Peterson, R. O. et al. 1984. Wolves of the Kenai Peninsula, Alaska. - Wildlife Monographs 88: 3–52.

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 Regions Sci. Tech. 37: 393–405.

Pontzer, H. 2007. Effective limb length and the scaling of locomotor cost in terrestrial animals. - J. Exp. Biol. 210: 1752–1761.

Post, E., Peterson, R. O., Stenseth, N. C. and McLaren, B. E. 1999. Ecosystem consequences of wolf behavioural response to climate. - Nature 401: 905–907.

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: 697–705.

Pulliainen, J., Luojus, K., Derksen, C., Mudryk, L., Lemmetyinen, J., Salminen, M., Ikonen, J., Takala, M., Cohen, J., Smolander, T. and Norberg, J. 2020. Patterns and trends of Northern Hemisphere snow mass from 1980 to 2018. - Nature 581: 294–298.

Rattenbury, K. L., Schmidt, J. H., Swanson, D. K., Borg, B. L., Mangipane, B. A. and Sousanes, P. J. 2018. Delayed spring onset drives declines in abundance and recruitment in a mountain ungulate. - Ecosphere 9: e02513.

Reinking, A. K., Pedersen, S. H., Elder, K., Boelman, N. T., Glass, T. W., Oates, B. A., Bergen, S., Roberts, S., Prugh, L. R., Brinkman, T. J., Coughenour, M. B., Feltner, J. A., Barker, K. J., Bentzen, T. W., Pedersen, Å. Ø., Schmidt, N. M. and Liston, G. E. 2022. Collaborative wildlife–snow science: Integrating wildlife and snow expertise to improve research and management. - Ecosphere 13: e4094.

Rezendes, P. 1999. *Tracking and the Art of Seeing: How to read animal tracks and sign*. - HarperCollins Publishers.

Riseth, J. Å., Tømmervik, H., Helander-Renvall, E., Labba, N., Johansson, C., Malnes, E., Bjerke, J. W., Jonsson, C., Pohjola, V., Sarri, L. E., Schanche, A. and Callaghan, T. V. 2011. Sámi traditional ecological knowledge as a guide to science: snow, ice and reindeer pasture facing climate change. - Polar Record 47: 202–217.

Robinson, D. A., Estilow, T. W. and NOAA CDR Program. 2014. NOAA Climate Data Record (CDR) of Northern Hemisphere (NH) Snow Cover Extent (SCE), Version 1. - NOAA Natl. Centers Envir. Infor.

Roebber, P. J., Bruening, S. L., Schultz, D. M. and Cortinas, J. V. 2003. Improving Snowfall Forecasting by Diagnosing Snow Density. - Wea. Forecasting 18: 264–287.

Scharf, I., Nulman, E., Ovadia, O. and Bouskila, A. 2006. Efficiency Evaluation of Two Competing Foraging Modes under Different Conditions. - Am. Nat. 3: 350-357.

Sivy, K. J., Nolin, A. W., Cosgrove, C. L. and Prugh, L. R. 2018. Critical snow density threshold for Dall's sheep (*Ovis dalli dalli*). - Can. J. Zool. 96: 1170–1177.

Smith, D. W., Peterson, R. O. and Houston, D. B. 2003. Yellowstone after Wolves. - BioScience 53: 330.

Sturm, M. and Liston, G. E. 2021. Revisiting the Global Seasonal Snow Classification: An Updated Dataset for Earth System Applications. - J. Hydromet. 21: 2917-2938.

Sturm, M., Holmgren, J. and Liston, G. E. 1995. A Seasonal Snow Cover Classification System for Local to Global Applications. - J. Clim. 8: 1261–1283.

Takeuchi, Y., Nohguchi, Y., Kawashima, K. and Izumi, K. 1998. Measurement of snow-hardness distribution. - Ann. Glaciol. 26: 27–30.

Telfer, E. S. and Kelsall, J. P. 1984. Adaptation of Some Large North American Mammals for Survival In Snow. - Ecology 65: 1828–1834.

Thackeray, C. W., Derksen, C., Fletcher, C. G. and Hall, A. 2019. Snow and Climate: Feedbacks, Drivers, and Indices of Change. - Curr. Clim. Change Rep. 5: 322–333.

Thurber, J. M. and Peterson, R. O. 1991. Changes in Body Size Associated with Range Expansion in the Coyote (*Canis latrans*). - J. Mammal. 72: 750–755.

Toms, J. D. and Lesperance, M. L. 2003. Piecewise regression: a tool for identifying ecological thresholds. - Ecology 84: 2034–2041.

van de Kerk, M., Verbyla, D., Nolin, A. W., Sivy, K. J. and Prugh, L. R. 2018. Range-wide variation in the effect of spring snow phenology on Dall sheep population dynamics. - Environ. Res. Lett. 13: 075008.

Wilmers, C. C., Post, E. and Hastings, A. 2007. The anatomy of predator–prey dynamics in a changing climate. - J Anim. Ecol. 76: 1037–1044.

Wood, S. N. 2003. Thin plate regression splines. - J. R. Statist. Soc. B 65: 95–114.

CHAPTER 3: APEX PREDATORS EXPLOIT ADVANTAGEOUS SNOW CONDITIONS ACROSS HUNTING MODES

Publication history: A version of this chapter was previously published in *Journal of Animal Ecology*. The full citation for this publication is:

> Sullender, B.K., T.R. Ganz, R. Mower, J.D. Lundquist, B.N. Kertson, T.M. Newsome, A.J. Wirsing, and L.R. Prugh. 2025. Apex predators exploit advantageous snow conditions across hunting modes. *Journal of Animal Ecology* https://doi.org/10.1111/1365-2656.70170.

3.1 Abstract

Apex predators balance functional traits, habitat features, and prey distribution to maximize hunting efficiency. As components of habitat such as snow cover are altered by climate change, functional traits may prove more or less effective given new environmental conditions, with ecosystem-wide impacts as a result of changing predator-prey interactions. Hunting mode is one such functional trait that shapes which environments are best for catching prey. Coursing large carnivores may exploit snow conditions that offer movement advantages, with long chase sequences maximizing their superior mobility over large-bodied ungulate prey that typically sink deeper into snow. However, comparatively little is known about whether stalking predators utilize snow similarly, despite similar theoretical movement advantages over prey. In this study, we examined the effects of snow on two sympatric predators with different hunting strategies: cougars (*Puma concolor*; stalking predators) and wolves (*Canis lupus*; coursing predators). We coupled a physically based snow model with kill site investigations and telemetry data from 50 cougars, 14 wolves, 142 mule deer (*Odocoileus hemionus*), and 90 white-tailed deer (*O. virginianus*) collected from 2017-2021 in Washington state, USA. We first created winter deer distribution models for each year to control for expected prey density. We then generated step selection functions for cougars and wolves using this deer index, snow properties, and other landscape characteristics hypothesized to influence the hunting process. The interaction between snow depth and density shaped both predators' movements and was an unexpectedly strong driver of cougar winter movements and kill site distribution. Wolves weakly selected for shallow (<35cm), low density (<200kg/m^3) snow, and avoided deeper snow unless sufficiently dense (>350kg/m^3). Cougars selected for very dense (>400kg/m^3), moderate-depth (<50cm) snow and avoided deep snow. Snow depth and density had similar effects on cougar kill site selection (n = 389 known and probable cougar kills; insufficient sample size for wolves). Our results indicate that snow is a critical component of large carnivore movements regardless of hunting mode. In a warming climate, the knock-on effects of a diminishing snowpack may reduce the hunting success of multiple large carnivore species, consequently altering predator-prey dynamics with cascading ecosystem-wide effects.

3.2 Introduction

Predator-prey interactions are critical to ecosystem structure and function (Estes et al., 2011; Ripple et al., 2014). Both the consumptive and non-consumptive components of these interactions are shaped by when and where predators most effectively hunt, which is itself a product of habitat domain and predator functional traits such as hunting mode (Huey & Pianka, 1981; Lima, 2002). For example, lions (*Panthera leo*) rely on tall grass for concealment to stalk their prey, which nearly quadruples hunting success rates when compared to short grass (Hopcraft et al., 2005; Orsdol, 1984). As climate change alters habitat characteristics, however, the places and times most productive for predators are shifting (Morin et al., 2021; Peers et al., 2020). New environmental conditions may better align with the functional traits of some predators while rendering other traits less effective or even maladaptive (Elmhagen et al., 2017; Peers et al., 2020). To better forecast what ecosystems will look like in the future, therefore, quantifying the interplay between predator functional traits and climate-sensitive habitat components remains a question of paramount importance.

Advances in animal tracking technology (Wilmers et al., 2015), statistical analysis (Thurfjell et al., 2014), and environmental data products (Reinking et al., 2022) have enabled researchers to examine the relationship between wildlife species and components of habitat that vary both spatially and temporally (Ganz, DeVivo, et al., 2024). In particular, seasonal snow cover has been increasingly identified for its capacity to transform predator-prey interactions (Reinking et al., 2022; Sullender et al., 2023). As wildlife move through a snow-covered landscape, their energy expenditure and overall mobility are largely determined by the depth that they sink into the snow with each step (Dailey & Hobbs, 1989; Parker et al., 1984), which is strongly influenced by snow properties such as depth and density (Glass et al., 2021; Mahoney et al., 2018; Sivy et al., 2018; Sullender et al., 2023). The foot morphology of carnivores generally provides more surface area per unit body mass (i.e., lower foot loading) than ungulate prey, so at a given snow depth and density, carnivores sink less into the snow and are afforded a relative movement advantage (Murray & Larivière, 2002; Sullender et al., 2023; Telfer & Kelsall, 1984). Furthermore, because snow restricts access to forage for herbivores and compounds increased energy expenditure during harsh winter conditions, ungulate body condition tends to deteriorate over the course of the winter as weaker individuals become more susceptible to predation (Ganz, Bassing, et al., 2024; Husseman et al., 2003; Wilmers et al., 2020). Snowy winters thus provide a two edges for predators: superior hunting conditions and increasing prey vulnerability. Consequently, snow has been implicated in altering both predator and prey activity patterns (Cunningham et al., 2022; Droghini & Boutin, 2018), habitat selection (Pedersen et al., 2021), and predation success rates (Horne et al., 2019; Mech et al., 2001), with potentially cascading effects on wildlife demography (Van de Kerk et al., 2020) and population dynamics (Borg & Schirokauer, 2022) across multiple trophic levels (Post et al., 1999).

Specific snow conditions give large carnivores a comparative movement advantage over ungulate prey (Sullender et al., 2023), but whether such predators actually exploit that theoretical advantage may depend on functional traits and habitat selection. Hunting mode is among the most important functional traits for predators (Huey & Pianka, 1981; Schmitz, 2008; Schmitz et al., 2004). Predators can be broadly categorized as using either cursorial or stalking hunting modes, although there may be more of a gradient than discrete states (Scharf et al., 2006). Cursorial predators like gray wolves (*Canis lupus,* hereafter referred to as wolves) and cheetahs (*Acinonyx jubatus*) typically undertake long chases when targeting mobile ungulate prey, and utilize open and relatively flat habitat to enhance prey detection and initiate pursuit (Bergman et al., 2006; Mills et al., 2004; A. M. Wilson et al., 2013). Cougars (*Puma concolor*), leopards (*Panthera pardus*), and other stalking predators, in contrast, prefer to utilize rugged terrain and habitat with structural complexity that enables undetected approaches and a sudden attack with minimal chase distance (Hopcraft et al., 2005; Owen-Smith, 2019; J. A. Smith et al., 2019). Accumulated snow should enhance the predator movement advantage over the chase distance (Sullender et al., 2023), resulting in a potentially greater benefit for cursorial than stalking predators in snowy habitats. This distinction is hypothesized to explain why wolves, for example, appear to benefit from deeper snow with higher kill rates (Nelson & Mech, 1986) and larger prey size (Horne et al., 2019; Post et al., 1999), whereas the limited evidence examining how snow affects cougar predation suggests that snow has weak, if any, influence (Atwood et al., 2009).

In this paper, we integrate physically-based snow model outputs with GPS location data of two sympatric apex predators – cougars and wolves – and their ungulate prey in Washington state, USA, to test the hypothesis that snow properties have a stronger influence on winter movements of coursing predators than stalking predators. The energetic costs of moving through snow can increase exponentially as the animal's sink depth exceeds half of its chest height, and this sink depth is jointly influenced by the depth and density of snow (Dailey & Hobbs, 1989; Fancy & White, 1987; Parker et al., 1984; Sullender et al., 2023). Thus, we expect snow density to have the greatest influence on animal movement in areas with deep snow, which should result in an interaction between snow depth and density as predictors of apex predator habitat selection. Additionally, we expect a similar directional influence of these two snow properties on cougar kill site locations, with kills more likely to occur in areas with deep, dense snow. By examining the interplay between functional traits and the dynamic components of predator habitat selection, our study provides new insights on the influence of snow conditions on apex predators in a rapidly warming world.

3.3 Materials and Methods

3.3.1 Study Area

Our study occurred in two areas within Washington state, USA (Fig. 1). The Okanogan Study Area (approx. 47.9–49.4N, ~119.3–120.8W) and the Northeast Study Area (approx. 47.7–49.2N, ~116.5–118.4W) span about 5,000 km^2 each. These areas encompass a diverse range of vegetation and landforms, from steep, barren mountain sides at high elevations to dense conifer forests and open sagebrush (*Artemisia* spp.) slopes at lower elevations. The upper elevations (i.e., >1200m) of both regions are typically snow-covered from mid-November until early May (Natural Resources Conservation Service, 2023, 2024). Lower elevations (~400m) present a greater human footprint with communities, roads, timber harvest, and agriculture. A diverse large mammal community inhabits both areas, with widespread mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), cougar, wolf, coyote (*Canis latrans*), and bobcat (*Lynx rufus*) populations. Although alternate prey such as elk (*Cervus canadensis*) and moose (*Alces alces*) are also present, mule deer and white-tailed deer comprise the vast majority of our focal carnivores' winter diets in both areas (author paper, unpublished).

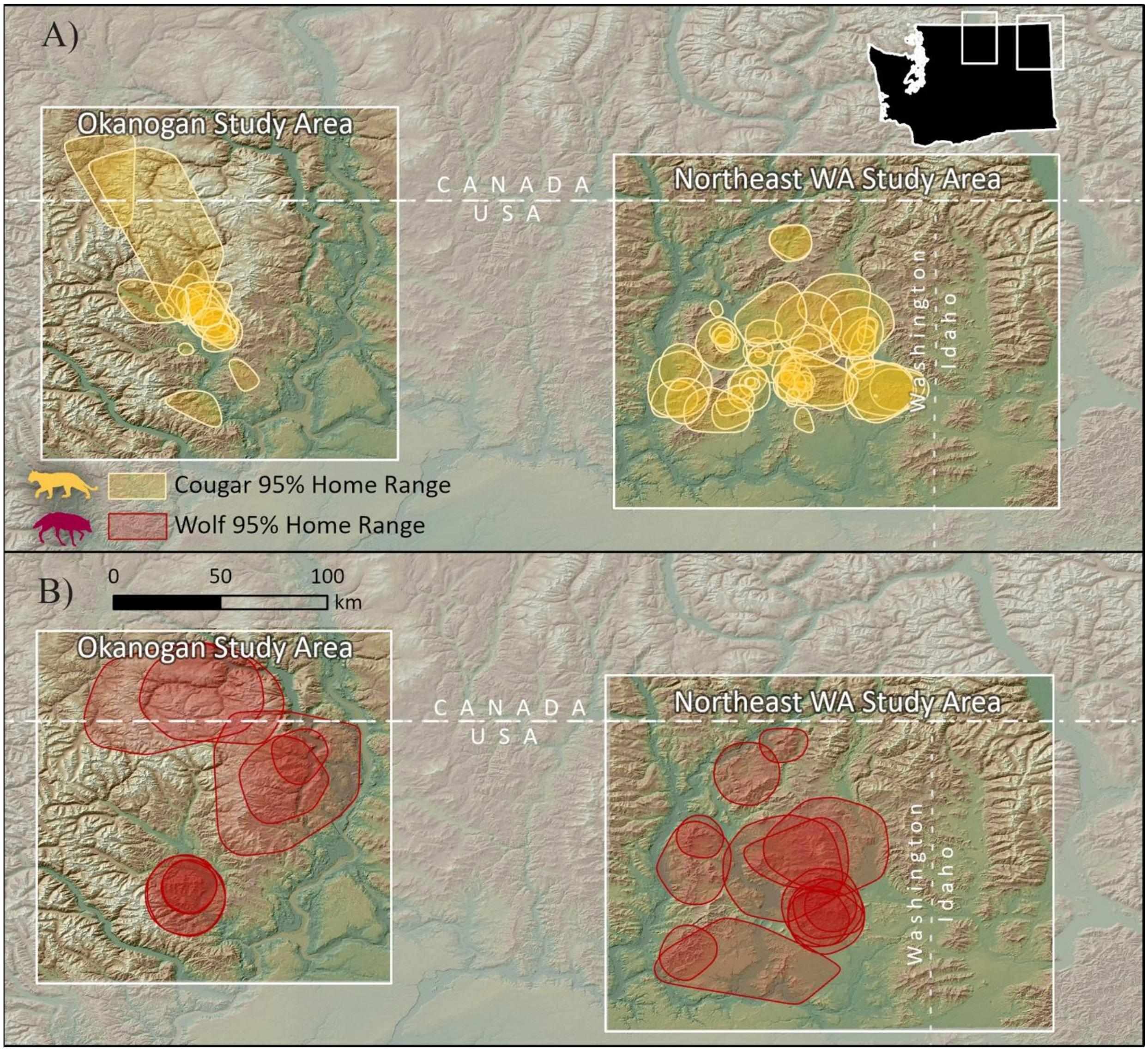

Figure 3.1. Location of Okanogan and Northeast study areas within the state of Washington, USA (top-right inset) and apex predator home ranges for cougars (a) and wolves (b).

3.3.2 Collar Data

We used wildlife telemetry data from the Washington Predator-Prey Project, as described in Bassing et al. (2023). GPS collars were deployed on cougars, wolves, mule deer, and white-tailed deer between 2016 and 2021, and programmed to collect locations every four hours for all species except wolves, whose fix rates varied between 2-12 hours. Mule deer were collared in the Okanogan study area, white-tailed deer were collared in the Northeast study area, and wolves and cougars were collared in both areas (Fig. 1). All animal handling was performed in accordance with University of Washington Institutional Animal Care and Use Committee guidelines under Protocols 4226-01 and 4381-01, Washington Department of Fish & Wildlife permits 20-290 and 17-162, and followed standards recommended by American Society of Mammalogists (Sikes & Gannon, 2011).

We used winter-only GPS locations of collared deer (*n* = 361 animal-years for 142 unique mule deer; *n* = 143 animal-years for 90 unique white-tailed deer; 2016-2021) to construct resource selection functions (RSFs; C. J. Johnson et al., 2006) that quantified relative habitat selection for deer at a 30m spatial resolution and on an annual time step (full details presented in Appendix B). These RSFs model the likely distribution of both predators' primary prey across our two study areas, with the outputs combined into a single output (hereafter, deer index).

For carnivores, we filtered all GPS data to keep only winter (December 1 - March 15; Ganz et al., 2022) locations. Because the fix rate on wolves varied depending on individual, collar, and year, we resampled all data to a common four-hour fix rate using a 30-minute tolerance. We omitted all individuals with 50 or fewer observations per winter, resulting in 50 unique cougars and 14 unique wolves (from 11 packs) distributed across the five years of our study (Table 1).

Table 3.1. Summary of carnivore collar data used in this study.

Species	**Region**	***n* collared 2017**	***n* collared 2018**	***n* collared 2019**	***n* collared 2020**	***n* collared 2021**	**All Years**
Cougar	Okanogan	6	9	11	4	1	**31**
Cougar	Northeast WA	6	11	23	17	8	**65**
Cougar	**Total**	**12**	**20**	**34**	**21**	**9**	**96***
Wolf	Okanogan	0	1	2	3	3	**9**
Wolf	Northeast WA	1	5	4	1	3	**14**
Wolf	**Total**	**1**	**6**	**6**	**4**	**6**	**23***

Notes: *Because some individuals were collared for multiple years, a total of 50 unique cougars were included in the 96 total cougar animal-years of data, and a total of 14 unique wolves from 11 packs were included in the 23 total wolf animal-years of data.

3.3.3 Snow Properties and Landscape Covariates

We used a distributed snow-evolution modeling system to model wildlife-relevant snow properties (SnowModel; Liston & Elder, 2006). SnowModel combines spatially and temporally distributed meteorological variables with topography and land cover type, numerically solving physical processes such as blowing-snow redistribution, canopy interception, and snow density evolution at user-specified spatial and temporal steps (Liston & Elder, 2006). We used NASA's Center for Climate Simulation Discover supercomputer to run a parallelized version of

SnowModel (Mower et al., 2024) at a 30m grid increment with a 3-hour forcing time step, and daily aggregated output snow depth (m) and snow density (kg/m^3). To validate the model, we intersected output with observations from the Natural Resources Conservation Service Snow Telemetry stations and field measurements. Full details are presented in Appendix B.

To account for landscape features aside from snow and prey distribution that could influence predator movements, we used a combination of static and dynamic variables. Terrain ruggedness index (TRI; M. F. J. Wilson et al., 2007) and slope remained unchanged throughout our study period and have been shown to be important components of suitable habitat for large mammals in our system (Bassing et al., 2023; Ganz et al., 2022). We first accessed elevation data for both study areas (30m resolution; Farr et al., 2007) and used the R package *terra* (Hijmans, 2024) to calculate TRI and slope.

Because we were interested in predator responses to dynamic covariates, we used annually updated land-cover data from TerrAdapt:Cascadia (30m resolution; TerrAdapt, 2022). These datasets use remote sensing to identify changes in land cover. We used canopy cover and combined vegetation classes into three broad categories: open (snow/ice, barren, emergent wetland, mesic grass forb, and xeric grass forb), shrub (mesic shrub and xeric shrub), and forest (woody wetlands, deciduous, and conifer). We used the median step length to extract percent cover within a species-specific moving window (180 m radius for cougars and 570 m radius for wolves) to better assess perceived availability (Ganz et al., 2022). We split predator GPS location data by year and extracted each year's landscape covariates – TRI, slope, and land cover – using *terra* (Hijmans, 2024). With the annually updated deer indices predicting the relative winter distribution of deer across the landscape, we extracted the deer index value at each used and available predator location.

3.3.4 Modeling Framework

We used step-selection functions (SSFs) to quantify the relative influence of snow properties, deer distribution, and other landscape variables on cougar and wolf movements (Fortin et al., 2005; Thurfjell et al., 2014). By parameterizing available steps using the observed distribution of turn angles and step lengths, SSFs explicitly account for both the non-independence of sequential locations and individual-specific movement patterns (Avgar et al., 2017; Thurfjell et al., 2014). Our use of SSFs aligns with 3rd-order habitat selection, assessing animal movement within home ranges (D. H. Johnson, 1980). We used the *amt* package (Signer et al., 2019) to randomly generate 10 available points per observed location, using a von Mises distribution for turning angle and a gamma distribution for step length (Thurfjell et al., 2014).

We constructed a set of conditional generalized additive models (GAMs) to predict how environmental covariates influence predator step selection. GAMs use splines to model non-linear relationships between predictors and the response variable, and are particularly useful when thresholds or complex interactions are expected (Wood, 2017). We used tensor products to model interactions between smoothed terms (Wood et al., 2013). We used the Cox proportional hazard model to fit a conditional logistic regression (i.e, the SSF) using the *mgcv* package in R with restricted maximum likelihood (Klappstein et al., 2024; Wood, 2017). In all GAMs, we used thin-plate splines and four basis functions (i.e., $k = 5$) as a compromise between precision and computational efficiency. We first screened all covariates for collinearity and excluded highly correlated variables ($|r| > 0.7$) from the same model. We then ranked candidate models based on Akaike's information criterion (AIC), which accounts for goodness of fit while penalizing models with additional parameters (Anderson & Burnham, 2002). We selected the models with lowest AIC as the best habitat covariates for use in both full predator-specific models. We validated our SSF models using the *k*-fold cross validation approach recommended by Boyce et al. (2002), calculating Spearman rank correlation coefficient for five folds of cougar and wolf data, each with an equal number of animal-years. For each covariate, we generated partial effects plots, which represent the change in response variable (i.e., step selection) for every unit change in the predictor variable with all other variables set to zero.

Finally, we constructed average effects plots for both carnivores to aid in interpretation of how snow properties impact the relative probability of use. Average effects plots illustrate the change in the relative probability of use as one focal covariate changes, averaged over all observed values of other covariates, thus better visualizing natural variability and correlation among covariates (Avgar et al., 2017). Although cougars and wolves experienced slightly different snow conditions owing to differing home range locations (Appendix B: Figure B2), we pooled all snow data from both predators' available steps and calculated lower (<25%) and upper (>75%) quartiles from the combined distributions to facilitate comparison. We selected the lower and upper quartiles for density (<200kg/m^3 and >350kg/m^3) and snow depth (<5cm and >30cm), binning data using these values. Comparing the effect of lower and upper quartiles depicts the non-linear interaction effects on step selection modeled by our GAMs.

3.3.5 Kill Sites

To determine the location of deer killed by predators in both study areas, we combined known deer kills from three winters of intensive predator GPS cluster investigations and mortality locations of collared ungulates (Ganz et al., 2023). We identified and included probable deer kills by analyzing GPS locations of collared predators (Clark et al., 2014; full details in Appendix S1: Section S2; Knopff et al., 2009). Due primarily to the challenges of inferring wolf behavior from a four-hour GPS collar fix rate, we were only able to field-validate five kill sites for wolves during our first field season. This low sample size for wolf kills precluded formal statistical investigation and prevented us from developing a satisfactory algorithm to predict kill sites from wolf clusters; thus, we limited kill site analysis to cougar clusters.

Because a verified cougar cluster may represent a cached carcass, rather than the actual kill site, we buffered each cluster location by the typical maximum distance cougars are known to drag predated deer (i.e., 95m; Blake & Gese, 2016). For each individual cougar in each year, we conditioned each 95-m buffered kill site (observed locations) against five randomly generated, 95m-buffered points (available locations) within that individual's winter home range, using the same date at observed and available locations to time-match snow conditions. We used the *pandas* and *xarray* libraries in Python (Hoyer & Hamman, 2017; The pandas development team, 2024) to calculate and extract the median snow depth and density for each buffered observed and available area. To determine how snow influenced kill site selection, we constructed a binomial GAM from the *mgcv* package (Wood, 2017) that fit each habitat covariate from our predator models (i.e., TRI, canopy cover, percent shrub, and deer index), snow depth, snow density, and an interaction of snow depth and density with four thin-plate spline smooths ($k = 5$). We visualized our results by plotting relative selection strength (Avgar et al., 2017) against the minimum observed values of snow depth and density, allowing us to quantify the relative change in kill site selection as these snow variables changed. To represent nonlinear interactions of snow properties in these relative selection plots, we generated predictions from our kill site GAM using the same depth and density quartiles as our predator movement modeling.

3.4 Results

3.4.1 Carnivore Movement

In our predator SSFs, the most parsimonious combination of variables included canopy cover, deer index, shrub cover, terrain ruggedness (TRI; Figure 3.2), and the tensor product of snow depth and density as predictors (Figure 3.3). TRI was a better predictor of predator habitat selection than slope (ΔAIC > 2; Appendix B: Table B4), and percent shrub and canopy cover were the most parsimonious, non-correlated vegetation predictors of habitat selection (Appendix B: Table B5). For both predators, the full tensor product of snow depth and density – analogous in a generalized linear regression framework to main effects of snow depth and density as well as an interaction term (Wood, 2017) – performed better than any other combination of snow variables (ΔAIC > 2; Appendix B: Tables B6 and B7), either alone, together as separate main effects, or as an interaction term only. Thus, models for each predator took the general form:

$$\eta_{it} = f(cc_{it}) + f(deer_{it}) + f(shr_{it}) + f(tri_{it}) + g(snod_{it}, dens_{it}), \qquad (1)$$

where, following Klappstein et al. (2024), η is the linear predictor of the SSF for the *i*-th location of stratum t, *f(x)* is the smooth function of variable x, *cc* is canopy cover, *deer* is deer habitat suitability, *shr* is shrub cover, *tri* is terrain ruggedness, *g(x,y)* is the tensor product of variables x and y, *snod* is snow depth, and *dens* is snow density. Our five-fold cross-validation indicated excellent model performance, with Spearman rank correlation coefficients of 0.949 and 0.940 for cougars and wolves, respectively.

Terrain ruggedness had the strongest effect on both predators' step selection patterns, with cougars strongly selecting for and wolves strongly avoiding rugged areas (> 8 TRI; Figure 3.2d). Cougars avoided open areas and selected moderate-to-high canopy cover (at 0% canopy cover, partial effect = -0.61 [95% confidence interval: -0.56 - -0.65]; at 60% canopy cover, partial effect = 0.43 [95% confidence interval: 0.39-0.46]), whereas wolves selected open areas and avoided densely forested areas (at 28% canopy cover, partial effect = 0.32 [95% CI: 0.26-0.39]; at 85% canopy cover, partial effect = -0.69 [95% CI: -0.48- -0.90]; Figure 3.2a). Both predators weakly avoided areas with very low deer index, but the effects of higher deer index values on predator movement were less clear (Figure 3.2b). Cougars weakly selected for higher shrub cover and wolves very weakly avoided moderate shrub cover (all partial effects between -0.17 and 0.22; Figure 3.2c).

To visualize the effects of interacting snow properties on predator movement patterns, we constructed average effects plots for cougars (Figure 3.4a,c) and wolves (Figure 3.4b,d). Wolves selected for low-density snow when it was shallow and avoided low-density snow when deep (Figure 3.4b), with weak selection for denser snow when deep (Figure 3.4d). However, snow conditions had a weaker influence on wolf movements than other habitat covariates. Cougars, in contrast, had strong responses to both snow depth and density (Figure 3.4a,c). Across the range of snow densities, cougars avoided deeper snow when possible (Figure 3.4a), but if moving through deep snow, cougars selected for densities > 400kg/m^3 (Figure 3.4c).

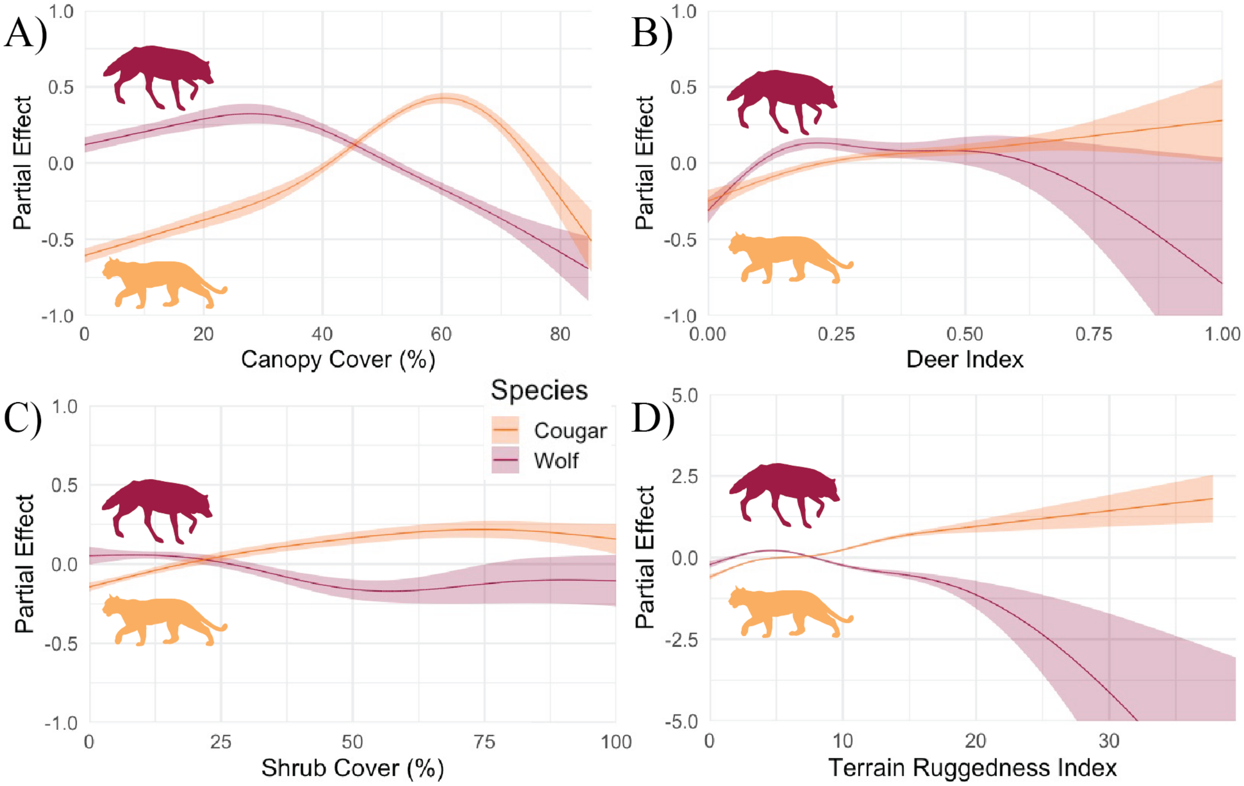

Figure 3.2. Partial effects plots indicating the relative influence of four predation-relevant variables (a, canopy cover; b, deer index; c, shrub cover; d, terrain ruggedness) on cougar (orange) and wolf (red) movement. Cougars select for medium-to-high canopy cover (40-75%), greater deer index (>0.25), higher shrub cover (>25%), and strongly select for high terrain ruggedness (>8 TRI). Wolves, in contrast, select for lower canopy cover (<50%) and low-to-moderate deer index (0.1-0.5), avoid moderate shrub cover (30-75%), and strongly avoid rugged terrain (>8 TRI). Both cougars and wolves avoid areas with a very low deer index.

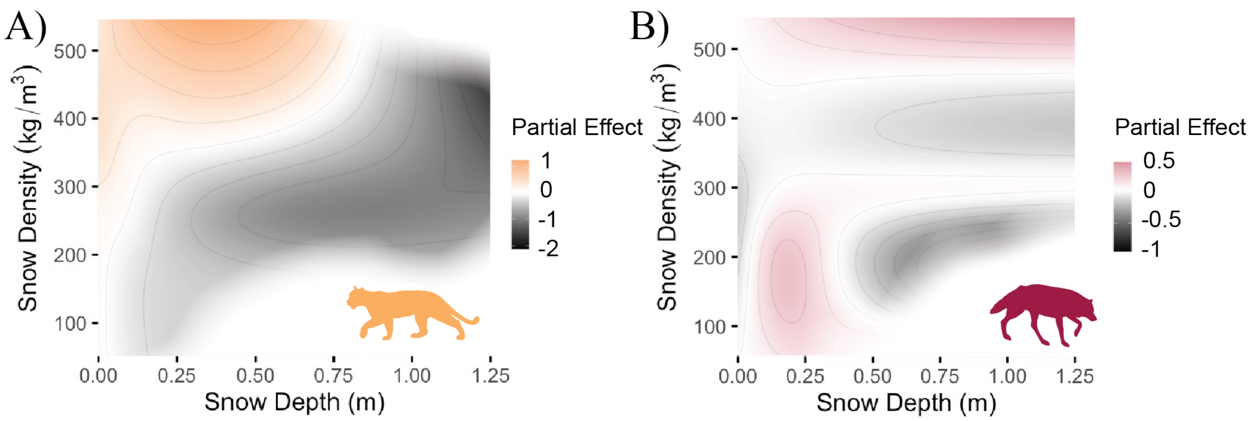

Figure 3.3. Tensor product plots showing the interaction of snow depth (x-axis) and snow density (y-axis) for (a) cougar step selection and (b) wolf step selection. Colors represent the partial effect of each combination of values, with black indicating a strong negative effect and saturated colors indicating strong positive effects (orange for cougars; red for wolves). Cougars tend to strongly select for very dense (>400 kg/m^3) snow of intermediate depth (0.25-0.75 m), whereas wolf selection is relatively weaker, with selection for low-density, shallow (200 kg/m^3, <0.3 m) and extremely dense (>450 kg/m^3) snow.

3.4.2 Kill Sites

Although we did not gather enough field data (*n* = 5 confirmed wolf kill sites) to delineate likely wolf kill sites, three winters of cougar cluster investigation yielded 389 known and probable cougar kills across the two study areas. Cougar kill site GAMs (Figure 3.5a,b) largely mirrored the effects of covariates on cougar habitat selection (Figure 3.4b,d). Relative selection strength plots indicated that kills were less common when snow was dense (350 kg/m^3), but only if snow depth exceeded ~60 cm (Figure 3.5a). Notably, snow density had no effect on kill location in shallow snow (Figure 3.5a) but had a strong positive effect if the snow was 30 cm deep. If the kill occurred in deep snow (30 cm), it was 1.7 times (95% CI: 1.4-1.9) as likely to occur in moderately dense (300 kg/m^3) snow and 2 times (95% CI: 1.7-2.4) as likely in very dense (400 kg/m^3) snow compared with the minimum observed snow density (60 kg/m^3).

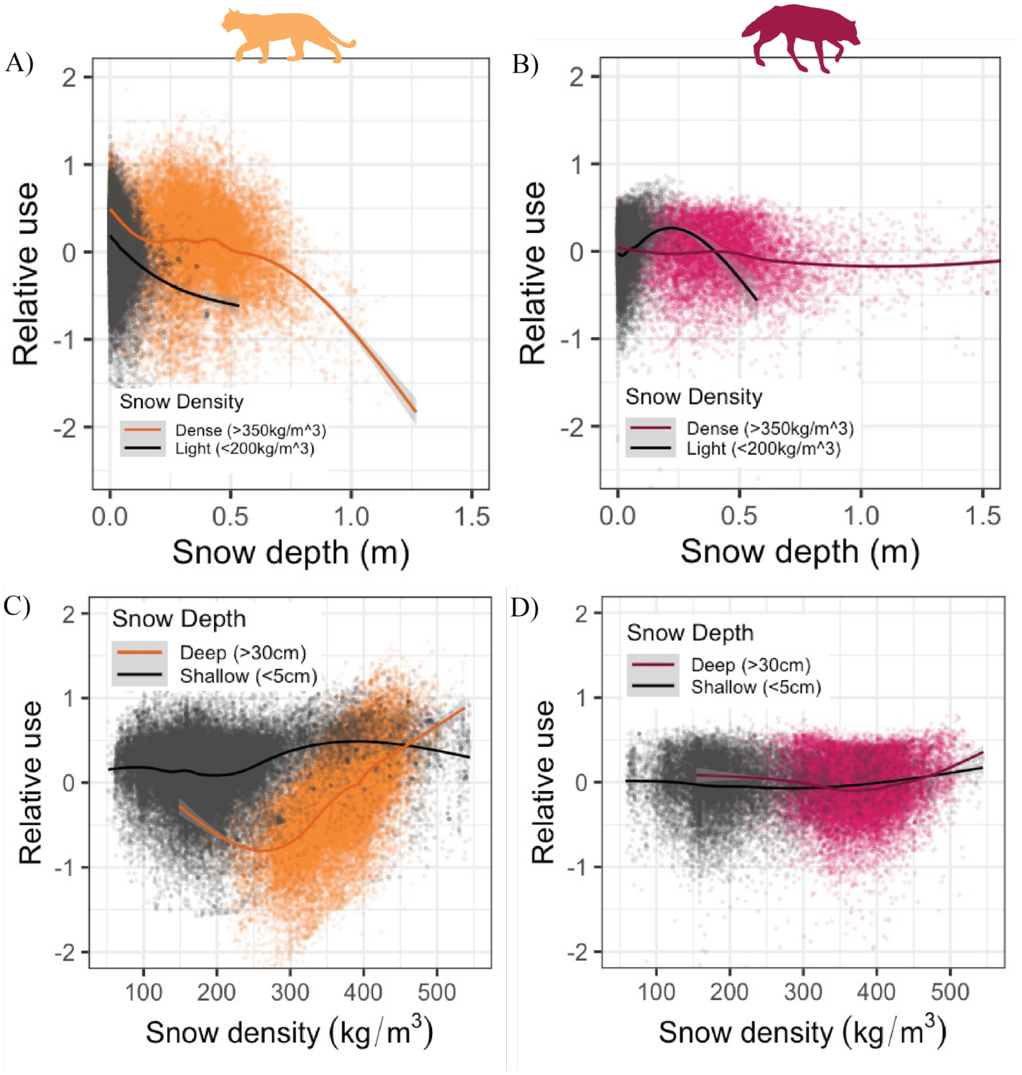

Figure 3.4. The relative effects of snow depth and density on step selection for (a,c) cougars and (b,d) wolves. These average-effects plots show the selection score plotted against the range of a focal covariate (i.e., [a,b] snow depth or [c,d] snow density) in the dataset, with all other relevant covariates (i.e., TRI, canopy cover, percent shrub, and deer index) kept at their observed values for all available steps. Values above 0 indicate selection and values below 0 indicate avoidance.

3.5 Discussion

Hunting opportunity is a key driver of habitat selection for apex predators, and their success is a product of prey encounter probability and capture success rate (Bergman et al., 2006; Prugh et al., 2019; J. A. Smith et al., 2020). Hunting mode – whether coursing, stalking, or a hybrid approach – is thought to influence multiple components of this optimization problem (Peterson et al., 2021; Preisser et al., 2007; Schmitz et al., 2017). However, our study revealed that advantageous snow conditions are an important feature of the winter landscape for two apex predators, regardless of hunting strategy. Our models indicated that variables related to capture success influenced predator movements more strongly than a proxy for prey availability, supporting recent evidence that prey vulnerability may influence hunting success to an even greater extent than prey density (Peterson et al., 2021; J. A. Smith et al., 2019). As hypothesized, the interaction between snow depth and density was an important component of all models. Contrary to our expectations, however, we found that both cougar movements in general and the location of their kill sites were strongly influenced by snow conditions. Specifically, cougars strongly selected areas of moderately deep, dense snow, whereas wolves marginally selected shallower, lower-density snow. We suggest that apex predators select these snow conditions because they provide a relative movement advantage over ungulate prey (Penczykowski et al., 2017; Sullender et al., 2023).

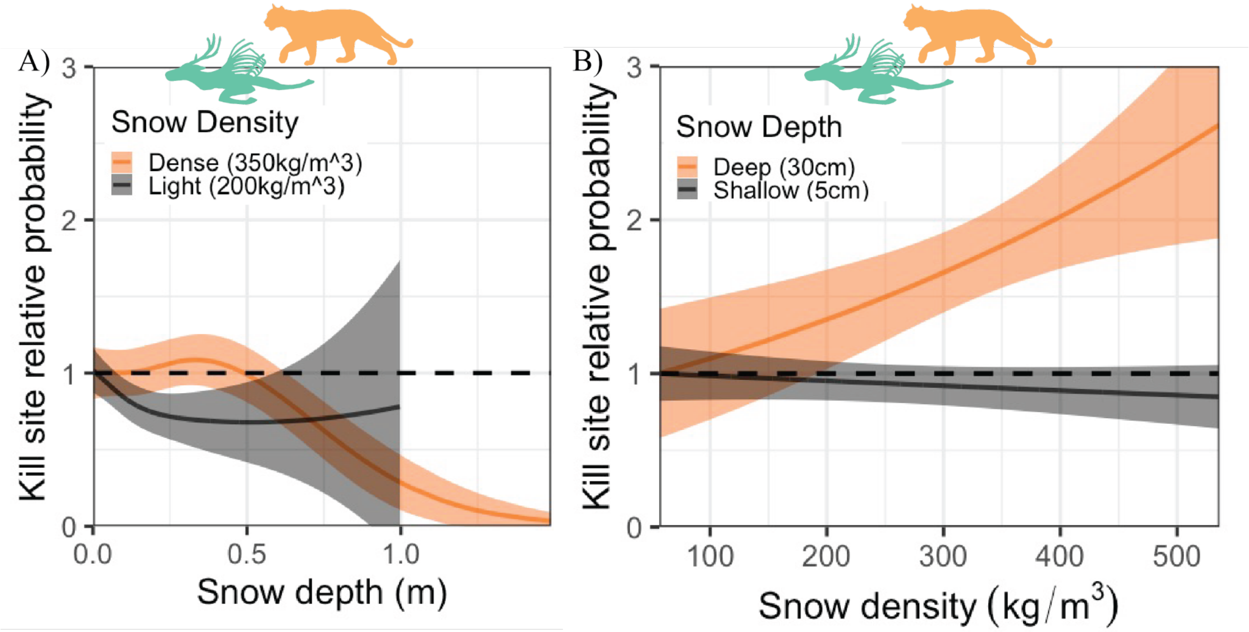

Figure 3.5. Relative selection strength of different (a) snow depths and (b) densities compared with observed minimum snow depth (1cm; a) and minimum snow density (60kg/m^3; b) at cougar kill site locations. Using these minimum values as the reference points enables illustration of how selection changes as snow becomes (a) deeper or (b) denser. Values above 1 indicate increased probability and values below 1 indicate decreased probability relative to these baselines. We did not analyze how landscape covariates influence wolf kill locations because of low sample size (*n* = 5).

In a changing climate, shifting snowpack properties may undermine seasonal advantages currently exploited by some large carnivores (Kunkel et al., 1999; Peers et al., 2020). Total precipitation and precipitation intensity are expected to increase as the climate warms, and more mid-winter melt may locally increase snow densities (Scaff et al., 2024; Thackeray et al., 2019). However, the reductions in the fraction of precipitation falling as snow as well as greater snowmelt are stronger signals projected to globally result in shorter snow cover duration, less snow cover extent, and less overall snow (Musselman et al., 2021; Thackeray et al., 2019). Together, these trends are forecasted to dramatically reduce snowpacks within our study region (Gergel et al., 2017; Salathé et al., 2010), which we suggest will reduce the extent and duration of predator-preferred snow conditions. For wolves and cougars specifically, the consequences of these changes to snow conditions may manifest as reduced ability to take down large, healthy prey (Nelson & Mech, 1986; Post et al., 1999) and, as negative impacts accumulate from consecutive low-snow years, may scale up to population-level impacts such as lower adult survival or reproductive success (Borg & Schirokauer, 2022).

Surprisingly, our results suggest that cougars exploit favorable snow conditions to a greater extent than wolves. Wolf selection varied relatively little across snow depths and densities, whereas snow conditions strongly influenced cougar habitat selection. We propose two potential explanations for this difference, one functional and one morphological. First, because wolves generally hunt and travel in packs, they can share the otherwise enormous energetic costs of breaking trail in challenging snow conditions (Mech & Boitani, 2003; Parker et al., 1984). Thus, sociality may largely mitigate differences in energy expenditure when traveling through easy versus difficult snow conditions. As typically solitary animals (Beausoleil et al., 2013), cougars must independently meet the full energetic demands of locomotion in snow and thus may benefit more from seeking out snow conditions that confer easier travel. Second, wolves are morphologically better adapted to snow than cougars, with greater paw surface area in comparison to body weight (Murray & Larivière, 2002; i.e., a lower foot-load; Telfer & Kelsall, 1984). Sullender et al. (2023) measured snow track sink depths of cougars, wolves, and deer in relation to snow density to identify “danger zones” of snow density whereby deep sink deeper into the snow (relative to leg length) than each predator. Although both predators have lower foot-loads than their ungulate prey, this study revealed that wolves gain a significant locomotion advantage over deer across all snow densities and may not need to select for specific conditions to realize this advantage. Cougars, in contrast, have no movement advantage over deer at low snow densities and their advantage has a distinct maximum at 340kg/m^3 – approximately where our tensor product plot indicates a positive partial effect (Figure 3.3a) and near where selection increases in our average effects plot (Figure 3.4c). The concordance between field measurements of snow track sink depths reported in Sullender et al. (2023) and our modeled predator movement preferences suggests that the patterns we observed are robust.

Our results indicate that snow is an under-appreciated factor in cougar movement and predation patterns. Prior studies have found little evidence of snow depth altering cougar movement patterns (Alexander et al., 2006; Blake & Gese, 2016) or kill site locations (Atwood et al., 2007). To our knowledge, our study is the first to explicitly model how cougars respond to the interaction between snow depth and density. Low-density snow is insufficient to support cougars on the snow surface, slowing down stalking approaches and reducing the effective range of a pouncing attack. At shallow snow depths, however, cougars may not sink in sufficiently to change their mobility regardless of snow density. In very deep snow, density also becomes less important, potentially due to prey avoidance of extremely deep snow (Gilbert et al., 2017) and partially due to a combination of sub-model-scale heterogeneity and the risk of incurring large energetic costs. The 30m resolution of our SnowModel output represents an average of local variations in depth and density, as snow properties vary on spatial scales as fine as the molecular level (Sexstone et al., 2016). Even within a grid cell classified as high-density snow, then, locally lower-density snow may exist. Any cougar misstep into locally lower-density snow would cause the animal to sink in deeply and expend enormous energy to climb back to the snow surface, a risk intensified in increasingly deep snow. Between these snow depth extremes, both our movement and kill site location models indicate that cougars select for more dense snow that supports cougars on the snow surface but not their ungulate prey (Sullender et al., 2023).

Although important, snow is merely one component of a broader suite of environmental variables shaping habitat selection by apex predators. Terrain ruggedness was the single most influential variable for both cougars and wolves, which further underscores the connection between predator terrain selection and hunting mode as predators seek to maximize hunting success (Bergman et al., 2006; J. A. Smith et al., 2019). Although hunting mode helps explain cougars' and wolves' diverging use of rugged, dense-canopy landscapes conducive to stalking but not coursing, the selection of similar snow conditions by both of these predators indicates that other traits - such as morphology and sociality that can affect sensitivity to snow conditions - should not be overlooked. Taken collectively, our findings situate snow within a broader understanding of how landscape features influence predator-prey interactions, both in concert with and independent of functional traits such as hunting mode.

When sympatric predators share common food resources, spatial or temporal habitat partitioning has been proposed as a means to mitigate some of the negative effects of competition (Rafiq et al., 2023; Schoener, 1974). Within the Pacific Northwest, the hierarchical dominance of wolves and their extensive dietary overlap with cougars (Kunkel et al., 1999) suggests that recovering populations of wolves will likely expose cougars to increased competition. The impacts of Washington's returning wolves are only beginning to be understood (Prugh et al., 2023), as the state population has grown from a single resident pack in 2008 to 43 packs with a combined 230 wolves as of 2024 (Washington Department of Fish & Wildlife, 2025). We found that cougars and wolves exhibit diverging use of canopy cover, terrain ruggedness, and shrub cover (Fig. 3.2), echoing the apex predator habitat partitioning observed in other systems with recovering wolf populations (Atwood et al., 2007; Bartnick et al., 2013; Kortello et al., 2007). We suggest that, first, snow may further contribute to niche separation because cougars and wolves select for somewhat different snow conditions, although prey distributional responses to snow could mediate this niche separation (Ganz et al., 2022; Gilbert et al., 2017). Second, certain combinations of snow depth and density may allow cougars to hunt effectively across a broader habitat domain, thus temporarily expanding niche space. For a subordinate competitor, such an expansion of niche space may foster short-term persistence or even longer-term coexistence (Monterroso et al., 2016).

More broadly, the close connection we demonstrate between snow and predator-prey interactions provides a framework for future ecological inquiry. Although we have outlined likely impacts of climate change across our study region, geophysical features may locally preserve snow conditions preferred by some wildlife, thus creating networks of refugia (Rivrud et al., 2019). Furthermore, other regions such as the Western Himalaya and East Siberia are forecasted to diverge from global climate trends and have increasing snow mass (Pulliainen et al., 2020; T. Smith & Bookhagen, 2020), which could benefit local predator populations. To capture these nuances of how climate change will alter predator-prey interactions, therefore, a geographically specific focus and a wildlife-relevant scale are critical (Reinking et al., 2022). As we move from quantifying predation-relevant landscape features toward integrative models that better bound community population dynamics, for example, additional fieldwork examining how snow influences predation outcomes (i.e., predation success rates or kill rates) would further enhance our forecasting efforts. Our study provides an essential step towards these eventual goals. Namely, by showing that snow shapes large carnivore movements across hunting mode, we demonstrate that suitable snow conditions can provide a predation advantage that overpowers even functional traits.

3.6 References

Alexander, S. M., Logan, T. B., & Paquet, P. C. (2006). Spatio-temporal co-occurrence of cougars (Felis concolor), wolves (Canis lupus) and their prey during winter: A comparison of two analytical methods. *Journal of Biogeography*, *33*(11), 2001–2012. https://doi.org/10.1111/j.1365-2699.2006.01564.x

Anderson, D. R., & Burnham, K. P. (2002). Avoiding Pitfalls When Using Information-Theoretic Methods. *The Journal of Wildlife Management*, *66*(3), 912. https://doi.org/10.2307/3803155

Atwood, T. C., Gese, E. M., & Kunkel, K. E. (2007). Comparative Patterns of Predation by Cougars and Recolonizing Wolves in Montana's Madison Range. *The Journal of Wildlife Management*, *71*(4), 1098–1106. https://doi.org/10.2193/2006-102

Atwood, T. C., Gese, E. M., & Kunkel, K. E. (2009). Spatial Partitioning of Predation Risk in a Multiple Predator–Multiple Prey System. *Journal of Wildlife Management*, *73*(6), 876–884. https://doi.org/10.2193/2008-325

Avgar, T., Lele, S. R., Keim, J. L., & Boyce, M. S. (2017). Relative Selection Strength: Quantifying effect size in habitat- and step-selection inference. *Ecology and Evolution*, *7*(14), 5322–5330. https://doi.org/10.1002/ece3.3122

Bartnick, T. D., Van Deelen, T. R., Quigley, H. B., & Craighead, D. (2013). Variation in cougar (*Puma concolor*) predation habits during wolf (*Canis lupus*) recovery in the southern Greater Yellowstone Ecosystem. *Canadian Journal of Zoology*, *91*(2), 82–93. https://doi.org/10.1139/cjz-2012-0147

Bassing, S. B., DeVivo, M., Ganz, T. R., Kertson, B. N., Prugh, L. R., Roussin, T., Satterfield, L., Windell, R. M., Wirsing, A. J., & Gardner, B. (2023). Are we telling the same story?

Comparing inferences made from camera trap and telemetry data for wildlife monitoring. *Ecological Applications*, *33*(1), e2745. https://doi.org/10.1002/eap.2745

Beausoleil, R. A., Koehler, G. M., Maletzke, B. T., Kertson, B. N., & Wielgus, R. B. (2013). Research to regulation: Cougar social behavior as a guide for management: RH Behavior-Based Cougar Management. *Wildlife Society Bulletin*, n/a-n/a. https://doi.org/10.1002/wsb.299

Bergman, E. J., Garrott, R. A., Creel, S., Borkowski, J. J., Jaffe, R., & Watson, F. G. R. (2006). Assessment Of Prey Vulnerability Through Analysis Of Wolf Movements And Kill Sites. *Ecological Applications*, *16*(1), 273–284. https://doi.org/10.1890/04-1532

Blake, L. W., & Gese, E. M. (2016). Resource selection by cougars: Influence of behavioral state and season. *The Journal of Wildlife Management*, *80*(7), 1205–1217. https://doi.org/10.1002/jwmg.21123

Borg, B. L., & Schirokauer, D. W. (2022). The Role of Weather and Long-Term Prey Dynamics as Drivers of Wolf Population Dynamics in a Multi-Prey System. *Frontiers in Ecology and Evolution*, *10*, 791161. https://doi.org/10.3389/fevo.2022.791161

Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecological Modelling*, *157*(2–3), 281–300. https://doi.org/10.1016/S0304-3800(02)00200-4

Clark, D. A., Davidson, G. A., Johnson, B. K., & Anthony, R. G. (2014). Cougar kill rates and prey selection in a multiple-prey system in northeast Oregon: Cougar Kill Rates and Prey Selection. *The Journal of Wildlife Management*, *78*(7), 1161–1176. https://doi.org/10.1002/jwmg.760

Cunningham, C. X., Liston, G. E., Reinking, A. K., Boelman, N. T., Brinkman, T. J., Joly, K., Hebblewhite, M., Boutin, S., Czetwertynski, S., Sielecki, L. E., & Prugh, L. R. (2022). Human and animal movements combine with snow to increase moose-vehicle collisions in winter. *Environmental Research Letters*, *17*(12), 125007. https://doi.org/10.1088/1748-9326/aca8bf

Dailey, T. V., & Hobbs, N. T. (1989). Travel in alpine terrain: Energy expenditures for locomotion by mountain goats and bighorn sheep. *Canadian Journal of Zoology*, *67*(10), 2368–2375. https://doi.org/10.1139/z89-335

Droghini, A., & Boutin, S. (2018). The calm during the storm: Snowfall events decrease the movement rates of grey wolves (Canis lupus). *PLOS ONE*, *13*(10), e0205742. https://doi.org/10.1371/journal.pone.0205742

Elmhagen, B., Berteaux, D., Burgess, R. M., Ehrich, D., Gallant, D., Henttonen, H., Ims, R. A., Killengreen, S. T., Niemimaa, J., Norén, K., Ollila, T., Rodnikova, A., Sokolov, A. A., Sokolova, N. A., Stickney, A. A., & Angerbjörn, A. (2017). Homage to Hersteinsson and Macdonald: Climate warming and resource subsidies cause red fox range expansion and Arctic fox decline. *Polar Research*, *36*(sup1), 3. https://doi.org/10.1080/17518369.2017.1319109

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., … Wardle, D. A. (2011). Trophic Downgrading of Planet Earth. *Science*, *333*(6040), 301–306. https://doi.org/10.1126/science.1205106

Fancy, S. G., & White, R. G. (1987). Energy expenditures for locomotion by barren-ground caribou. *Canadian Journal of Zoology*, *65*(1), 122–128. https://doi.org/10.1139/z87-018

Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., & Alsdorf, D. (2007). The Shuttle Radar Topography Mission. *Reviews of Geophysics*, *45*(2), 2005RG000183. https://doi.org/10.1029/2005RG000183

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, *86*(5), 1320–1330. https://doi.org/10.1890/04-0953

Ganz, T. R., Bassing, S. B., DeVivo, M. T., Gardner, B., Kertson, B. N., Satterfield, L. C., Shipley, L. A., Turnock, B. Y., Walker, S. L., Abrahamson, D., Wirsing, A. J., & Prugh, L. R. (2024). White-tailed deer population dynamics in a multipredator landscape shaped by humans. *Ecological Applications*, *34*(5), e3003. https://doi.org/10.1002/eap.3003

Ganz, T. R., DeVivo, M. T., Kertson, B. N., Roussin, T., Satterfield, L., Wirsing, A. J., & Prugh, L. R. (2022). Interactive effects of wildfires, season and predator activity shape mule deer movements. *Journal of Animal Ecology*, *91*(11), 2273–2288. https://doi.org/10.1111/1365-2656.13810

Ganz, T. R., DeVivo, M. T., Reese, E. M., & Prugh, L. R. (2023). Wildlife whodunnit: Forensic identification of predators to inform wildlife management and conservation. *Wildlife Society Bulletin*, *47*(1), e1386. https://doi.org/10.1002/wsb.1386

Ganz, T. R., DeVivo, M. T., Wirsing, A. J., Bassing, S. B., Kertson, B. N., Walker, S. L., & Prugh, L. R. (2024). Cougars, wolves, and humans drive a dynamic landscape of fear for elk. *Ecology*, *105*(4), e4255. https://doi.org/10.1002/ecy.4255

Gergel, D. R., Nijssen, B., Abatzoglou, J. T., Lettenmaier, D. P., & Stumbaugh, M. R. (2017). Effects of climate change on snowpack and fire potential in the western USA. *Climatic Change*, *141*(2), 287–299. https://doi.org/10.1007/s10584-017-1899-y

Gilbert, S. L., Hundertmark, K. J., Person, D. K., Lindberg, M. S., & Boyce, M. S. (2017). Behavioral plasticity in a variable environment: Snow depth and habitat interactions drive deer movement in winter. *Journal of Mammalogy*, *98*(1), 246–259. https://doi.org/10.1093/jmammal/gyw167

Glass, T. W., Breed, G. A., Liston, G. E., Reinking, A. K., Robards, M. D., & Kielland, K. (2021). Spatiotemporally variable snow properties drive habitat use of an Arctic mesopredator. *Oecologia*, *195*(4), 887–899. https://doi.org/10.1007/s00442-021-04890-2

Hijmans, R. J. (2024). *terra: Spatial Data Analysis* (Version R package version 1.7-78) [Computer software]. https://CRAN.R-project.org/package=terra

Hopcraft, J. G. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, *74*(3), 559–566. https://doi.org/10.1111/j.1365-2656.2005.00955.x

Horne, J. S., Hurley, M. A., White, C. G., & Rachael, J. (2019). Effects of wolf pack size and winter conditions on elk mortality. *The Journal of Wildlife Management*, *83*(5), 1103–1116. https://doi.org/10.1002/jwmg.21689

Hoyer, S., & Hamman, J. (2017). xarray: N-D labeled Arrays and Datasets in Python. *Journal of Open Research Software*, *5*(1), 10. https://doi.org/10.5334/jors.148

Huey, R. B., & Pianka, E. R. (1981). Ecological Consequences of Foraging Mode. *Ecology*, *62*(4), 991–999. https://doi.org/10.2307/1936998

Husseman, J. S., Murray, D. L., Power, G., Mack, C., Wenger, C. R., & Quigley, H. (2003). Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos*, *101*(3), 591–601. https://doi.org/10.1034/j.1600-0706.2003.12230.x

Johnson, C. J., Nielsen, S. E., Merrill, E. H., Mcdonald, T. L., & Boyce, M. S. (2006). Resource Selection Functions Based on Use–Availability Data: Theoretical Motivation and Evaluation Methods. *Journal of Wildlife Management*, *70*(2), 347–357. https://doi.org/10.2193/0022-541X(2006)70%255B347:RSFBOU%255D2.0.CO;2

Johnson, D. H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, *61*(1), 65–71. https://doi.org/10.2307/1937156

Klappstein, N. J., Michelot, T., Fieberg, J., Pedersen, E. J., & Mills Flemming, J. (2024). Step selection functions with non-linear and random effects. *Methods in Ecology and Evolution*, 2041-210X.14367. https://doi.org/10.1111/2041-210X.14367

Knopff, K. H., Knopff, A. A., Warren, M. B., & Boyce, M. S. (2009). Evaluating Global Positioning System Telemetry Techniques for Estimating Cougar Predation Parameters. *The Journal of Wildlife Management*, *73*(4), 586–597. https://doi.org/10.2193/2008-294

Kortello, A. D., Hurd, T. E., & Murray, D. L. (2007). Interactions between cougars (Puma concolor) and gray wolves (Canis lupus) in Banff National Park, Alberta. *Ecoscience*, *14*(2), 214–222. https://doi.org/10.2980/1195-6860(2007)14%255B214:IBCPCA%255D2.0.CO;2

Kunkel, K. E., Ruth, T. K., Pletscher, D. H., & Hornocker, M. G. (1999). Winter Prey Selection by Wolves and Cougars in and Near Glacier National Park Montana. *The Journal of Wildlife Management*, *63*(3), 901. https://doi.org/10.2307/3802804

Lima, S. L. (2002). Putting predators back into behavioral predator–prey interactions. *Trends in Ecology & Evolution*, *17*(2), 70–75. https://doi.org/10.1016/S0169-5347(01)02393-X

Liston, G. E., & Elder, K. (2006). A Distributed Snow-Evolution Modeling System (SnowModel). *Journal of Hydrometeorology*, *7*(6), 1259–1276. https://doi.org/10.1175/JHM548.1

Mahoney, P. J., Liston, G. E., LaPoint, S., Gurarie, E., Mangipane, B., Wells, A. G., Brinkman, T. J., Eitel, J. U. H., Hebblewhite, M., Nolin, A. W., Boelman, N., & Prugh, L. R. (2018). Navigating snowscapes: Scale-dependent responses of mountain sheep to snowpack properties. *Ecological Applications*, *28*(7), 1715–1729. https://doi.org/10.1002/eap.1773

Mech, L. D., & Boitani, L. (2003). Wolf Social Ecology. In *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press.

Mech, L. D., Smith, D. W., Murphy, K. M., & MacNulty, D. R. (2001). Winter Severity and Wolf Predation on a Formerly Wolf-Free Elk Herd. *The Journal of Wildlife Management*, *65*(4), 998. https://doi.org/10.2307/3803048

Mills, M. G. L., Broomhall, L. S., & Du Toit, J. T. (2004). Cheetah *Acinonyx jubatus* feeding ecology in the Kruger National Park and a comparison across African savanna habitats: Is the cheetah only a successful hunter on open grassland plains? *Wildlife Biology*, *10*(3), 177–186. https://doi.org/10.2981/wlb.2004.024

Monterroso, P., Rebelo, P., Alves, P. C., & Ferreras, P. (2016). Niche partitioning at the edge of the range: A multidimensional analysis with sympatric martens. *Journal of Mammalogy*, *97*(3), 928–939. https://doi.org/10.1093/jmammal/gyw016

Morin, A., Chamaillé-Jammes, S., & Valeix, M. (2021). Climate Effects on Prey Vulnerability Modify Expectations of Predator Responses to Short- and Long-Term Climate

Fluctuations. *Frontiers in Ecology and Evolution*, *8*, 601202. https://doi.org/10.3389/fevo.2020.601202

Mower, R., Gutmann, E. D., Liston, G. E., Lundquist, J., & Rasmussen, S. (2024). Parallel SnowModel (v1.0): A parallel implementation of a distributed snow-evolution modeling system (SnowModel). *Geoscientific Model Development*, *17*(10), 4135–4154. https://doi.org/10.5194/gmd-17-4135-2024

Murray, D. L., & Larivière, S. (2002). The relationship between foot size of wild canids and regional snow conditions: Evidence for selection against a high footload? *Journal of Zoology*, *256*(3), 289–299. https://doi.org/10.1017/S095283690200033X

Musselman, K. N., Addor, N., Vano, J. A., & Molotch, N. P. (2021). Winter melt trends portend widespread declines in snow water resources. *Nature Climate Change*, *11*(5), 418–424. https://doi.org/10.1038/s41558-021-01014-9

Natural Resources Conservation Service. (2023). *Air & Water Database Reports, Station 1175* [Dataset]. National Water & Climate Center. https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=1175

Natural Resources Conservation Service. (2024). *Air & Water Database Reports, Station 1259* [Dataset]. National Water & Climate Center. https://nwcc-apps.sc.egov.usda.gov/awdb/site-plots/POR/WTEQ/WA/Muckamuck.html

Nelson, M. E., & Mech, L. D. (1986). Relationship between Snow Depth and Gray Wolf Predation on White-Tailed Deer. *The Journal of Wildlife Management*, *50*(3), 471. https://doi.org/10.2307/3801108

Orsdol, K. G. V. (1984). Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. *African Journal of Ecology*, *22*(2), 79–99. https://doi.org/10.1111/j.1365-2028.1984.tb00682.x

Owen-Smith, N. (2019). Ramifying effects of the risk of predation on African multi-predator, multi-prey large-mammal assemblages and the conservation implications. *Biological Conservation*, *232*, 51–58. https://doi.org/10.1016/j.biocon.2019.01.027

Parker, K. L., Robbins, C. T., & Hanley, T. A. (1984). Energy Expenditures for Locomotion by Mule Deer and Elk. *The Journal of Wildlife Management*, *48*(2), 474. https://doi.org/10.2307/3801180

Pedersen, S. H., Bentzen, T. W., Reinking, A. K., Liston, G. E., Elder, K., Lenart, E. A., Prichard, A. K., & Welker, J. M. (2021). Quantifying effects of snow depth on caribou winter range selection and movement in Arctic Alaska. *Movement Ecology*, *9*(1), 48. https://doi.org/10.1186/s40462-021-00276-4

Peers, M. J. L., Majchrzak, Y. N., Menzies, A. K., Studd, E. K., Bastille-Rousseau, G., Boonstra, R., Humphries, M., Jung, T. S., Kenney, A. J., Krebs, C. J., Murray, D. L., & Boutin, S. (2020). Climate change increases predation risk for a keystone species of the boreal forest. *Nature Climate Change*, *10*(12), 1149–1153. https://doi.org/10.1038/s41558-020-00908-4

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

Peterson, C. J., Mitchell, M. S., DeCesare, N. J., Bishop, C. J., & Sells, S. S. (2021). Habitat selection by wolves and mountain lions during summer in western Montana. *PLOS ONE*, *16*(7), e0254827. https://doi.org/10.1371/journal.pone.0254827

Post, E., Peterson, R. O., Stenseth, N. Chr., & McLaren, B. E. (1999). Ecosystem consequences of wolf behavioural response to climate. *Nature*, *401*(6756), 905–907. https://doi.org/10.1038/44814

Preisser, E. L., Orrock, J. L., & Schmitz, O. J. (2007). PREDATOR HUNTING MODE AND HABITAT DOMAIN ALTER NONCONSUMPTIVE EFFECTS IN PREDATOR–PREY INTERACTIONS. *Ecology*, *88*(11), 2744–2751. https://doi.org/10.1890/07-0260.1

Prugh, L. R., Cunningham, C. X., Windell, R. M., Kertson, B. N., Ganz, T. R., Walker, S. L., & Wirsing, A. J. (2023). Fear of large carnivores amplifies human-caused mortality for mesopredators. *Science*, *380*(6646), 754–758. https://doi.org/10.1126/science.adf2472

Prugh, L. R., Sivy, K. J., Mahoney, P. J., Ganz, T. R., Ditmer, M. A., Van De Kerk, M., Gilbert, S. L., & Montgomery, R. A. (2019). Designing studies of predation risk for improved inference in carnivore-ungulate systems. *Biological Conservation*, *232*, 194–207. https://doi.org/10.1016/j.biocon.2019.02.011

Pulliainen, J., Luojus, K., Derksen, C., Mudryk, L., Lemmetyinen, J., Salminen, M., Ikonen, J., Takala, M., Cohen, J., Smolander, T., & Norberg, J. (2020). Patterns and trends of Northern Hemisphere snow mass from 1980 to 2018. *Nature*, *581*(7808), 294–298. https://doi.org/10.1038/s41586-020-2258-0

Rafiq, K., Jordan, N. R., Golabek, K., McNutt, J. W., Wilson, A., & Abrahms, B. (2023). Increasing ambient temperatures trigger shifts in activity patterns and temporal partitioning in a large carnivore guild. *Proceedings of the Royal Society B: Biological Sciences*.

Reinking, A. K., Højlund Pedersen, S., Elder, K., Boelman, N. T., Glass, T. W., Oates, B. A., Bergen, S., Roberts, S., Prugh, L. R., Brinkman, T. J., Coughenour, M. B., Feltner, J. A., Barker, K. J., Bentzen, T. W., Pedersen, Å. Ø., Schmidt, N. M., & Liston, G. E. (2022). Collaborative wildlife–snow science: Integrating wildlife and snow expertise to improve research and management. *Ecosphere*, *13*(6). https://doi.org/10.1002/ecs2.4094

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science*, *343*(6167), 1241484. https://doi.org/10.1126/science.1241484

Rivrud, I. M., Meisingset, E. L., Loe, L. E., & Mysterud, A. (2019). Future suitability of habitat in a migratory ungulate under climate change. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1899), 20190442. https://doi.org/10.1098/rspb.2019.0442

Salathé, E. P., Leung, L. R., Qian, Y., & Zhang, Y. (2010). Regional climate model projections for the State of Washington. *Climatic Change*, *102*(1–2), 51–75. https://doi.org/10.1007/s10584-010-9849-y

Scaff, L., Krogh, S. A., Musselman, K., Harpold, A., Li, Y., Lillo-Saavedra, M., Oyarzún, R., & Rasmussen, R. (2024). The Impacts of Changing Winter Warm Spells on Snow Ablation Over Western North America. *Water Resources Research*, *60*(5), e2023WR034492. https://doi.org/10.1029/2023WR034492

Scharf, I., Nulman, E., Ovadia, O., & Bouskila, A. (2006). *Efficiency Evaluation of Two Competing Foraging Modes under Different Conditions.* 8.

Schmitz, O. J. (2008). Effects of Predator Hunting Mode on Grassland Ecosystem Function. *Science*, *319*(5865), 952–954. https://doi.org/10.1126/science.1152355

Schmitz, O. J., Krivan, V., & Ovadia, O. (2004). Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecology Letters*, *7*(2), 153–163. https://doi.org/10.1111/j.1461-0248.2003.00560.x

Schmitz, O. J., Miller, J. R. B., Trainor, A. M., & Abrahms, B. (2017). Toward a community ecology of landscapes: Predicting multiple predator–prey interactions across geographic space. *Ecology*, *98*(9), 2281–2292. https://doi.org/10.1002/ecy.1916

Schoener, T. W. (1974). Resource Partitioning in Ecological Communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science*, *185*(4145), 27–39. https://doi.org/10.1126/science.185.4145.27

Sexstone, G. A., Fassnacht, S. R., López-Moreno, J. I., & Hiemstra, C. A. (2016). Subgrid snow depth coefficient of variation within complex mountainous terrain. *The Cryosphere*. https://doi.org/10.5194/tc-2016-188

Signer, J., Fieberg, J., & Avgar, T. (2019). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and Evolution*, *9*(2), 880–890. https://doi.org/10.1002/ece3.4823

Sikes, R. S., & Gannon, W. L. (2011). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, *92*(1), 235–253. https://doi.org/10.1644/10-MAMM-F-355.1

Sivy, K. J., Nolin, A. W., Cosgrove, C. L., & Prugh, L. R. (2018). Critical snow density threshold for Dall's sheep (*Ovis dalli dalli*). *Canadian Journal of Zoology*, *96*(10), 1170–1177. https://doi.org/10.1139/cjz-2017-0259

Smith, J. A., Donadio, E., Bidder, O. R., Pauli, J. N., Sheriff, M. J., Perrig, P. L., & Middleton, A. D. (2020). Where and when to hunt? Decomposing predation success of an ambush carnivore. *Ecology*, *101*(12), e03172. https://doi.org/10.1002/ecy.3172

Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., Bidder, O. R., & Middleton, A. D. (2019). Habitat complexity mediates the predator–prey space race. *Ecology*, *100*(7), e02724. https://doi.org/10.1002/ecy.2724

Smith, T., & Bookhagen, B. (2020). Assessing Multi-Temporal Snow-Volume Trends in High Mountain Asia From 1987 to 2016 Using High-Resolution Passive Microwave Data. *Frontiers in Earth Science*, *8*, 559175. https://doi.org/10.3389/feart.2020.559175

Sullender, B. K., Cunningham, C. X., Lundquist, J. D., & Prugh, L. R. (2023). Defining the danger zone: Critical snow properties for predator–prey interactions. *Oikos*, *2023*(10), e09925. https://doi.org/10.1111/oik.09925

Telfer, E. S., & Kelsall, J. P. (1984). Adaptation of Some Large North American Mammals for Survival In Snow. *Ecology*, *65*(6), 1828–1834. https://doi.org/10.2307/1937779

TerrAdapt. (2022). *TerrAdapt:Cascadia* [Dataset]. https://terradapt.org/regions/cascadia/

Thackeray, C. W., Derksen, C., Fletcher, C. G., & Hall, A. (2019). Snow and Climate: Feedbacks, Drivers, and Indices of Change. *Current Climate Change Reports*, *5*(4), 322–333. https://doi.org/10.1007/s40641-019-00143-w

The pandas development team. (2024). *pandas-dev/pandas: Pandas* (Version v2.2.3) [Computer software]. Zenodo. https://doi.org/10.5281/ZENODO.3509134

Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology*, *2*(1), 4. https://doi.org/10.1186/2051-3933-2-4

Van de Kerk, M., Arthur, S., Bertram, M., Borg, B., Herriges, J., Lawler, J., Mangipane, B., Lambert Koizumi, C., Wendling, B., & Prugh, L. (2020). Environmental Influences on Dall's Sheep Survival. *The Journal of Wildlife Management*, *84*(6), 1127–1138. https://doi.org/10.1002/jwmg.21873

Washington Department of Fish & Wildlife. (2025). *Washington Gray Wolf Conservation and Management 2024 Annual Report*. Washington Department of Fish & Wildlife.

Wilmers, C. C., Metz, M. C., Stahler, D. R., Kohl, M. T., Geremia, C., & Smith, D. W. (2020). How climate impacts the composition of wolf-killed elk in northern Yellowstone National Park. *Journal of Animal Ecology*, *89*(6), 1511–1519. https://doi.org/10.1111/1365-2656.13200

Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., & Yovovich, V. (2015). The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. *Ecology*, *96*(7), 1741–1753. https://doi.org/10.1890/14-1401.1

Wilson, A. M., Lowe, J. C., Roskilly, K., Hudson, P. E., Golabek, K. A., & McNutt, J. W. (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature*, *498*(7453), 185–189. https://doi.org/10.1038/nature12295

Wilson, M. F. J., O'Connell, B., Brown, C., Guinan, J. C., & Grehan, A. J. (2007). Multiscale Terrain Analysis of Multibeam Bathymetry Data for Habitat Mapping on the Continental Slope. *Marine Geodesy*, *30*(1–2), 3–35. https://doi.org/10.1080/01490410701295962

Wood, S. N. (2017). *Generalized additive models: An introduction with R* (2nd ed.). Chapman and Hall/CRC.

Wood, S. N., Scheipl, F., & Faraway, J. J. (2013). Straightforward intermediate rank tensor product smoothing in mixed models. *Statistics and Computing*, *23*(3), 341–360. https://doi.org/10.1007/s11222-012-9314-z

CHAPTER 4: WARM WINTERS, HOT MOOSE: TEMPERATURE DRIVES ACTIVITY AND HABITAT TRADE-OFFS ACROSS A COLD-ADAPTED SPECIES' RANGE

Publication history: A version of this chapter was previously published in *Environmental Research Letters*. The full citation for this publication is:

> Sullender, B.K., C.X. Cunningham, A.K. Reinking, G.E. Liston, R.L. Levine, T.L. Verzuh, N.T. Boelman, S. Boutin, M. Suitor, K.L. Monteith, M. Hebblewhite, T.J. Brinkman, and L.R. Prugh. (*in press)*. Warm winters, hot moose: temperature drives activity and habitat trade-offs across a cold-adapted species' range. *Environmental Research Letters*. https://doi.org/10.1088/1748-9326/ae263a.

4.1 Abstract

Moose (*Alces alces*) are a cold-adapted species that may be vulnerable to overheating at relatively low temperatures in winter. Moose have two main strategies for thermal regulation: shifting activity patterns and selecting habitat that provides thermal refuge. In this study, we compared how moose use these two strategies in response to winter temperature across their latitudinal range. First, we used hidden Markov models to delineate encamped and traveling movement states for five populations of GPS-collared moose in relation to time of day, temperature, and snow depth. Next, we used step-selection functions to determine influential covariates of encamped locations. As air temperatures and snow depths increased, moose from all populations were more likely to remain in an encamped, relatively stationary state. All moose became less diurnal and more nocturnal at high temperatures, although the magnitude of changes

in activity varied by population. Encamped northern moose selected shrubby habitat that presents foraging opportunities, whereas encamped southern moose selected for coniferous forest that provides poor forage but offers shade in southern regions. The only moose population to select for lower temperatures also experienced the warmest winter on record during our study period, which may explain this population's low overall activity rates. Our results indicate that moose along their southern range extent are responding to elevated mid-winter temperatures by initially altering activity patterns and subsequently selecting for potential thermal refugia at the expense of foraging habitat, while northern moose were unlikely to shift habitat selection based on temperature unless faced with an anomalously warm winter. As climate change is implicated in range contraction and population declines, our findings suggest that high winter temperatures may be causing moose to not only reduce overall activity but also to forgo preferred foraging habitat in favor of prioritizing thermal refuge, thus forcing a trade-off between nutrition and thermoregulation.

4.2 Introduction

Northern high-latitude ecosystems are warming at the fastest rates on Earth (Rantanen *et al* 2022), forcing wildlife species to adapt, shift range, or face extinction as temperatures exceed natural capabilities (Pecl *et al* 2017). In order for a species to persist in place, phenotypic plasticity – the ability of an individual to respond to rapidly changing environmental conditions – is of paramount importance due to the comparatively gradual pace of genetic adaptation (Berg *et al* 2010). For large endotherms, phenotypic plasticity is most immediately expressed as changes in behavior. For example, elk (*Cervus canadensis*) in the Greater Yellowstone Ecosystem alter migration timing based on meteorological conditions (Rickbeil *et al* 2019), and muskoxen (*Ovibos moschatus*) in Greenland increase movement rates during extremely cold periods to avoid thermal stress (Schmidt *et al* 2016). Thus, tracking conditions that cause a species to alter its behavior can help determine how and to what extent a species experiences environmental stressors.

As one of the northernmost ungulates, moose (*Alces alces*) are well-adapted to cold winters (Renecker and Hudson 1986, Lundmark 2008). A large body size and dense winter pelage allow moose to maintain core heat without expending additional energy at temperatures as low as -30°C (Renecker and Hudson 1986). However, these physiological adaptations, coupled with a limited ability to dissipate heat (Dussault *et al* 2004), may expose moose to thermal stress at surprisingly low temperatures (McCann *et al* 2013, Thompson *et al* 2020). Indeed, heat stress has been proposed as one reason for population declines and potential range contraction along the southern extent of moose range (Monteith *et al* 2015, Wattles *et al* 2018, Weiskopf *et al* 2019), as thermoregulation may compromise individual fitness by restricting foraging (Ditmer *et al* 2018, Van Beest *et al* 2012). As climate change increases both overall winter temperatures and the frequency, intensity, and duration of warm spells (Perkins *et al* 2012, Scaff *et al* 2024), midwinter heat stress may become more prevalent across the latitudinal range of moose populations.

Even without the added impact of thermal stress, high-latitude winters already present significant physiological challenges for ungulates (Schwartz 1992, Parker *et al* 2009, Kautz *et al* 2020). Snow accumulation constrains forage availability (Hansen *et al* 2011), impedes animal mobility (Sullender *et al* 2023, Mahoney *et al* 2018), and increases energy expenditure (Parker *et al* 1984, Fancy and White 1987), and thus has direct bearing on ungulate overwinter body conditions (Parker *et al* 2009, Garroway and Broders 2005). Vegetation senescence compounds this potential nutritional bottleneck by reducing forage quality and increasing required rumination time (Parker *et al* 1999, Massé and Côté 2012). Cumulatively, these pathways link winter meteorological conditions with changes in annual survival rate, calf body mass, birth rate, population trends, and even species range limits (Lenarz *et al* 2009, Ruprecht *et al* 2016, 2020, Hoy *et al* 2018). Thus, understanding the relationships between temperature, snow depth, and moose phenotypic plasticity holds importance not just for understanding moose behavior but also broader demographic drivers.

Although thermal stress in moose has been widely researched, most studies focus on summer (Felton *et al* 2024). Overall, there is general consensus that moose alter both activity and habitat selection patterns based on temperature: as ambient temperatures increase, moose rest more (Street *et al* 2015), move less during daytime (Montgomery *et al* 2019), and spend more time bedded down (up to 98.7% of daylight hours; Verzuh *et al* 2023). Similarly, moose seek thermal refugia as temperatures increase, selecting for shaded land-cover types (e.g., closed-canopy forests; Dussault *et al* 2006, Leblond *et al* 2010, Melin *et al* 2014, Jennewein *et al* 2020), cooler aspects (Harris *et al* 2023), and wetter sites that promote conductive cooling (Verzuh *et al* 2023). Because moose behavior exhibits such broad changes in response to temperature, the magnitude of these changes can serve as a proxy for heat stress in different populations, and gauge whether a population's thermal tolerance is exceeded.

In this study, we quantify how moose alter movement rates and habitat selection in response to elevated midwinter temperatures across their latitudinal range. First, we apply a physics-based model to generate spatially and temporally distributed temperature and snow information across all of our study areas. Second, we run a two-step analytical approach to quantify how moose respond to temperature changes. We use hidden Markov models (McClintock *et al* 2020) to delineate encamped (i.e., resting, bedded down, or foraging) and traveling (i.e., exploratory) states for each individual moose. We then use step selection functions (Thurfjell *et al* 2014, Klappstein *et al* 2024) to determine the habitat covariates that most influence selection of encamped locations, focusing on shrub-dominated landcover types that provide preferred winter forage and conifer forests that provide inferior forage but better shade in southern regions. Because moose along their southern range limit may be experiencing heat-related range contraction (Monteith *et al* 2015, Weiskopf *et al* 2019) – in contrast to northern moose's range expansion (Zhou *et al* 2020) – we hypothesize that southern moose endure warmer winter conditions that demand a higher degree of behavioral mitigation. Specifically, we expect that southern moose respond to warmer winter conditions by exhibiting stronger behavioral state changes as a function of temperature (*H1*), exhibiting greater shifts in timing of activity based on temperature (*H2*), and more strongly selecting habitat that provides thermal refuge rather than foraging opportunities (*H3*). In so doing, we investigate a unifying framework for how a changing climate may constrain moose distribution.

4.3 Methods

4.3.1 Study Areas

Our study took place across five study areas spanning the entire latitudinal range of moose in North America (Figure 4.1; Table 4.1), from dense coniferous forests in Colorado and Wyoming, USA (~41.4°N) to Arctic tundra in Alaska, USA and the Yukon Territory, Canada (~68.5°N). From south to north, these sites are: Snowy Range, Meeteetse, Alberta-British Columbia, Alberta-North, and Old Crow. Because extreme winter conditions can cause unusual movements of mammals (Prugh *et al* 2024), we compared meteorological conditions during our study period to typical trends for each study area. We defined typical trends using daily winter (December–February) maximum temperature for the last 30 years (NOAA's GHCNd; Menne *et al* 2012, NRCS' SNOTEL stations; Natural Resources Conservation Service 2025), using the station nearest the centroid of each of our study areas.

4.3.2 Moose Locations

We deployed satellite global positioning system (GPS) collars on a total of 126 moose across our five study areas (Figure 4.1; Table 4.1). All deployments followed regional and national animal care and handling standards (Peters *et al* 2013, Boutin *et al* 2015, Cooley *et al* 2019, Levine *et al* 2022, Verzuh *et al* 2023). Only female moose were collared in Snowy Range and Alberta-North, with a combination of male and female moose collared in the other regions. We filtered all data to retain only winter locations, defined as 1 December – 28/29 February. All collars had on-board thermometers, which we bias corrected with generalized linear mixed models to account for known sources of measurement error (Ericsson *et al* 2015, Messeri *et al* 2019, Studd *et al* 2019; details in Appendix C).

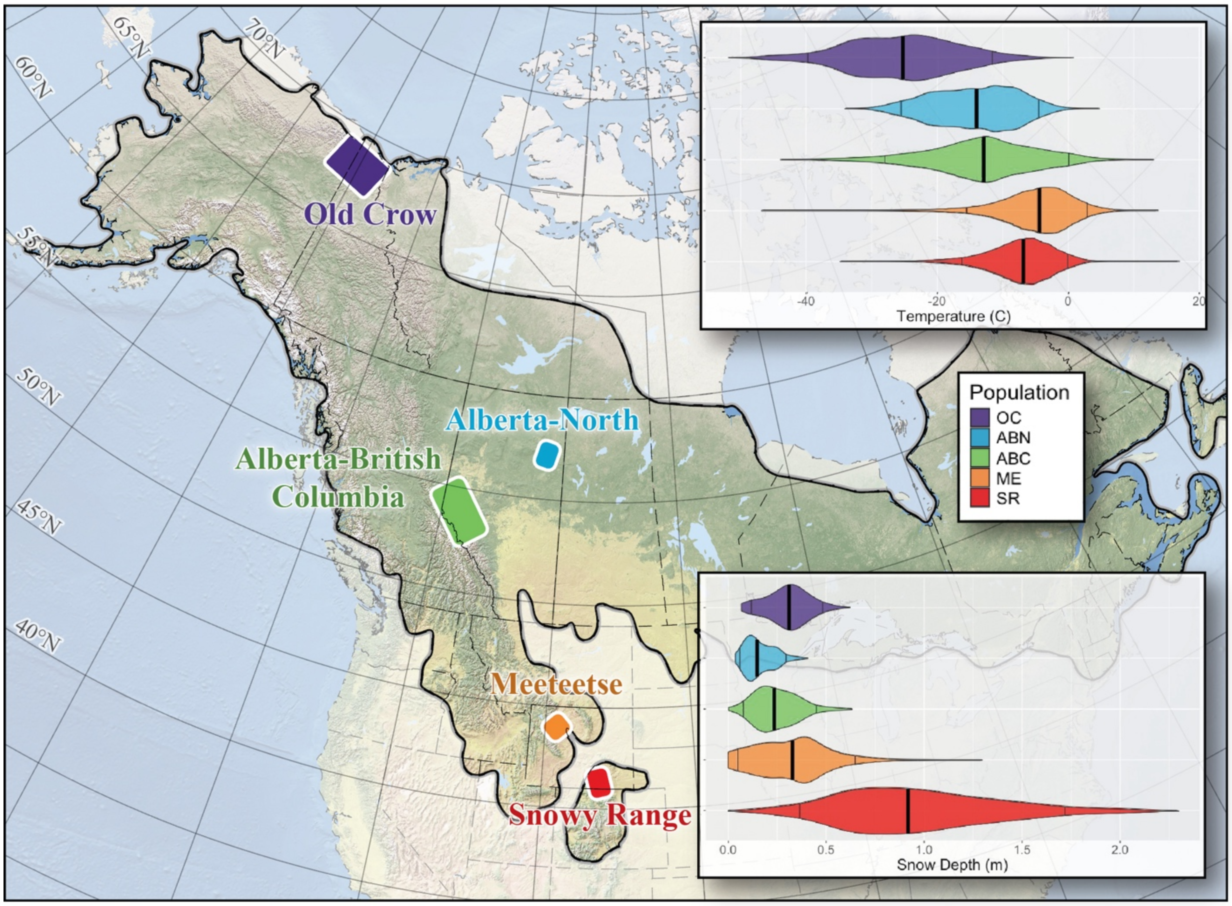

Figure 4.1. Study areas with the five moose populations shown (left) and inset violin plots of winter (i.e., 1 December through 28/29 February) conditions during the years studied. Upper-right inset shows bias-corrected temperature (°C) and lower-right inset shows snow depth (m), with thick lines representing median value for each population and thin lines representing 5th and 95th percentiles.

4.3.3 SnowModel

We used SnowModel, a physics-based modeling system, to derive temperature (Liston and Elder 2006b) and snow depth (Liston and Elder 2006a) at a 100m daily resolution across each study area (Appendix C). To validate SnowModel results, we compared output temperatures with observed weather station data (GHCNh; Menne *et al* 2012) and compared output snow depth with observations from SNOTEL stations for Meeteetse and Snowy Range (Natural Resources Conservation Service 2025). Because there were no SNOTEL stations in Canada, we validated snow depth for Alberta-British Columbia, Alberta-North, and Old Crow with gridded, daily snow reanalysis derived from in-situ observations (Brown and Brasnett 2010).

Table 4.1. Summary of GPS-collared moose analyzed in this study. Because Alberta-British Columbia moose included both 2-hour and 4-hour fix rates, we resampled individuals with a 2-hour fix rate to a common 4-hour interval. For hidden Markov model analysis, all moose fixes were left in their native fix rate resolution. For step-selection function analyses, Meeteetse and Snowy Range moose were resampled to a 4-hour rate to facilitate comparison with other populations and better align with our 100-m resolution temperature and snow depth covariate data.

Study Area	**Centroid Latitude (°N)**	**Date Range**	**Fix Rate (hours)**	***n* fixes**	***n* Animal-Years**
Old Crow	68.5	Dec 2007 - Feb 2009	5	5085	19
Alberta North	57.1	Dec 2010 - Feb 2012	3	17941	35
Alberta-British Columbia	54.1	Dec 2008 - Feb 2010	4	8007	18
Meeteetse	44.0	Dec 2020 - Jan 2023	1	96301	60
Snowy Range	41.4	Dec 2017 - Feb 2021	1	134881	73

4.3.4 Behavioral State Delineation

We generated a series of two-state hidden Markov models (HMMs; McClintock *et al* 2020, Klappstein *et al* 2023) with one state characterized by more localized movements (hereafter, "encamped") and the other characterized by more directional, longer-distance movements (hereafter, "traveling"; Table 4.2). We implemented a two-step approach (details in Appendix C; Klappstein et al. 2023) to model transition probabilities between these two states as a function of time, bias-corrected temperature (as recorded by GPS collar), and snow depth (as modeled by SnowModel). We used the Viterbi algorithm to predict the behavioral state of each moose location (Viterbi 1967, McClintock *et al* 2020). We used the *momentuHMM* package in R for all HMM analyses (McClintock and Michelot 2018).

Next, we tested whether moose altered diurnal activity patterns at different temperatures. Due to pitfalls related to random effect implementation in HMMs (McClintock 2021), we used generalized additive mixed models (GAMMs) to account for both individual variation and nonlinear effects (Pedersen *et al* 2019, Klappstein *et al* 2024), which are prevalent in moose behavior (Graf *et al* 2024, Borowik *et al* 2024). Thus, we combined the benefits of movement-specific HMMs with the flexibility of GAMMs.

We converted clock time to "suntimes" using the *suncalc* package in R (Thieurmel and Elmarhraoui 2022), which better represents seasonal variation in studies that cover a wide range of latitudes (Bonnot *et al* 2020). All activity data were classified as dawn, day, dusk, or night based on astronomical twilight (Appendix C). For each suntime category and population, we modeled moose behavioral state (a binomial response; encamped or traveling) as a function of a global smooth of temperature and an individual-specific deviation from that population-level smooth (Klappstein *et al* 2024). We used the *mgcv* package (Wood 2017) in R for all GAMMs.

Table 4.2. Hidden Markov model (HMM) results and overall state distribution. The two-state model delineated one state with a shorter step length (encamped) from a second with a longer step length (traveling). Hourly movement rates were calculated by dividing the HMM-derived mean step lengths by the fix rate to enable comparison. State distribution calculated using the Viterbi algorithm to classify each location based on temperature, time of day, snow depth, and interactions between these variables.

Population	**Encamped Hourly Movement Rate (SD; meters)**	**Traveling Hourly Movement Rate (SD; meters)**	**Overall Percent of Locations Encamped**
Old Crow	27 (20)	121 (118)	74.3%
Alberta-North	25 (23)	99 (114)	82.2%
Alberta-British Columbia	21 (18)	89 (88)	67.0%
Meeteetse	31 (33)	295 (310)	90.4%
Snowy Range	11 (10)	112 (123)	74.8%

4.3.5 Habitat Selection

We coupled step-selection functions (SSFs; Thurfjell *et al* 2014) with our HMM-based behavioral segmentation output to model how covariates influence moose selection of encamped locations (Klappstein *et al* 2023, Beumer *et al* 2023). These steps were more likely to terminate in preferred habitat for some aspect of moose biology (i.e., foraging, thermal refuge, or safe resting habitat), whereas traveling steps could represent responses to disturbance or movement between suitable habitat patches (Roever *et al* 2014).

We used time-matched 30 m landcover datasets to define habitats offering good moose forage or shade (Latifovic *et al* 2017, Jin *et al* 2013, Commission for Environmental Cooperation 2023). Because moose browse on riparian shrubs and deciduous trees in winter (Schwartz 1992, Poole and Stuart-Smith 2006, Parikh *et al* 2017, Harris *et al* 2023), we selected temperate/subpolar shrub, temperate/subpolar deciduous forest, mixed forest, subpolar shrub-lichen-moss, and wetland areas as providing superior forage conditions. We then calculated the distance to these areas across each study area (hereafter, "forage"). To represent areas that may offer thermal refuge (via shade; Dussault *et al* 2006, Melin *et al* 2014) or reduced snow depth (Lundquist *et al* 2021) but poorer forage (Shipley and Spalinger 1992, Wam and Hjeljord 2010, Felton *et al* 2021), we selected areas with temperate or subpolar conifer forest and calculated the distance to these areas (hereafter, "conifer").

To facilitate comparison of SSF output across moose populations, we resampled all moose collar data to a common four-hour fix rate (Table 4.1). Using the *amt* package in R (Signer *et al* 2019), we randomly generated 20 available steps for each used step from turn angles (using a von Mises distribution) and step lengths (using a gamma distribution), parameterized by each individual's observed movement patterns. We assigned a weight of 5000 to the available locations and a weight of 1 to the used locations (Fieberg *et al* 2021). Finally, we extracted time-matched temperature and snow depth predictions from SnowModel at each location. Because SnowModel generated spatially distributed covariates, we were able to extract values at both used and available locations.

We developed conditional logistic mixed regression models with the *glmmTMB* package (Brooks *et al* 2017). Because snow has non-linear effects on moose movement (Cunningham *et al* 2022), we included a quadratic form of snow depth. We used random slopes to allow individual responses to forage, conifer, and temperature (Muff *et al* 2020) and predicted outcomes using a population-level estimate. Thus, following Klappstein et al. (2024), our model took the form:

$$\eta_{itj} = (\beta_1 + \gamma_{1j}) forage_{itj} + (\beta_2 + \gamma_{2j}) conifer_{itj} + (\beta_3 + \gamma_{3j}) T_{itj} + \beta_4 forage_{it} * T_{it} + \beta_5 conifer_{it} * T_{it} + \beta_6 snod_{it} + \beta_7 {snod_{it}}^2,$$

where η is the linear predictor for the *i*-ith location of stratum *t* for $j \in 1,2,..,n$ individuals, γ terms are vectors of random effects, *forage* and *conifer* are log-transformed distance to nearest forage or conifer cell, *T* is ambient temperature, and *snod* is snow depth. We used *k*-fold cross-validation to evaluate model fit, partitioning each study area's moose movement data into five equal-size subsets, generating an SSF model using four subsets, and using that model to predict SSF values for the withheld subset (Boyce *et al* 2002).

4.4 Results

4.4.1 SnowModel Validation

Overall, we found strong agreement between daily SnowModel temperatures and both hourly (Pearson's $r = 0.919$) and average daily (Pearson's $r = 0.973$) temperatures at a network of weather stations across our study areas, as well as strong agreement between modeled and observed snow depth across all study areas (Pearson's $r = 0.911$; Appendix C).

Compared with 30-year climate normals, three of the five study areas had typical maximum daily temperatures during our study period. Observed winter (December–February) conditions during our study period in Alberta-British Columbia, Meeteetse, and Snowy Range were within 0.8°C of observed 30-year climate means (Appendix C). Our two northernmost populations, however, included highly unusual periods. Our 2007–2009 Old Crow data included two of the coldest stretches on record: six nearly consecutive days when temperatures stayed below -40°C in January–February 2008, and four nearly consecutive days in January 2009 when temperatures stayed below -40°C. In contrast, in 2011-2012, our Alberta-North region experienced the highest average winter maximum temperatures on record: -5.4°C, 1.5 standard deviations above the -9.0°C long-term mean.

4.4.2 Behavioral State Delineation

Across study areas, moose in an encamped state moved on average 22 m/hr, whereas moose in a traveling state moved on average 141 m/hr (Table 4.2). Moose in a traveling state had more directed movements (i.e., a higher density of turning angles close to 0 radians), whereas encamped moose had a nearly-uniform distribution of turn angles (Appendix C). Meeteetse moose, which experienced the highest average temperature of all study areas, were encamped at 90% of observed locations. Alberta-North moose - experiencing the warmest winter in the last 30 years - were similarly in an encamped state at 82% of locations, whereas other moose populations were encamped at 67-75% of locations (Table 4.2).

As temperatures increased, moose were more likely to remain in an encamped state (Figure 4.2a) and were less likely to remain in a traveling state. Deeper snow had a significant effect on behavioral state for only Meeteetse and Snowy Range moose, with both populations more likely to switch from a traveling to an encamped state as snow depth increased (Figure 4.2b). All moose were most sedentary at night (Figure 4.3a-e). Northern moose (Old Crow, Alberta-North, and Alberta-British Columbia) demonstrated similar activity trends across suntimes, becoming more likely to be encamped as temperatures increased, although these trends were weak for Alberta-North moose (Figure 4.3a-c). Southern moose (Meeteetse and Snowy

Range) exhibited major declines in traveling movements as daytime temperatures increased, but were more active at both dawn/dusk and at night as temperatures increased (Figure 4.3d-e).

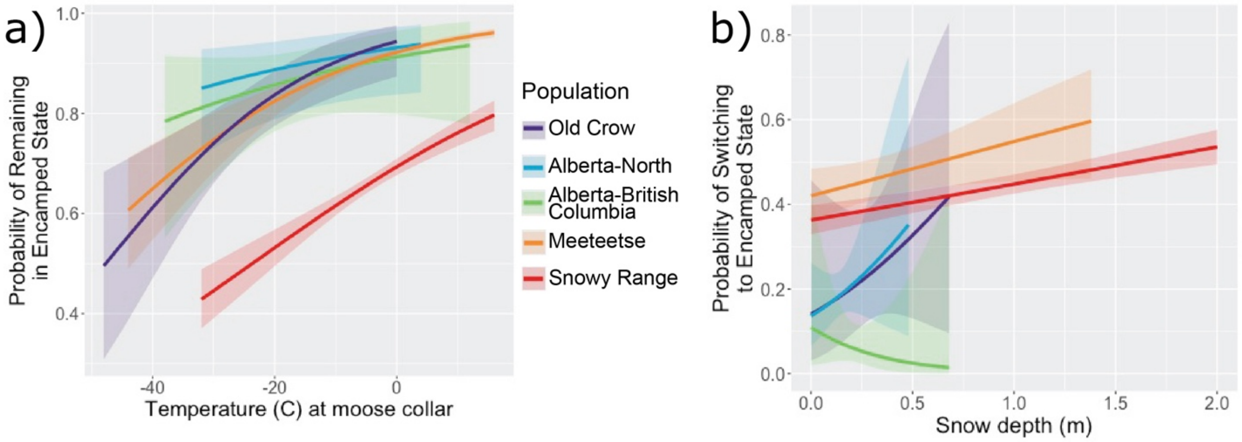

Figure 4.2. Probability of moose transitioning between behavioral states as a function of temperature (a; probability of remaining encamped) and snow depth (b; probability of switching from traveling to encamped). Moose in an encamped state have relatively stationary movement patterns, whereas moose in an traveling state demonstrate more directed and longer distance movements. For both a) and b), time was held constant at noon to control for diurnal activity patterns. For a), snow depth was held constant for all populations at the study-area-wide average (0.39 m). For b), temperature was held constant for all populations for the study-area-wide average (-12.7° C). Only observed ranges of temperatures and snow depths are modeled for each population.

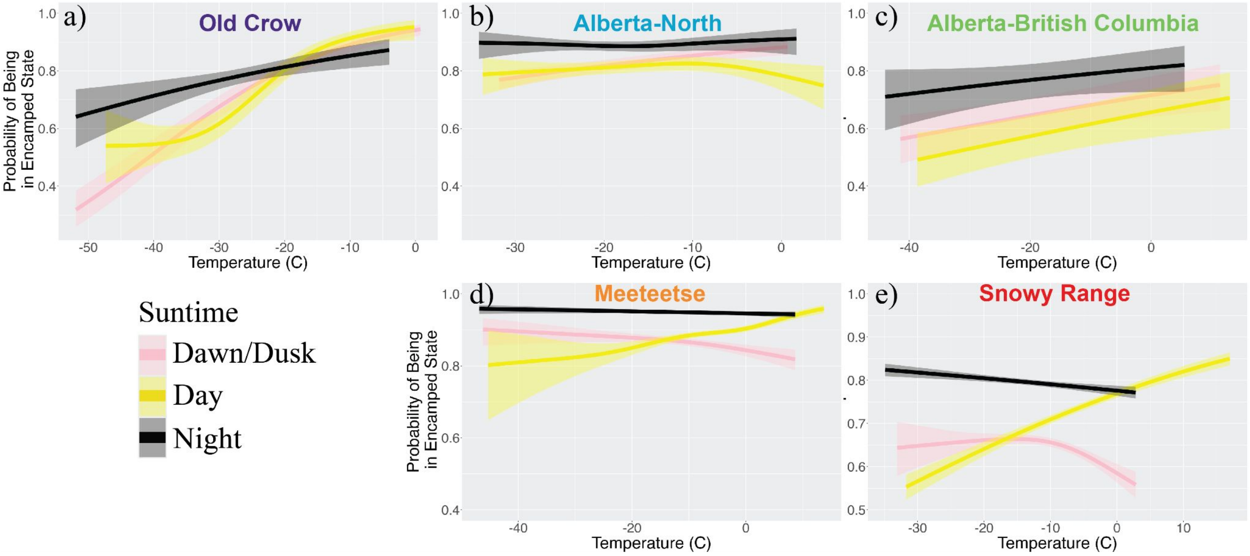

Figure 4.3. Moose activity state as a function temperature and solar time (suntime) across five study areas: (a) Old Crow (northernmost), (b) Alberta-North, (c) Alberta-British Columbia, (d) Meeteetse, (e) and Snowy Range (southernmost). The y-axis represents the probability of being in an encamped (inactive) state, as opposed to a more active (traveling) state. Pink lines show generalized additive mixed models for moose activity state during dawn or dusk (i.e., sun between 0 and 18 degrees on the horizon), yellow lines show moose activity state during daytime, and black lines show moose activity state at night (including polar night). Shaded areas represent 95% confidence intervals.

4.4.3 Habitat Selection

Predictive performance for SSFs was strong across all study areas, as indicated by an average Spearman-rank correlation of 0.786 with five-fold cross-validation (Boyce *et al* 2002). Four of the five moose populations selected for habitat closer to land-cover types that provided preferred forage (Figure 4.4a), with the fifth moose population, Meeteetse, demonstrating marginal selection ($P = 0.0722$). The two southern moose populations strongly selected for areas closer to conifers, with weaker selection from Alberta-North and neither selection nor avoidance from Old Crow and Alberta-British Columbia (Figure 4.4a). Only Alberta-North moose directly selected for lower temperatures. Snow depth had at least a marginal effect ($P < 0.1$) on moose movement for all populations except Alberta-British Columbia, with all populations avoiding snow deeper than 75 cm and selecting between 20 cm and 40 cm of snow (Figure 4.4b).

All moose populations except for Alberta-British Columbia altered habitat selection to some extent based on temperature (Figure 4.5). For the two southernmost moose populations, higher temperatures weakened relative selection for proximity to forage, although this trend was reversed for Old Crow moose (stronger selection for forage at higher temperatures). Only Alberta-North and Snowy Range altered selection towards conifer forest at different temperatures, exhibiting stronger selection at lower temperatures (Figure 4.5e-f). At high temperatures (defined for each study area as 95th percentile; compared to low temperatures at 5th percentile), Snowy Range moose were twice as likely to avoid areas close to forage and Alberta-North moose were twice as likely to select areas close to conifers.

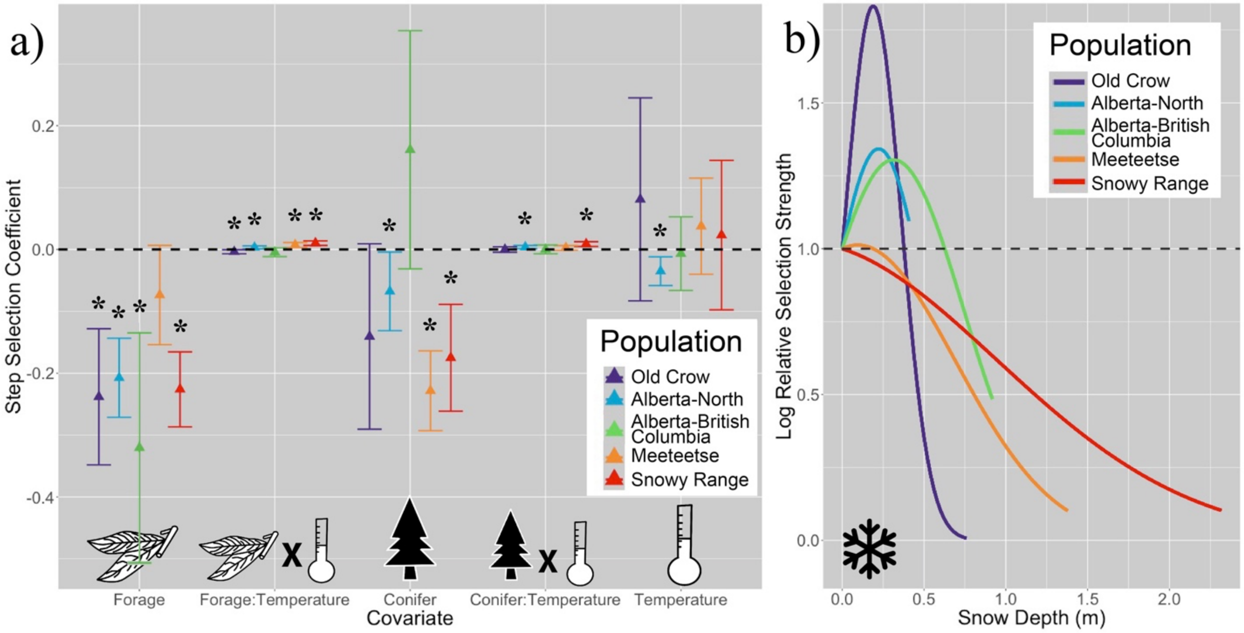

Figure 4.4. Results from step-selection analysis for encamped moose locations. Panel a) shows coefficients for habitat covariates: log of distance to land cover with forage ("Forage"), log of distance to coniferous forest ("Conifer"), temperature at moose collar height, an interaction between log distance to food and temperature ("Forage:Temperature"), and an interaction between log distance to shade and temperature ("Conifer:Temperature"). Asterisks indicate significant coefficients ($P < 0.05$). Panel b) shows the log-relative selection strength (log-RSS) for each moose population at different snow depths. Log-RSS calculated relative to a snow depth of 0m; 95% confidence intervals omitted for clarity, but snow depth and a quadratic form of snow depth were significant covariates for all populations except Alberta-North and Alberta-British Columbia.

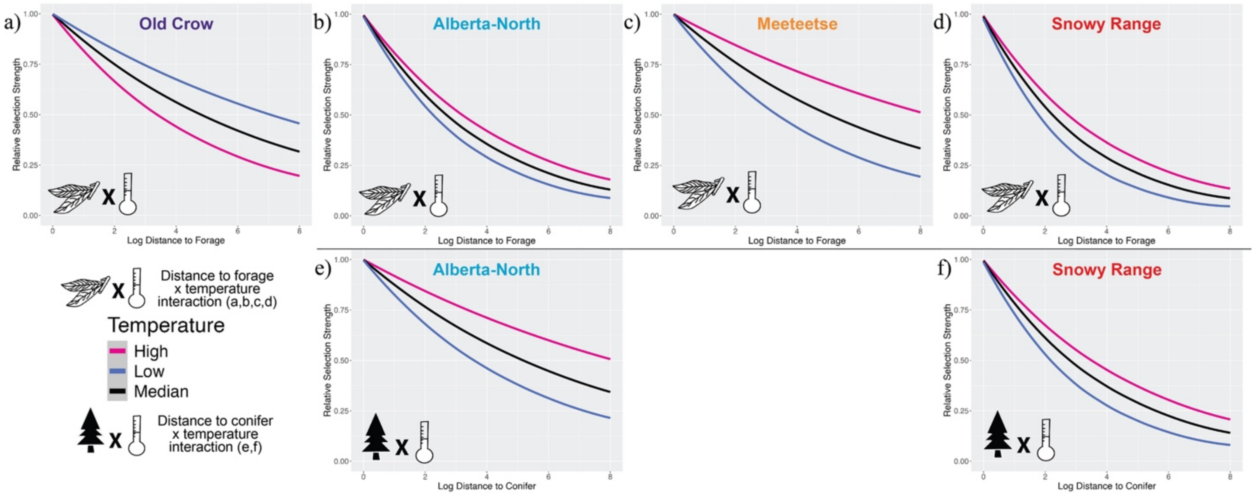

Figure 4.5. Relative selection strength plots comparing the effect of high (red line), median (black line), and low (blue line) temperatures on habitat selection for (a) Old Crow, (b, e) Alberta-North, (c) Meeteetse, and (d, f) Snowy Range moose. Panels a-d show the relative selection strength for distance to forage at different temperatures, and panels e-f show the relative selection strength for distance to conifer at different temperatures. Only predictors for populations with significant interaction terms are shown here; thus, Alberta-British Columbia moose are not included. In each panel, lines representing changes in selection at high (95th percentile of temperature, calculated separately for each study area), median, and low (5th percentile of temperature) temperatures are shown relative to a baseline distance of zero from the focal covariate.

4.5 Discussion

Moose inhabit environments with dramatic seasonal changes in temperature, and temperatures are known to drive their movement and habitat selection patterns in summer (Street *et al* 2015, Alston *et al* 2020, Jennewein *et al* 2020, Verzuh *et al* 2023). We offer novel evidence that, even in midwinter, moose across their latitudinal range experienced high enough temperatures to alter behavior and that the magnitudes of these responses varies by geographic region. Broadly, we found that during the winter, moose were more likely to remain encamped at higher temperatures, shift activity towards cooler times of day, and alter habitat selection based on temperature. By quantifying how different populations of moose responded to elevated temperatures, our work advances understanding of the phenotypic plasticity of moose and their capacity to behaviorally adapt to future climate change.

Despite finding broad patterns of shifting moose behavior, our results do not fully support our specific hypotheses that moose at their southern range limit exhibit stronger temperature-driven shifts in activity patterns and movement than northern moose (*H1-3*). Indeed, the northernmost population exhibited the greatest shift in diurnal timing of activity patterns in response to temperature (counter to *H2*), while the second-northernmost population demonstrated similar changes in temperature-mediated habitat selection as southern moose (counter to *H3*). The unusually warm winter during our study period in Alberta-North may explain some of these unexpected results: extremely low overall movement rates (82.2% in an encamped state; comparable only to Meeteetse at 90.4%) offered little capacity to adjust diurnal patterns (*H1-2*). Notably, Alberta-North moose were the only population to directly select for lower temperatures on the landscape, which may be a response to the sustained warm conditions during the record high winter temperatures.

Still, we noted major differences between moose along their southern range limit and moose in the central and northern portions of their range. Southern moose exhibited more marked behavioral shifts in response to higher temperatures and more strongly selected for areas closer to conifer forest than northern moose. Selection for areas closer to forage was weaker on hotter days than on cooler days for southern moose, whereas this trend was reversed for the northernmost moose. Taken together, these results suggest that cold days could constrain winter foraging for moose at their extreme northern limit, whereas warm days restrict foraging for moose at their southern limit. However, the two periods of unusual cold during our study may poorly reflect typical winter conditions in the Yukon region, especially given the strong local warming trend (1°C/decade in winter; Schetselaar *et al* 2023) since our data were collected - thus, winters may no longer be consistently cold enough to exceed moose's lower thermal tolerance.

The low overall activity rates of southern moose likely represent an adaptation to warm winters. Many endothermic animals respond to high temperatures by reducing activity during the hotter daytime hours (Mole *et al* 2016, Verzuh *et al* 2023). With restricted ability to relocate without incurring activity-induced thermal stress, habitat selection becomes critically important as an organism's thermoregulatory limit is approached (Verzuh *et al* 2023). With the exception of Alberta-North moose during the record-hot 2011-2012, northern moose altered activity patterns during rare hot winter days without shifting habitat selection patterns away from preferred forage. The similarities in habitat selection for southern and Alberta-North moose - especially in concert with their far more limited shifts in activity timing - suggests that shifts in daily activity patterns may be an initial response, whereas habitat shifts are more of a last resort. Moose adaptive capacity in response to warm winters may therefore be somewhat tiered, with widespread and immediate shifts in activity timing and, provided ambient temperatures remain high or are further elevated, a subsequent secondary shift in habitat selection.

The difference between selecting conifer and selecting preferred forage habitat likely has nutritional consequences. In winter, moose primarily forage on deciduous trees and riparian shrubs, especially willows (*Salix* spp.; Schwartz 1992, Poole and Stuart-Smith 2006, Parikh *et al*

2017). Nutritionally, these plants offer high digestible energy and digestible protein (Schrempp *et al* 2019), whereas conifers instead require more handling and rumination time (Shipley and Spalinger 1992, Felton *et al* 2021). Although moose can and do consume conifers, a conifer-based diet is often an indicator for suboptimal food resources (Danell *et al* 1991, Wam and Hjeljord 2010). Mature coniferous forest diminishes wind (Sexstone *et al* 2016), decreases snow accumulation (Lundquist *et al* 2013), and reduces surface-level shortwave radiation although solar radiation is negligible for northern regions in mid-winter (Lundquist *et al* 2013). We suggest that moose selection of conifers is most likely driven by this latter variable (i.e., shade) for southern moose, as our models explicitly account for snow depth and wind is less important than solar radiation for moose heat stress (Thompson *et al* 2020, Verzuh *et al* 2023). Furthermore, moose exploit shady coniferous forest to provide thermal refuge in summer (Melin *et al* 2014, Alston *et al* 2020), a behavior that we demonstrate happens in winter as well. The shift by southern moose towards coniferous areas – in contrast to northern moose selection for deciduous and shrub-dominated habitat – is an indication that thermoregulation limits foraging at the southern extent of moose range.

The response of moose to changes in their thermal environment is more complex than the relationships we quantify here. The secondary responses (behavioral patterns and habitat selection) we analyzed could be further strengthened by including physiological measurements of thermal stress (e.g., respiration rate, cortisol, piloerection; Thompson *et al* 2020). Additionally, time lags at multiple scales influence mammal thermoregulation: cumulative effects of daily environmental conditions (e.g., a previous day's hot weather raises current moose body temperature; Thompson *et al* 2020), seasonal adjustments to coat thickness and homeostatic body temperature ranges (Hetem *et al* 2016), and evolutionary-scale changes such as larger body size at northern latitudes (i.e., Bergmann's rule; Herfindal *et al* 2006). Moose may be able to compensate for inferior foraging habitat through other adaptations not analyzed here.

Climate change will not exert uniform pressures across the entirety of moose range. The climate-aided poleward expansion of shrubs appears to be a key factor in moose colonization of Arctic tundra (Tape *et al* 2016, Zhou *et al* 2020), and projected overall reductions in snow depth may enhance body condition and open new winter habitats (Poole and Stuart-Smith 2006, Holmes *et al* 2021, Cunningham *et al* 2022). However, climate change may also exacerbate moose range contraction: higher ambient temperatures are associated with elevated parasite loads (Debow *et al* 2021, DeCesare *et al* 2024, Pouchet *et al* 2024), declining moose survival (Lenarz *et al* 2009), reduced reproductive output (Ruprecht *et al* 2016), and, as we show, a potential decline in overall nutrition that may decrease individual fitness (Van Beest *et al* 2012). With thermoregulation already driving behavioral trade-offs for northern ungulates in summer (Williamsen *et al* 2019, Levine *et al* 2025), the effects of climate change may extend these trade-offs into winter, especially along the warmer margins of suitable habitat.

Thermoregulation contributes to moose activity patterns and habitat selection across their latitudinal range. This process is apparent even in mid-winter: high ambient temperatures drive moose to first adjust the daily timing of activity and subsequently prioritize thermal refugia. Because thermal refuge comes at the expense of foraging opportunities, these behavioral adaptations may compound a seasonal nutritional bottleneck for northern ungulates and exacerbate heat-related impacts at a demographic and population level (Ruprecht *et al* 2020, Kautz *et al* 2020). As midwinter warm spells increase in frequency, intensity, and duration (Perkins *et al* 2012, Scaff *et al* 2024), the aggregated costs of forgone foraging may prove detrimental for cold-adapted herbivores such as moose.

4.7 References

Alston J M, Joyce M J, Merkle J A and Moen R A 2020 Temperature shapes movement and habitat selection by a heat-sensitive ungulate *Landscape Ecol* **35** 1961–73

Berg M P, Kiers E T, Driessen G, Van Der Heijden M, Kooi B W, Kuenen F, Liefting M, Verhoef H A and Ellers J 2010 Adapt or disperse: understanding species persistence in a changing world *Global Change Biology* **16** 587–98

Beumer L T, Schmidt N M, Pohle J, Signer J, Chimienti M, Desforges J, Hansen L H, Højlund Pedersen S, Rudd D A, Stelvig M and Van Beest F M 2023 Accounting for behaviour in fine-scale habitat selection: A case study highlighting methodological intricacies *Journal of Animal Ecology* **92** 1937–53

Bonnot N C, Couriot O, Berger A, Cagnacci F, Ciuti S, De Groeve J E, Gehr B, Heurich M, Kjellander P, Kröschel M, Morellet N, Sönnichsen L and Hewison A J M 2020 Fear of the dark? Contrasting impacts of humans versus lynx on diel activity of roe deer across Europe ed E Vander Wal *Journal of Animal Ecology* **89** 132–45

Borowik T, Kowalczyk R, Ratkiewicz M, Maślanko W, Duda N and Żmihorski M 2024 A highly variable habitat selection in moose across diel and seasonal scales *Mov Ecol* **12** 69

Boutin S A, Bohm H, Neilson E, Droghini A and Mare C D L 2015 *Wildlife Habitat Effectiveness and Connectivity Final Report August 2015* (Unpublished) Online: http://rgdoi.net/10.13140/RG.2.2.35281.38240

Boyce M S, Vernier P R, Nielsen S E and Schmiegelow F K A 2002 Evaluating resource selection functions *Ecological Modelling* **157** 281–300

Brooks M E, Kristensen K, Benthem K J ,van, Magnusson A, Berg C W, Nielsen A, Skaug H J, Mächler M and Bolker B M 2017 glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling *The R Journal* **9** 378

Brown R and Brasnett B 2010 Canadian Meteorological Centre (CMC) daily snow depth analysis data, version 1 *NASA National Snow and Ice Data Center Distributed Active Archive Center (DAAC) data set* W9FOYWH0EQZ3

Commission for Environmental Cooperation 2023 2020 Land Cover of North America at 30 Meters Online: http://www.cec.org/north-american-environmental-atlas/land-cover-30m-2020/

Cooley D, Clarke H, Graupe S, Landry-Cuerrier M, Lantz T, Milligan H, Pretzlaw T, Larocque G and Humphries M M 2019 The Seasonliaty of a Migratory Moose Population in Northern Yukon *Alces* **55**

Cunningham C X, Liston G E, Reinking A K, Boelman N T, Brinkman T J, Joly K, Hebblewhite M, Boutin S, Czetwertynski S, Sielecki L E and Prugh L R 2022 Human and animal movements combine with snow to increase moose-vehicle collisions in winter *Environ. Res. Lett.* **17** 125007

Danell K, Niemela P, Varvikko T and Vuorisalo T 1991 Moose Browsing on Scots Pine along a Gradient of Plant Productivity *Ecology* **72** 1624–33

Debow J, Blouin J, Rosenblatt E, Alexander C, Gieder K, Cottrell W, Murdoch J and Donovan T 2021 Effects of Winter Ticks and Internal Parasites on Moose Survival in Vermont, USA *J Wildl Manag* **85** 1423–39

DeCesare N J, Harris R B, Atwood M P, Bergman E J, Courtemanch A B, Cross P C, Fralick G L, Hersey K R, Hurley M A, Koser T M, Levine R L, Monteith K L, Newby J R, Peterson

C J, Robertson S and Wise B L 2024 Warm places, warm years, and warm seasons increase parasitizing of moose by winter ticks *Ecosphere* **15** e4799

Ditmer M A, Moen R A, Windels S K, Forester J D, Ness T E and Harris T R 2018 Moose at their bioclimatic edge alter their behavior based on weather, landscape, and predators *Current Zoology* **64** 419–32

Dussault C, Courtois R and Ouellet J-P 2006 A habitat suitability index model to assess moose habitat selection at multiple spatial scales *Can. J. For. Res.* **36** 1097–107

Dussault C, Ouellet J-P, Courtois R, Huot J, Breton L and Larochelle J 2004 Behavioural responses of moose to thermal conditions in the boreal forest *Écoscience* **11** 321–8

Ericsson G, Dettki H, Neumann W, Arnemo J M and Singh N J 2015 Offset between GPS collar-recorded temperature in moose and ambient weather station data *Eur J Wildl Res* **61** 919–22

Fancy S G and White R G 1987 Energy expenditures for locomotion by barren-ground caribou *Can. J. Zool.* **65** 122–8

Felton A M, Wam H K, Borowski Z, Granhus A, Juvany L, Matala J, Melin M, Wallgren M and Mårell A 2024 Climate change and deer in boreal and temperate regions: From physiology to population dynamics and species distributions *Global Change Biology* **30** e17505

Felton A M, Wam H K, Felton A, Simpson S J, Stolter C, Hedwall P, Malmsten J, Eriksson T, Tigabo M and Raubenheimer D 2021 Macronutrient balancing in free-ranging populations of moose *Ecology and Evolution* **11** 11223–40

Fieberg J, Signer J, Smith B and Avgar T 2021 A 'How to' guide for interpreting parameters in habitat-selection analyses *Journal of Animal Ecology* **90** 1027–43

Garroway C J and Broders H G 2005 The quantitative effects of population density and winter weather on the body condition of white-tailed deer (*Odocoileus virginianus*) in Nova Scotia, Canada *Can. J. Zool.* **83** 1246–56

Graf L, Thurfjell H, Ericsson G and Neumann W 2024 Naivety dies with the calf: calf loss to human hunters imposes behavioral change in a long-lived but heavily harvested ungulate *Mov Ecol* **12** 66

Hansen B B, Aanes R, Herfindal I, Kohler J and Sæther B-E 2011 Climate, icing, and wild arctic reindeer: past relationships and future prospects *Ecology* **92** 1917–23

Harris R B, DeCesare N J, Newby J R and Peterson C J 2023 Habitat Use and Selection by Adult Female Moose in Northwestern Montana: Vegetation Types, Forest Disturbance, and Thermal Refuge *Alces* **59**

Herfindal I, Solberg E J, Sæther B-E, Høgda K A and Andersen R 2006 Environmental phenology and geographical gradients in moose body mass *Oecologia* **150** 213–24

Hetem R S, Maloney S K, Fuller A and Mitchell D 2016 Heterothermy in large mammals: inevitable or implemented? *Biological Reviews* **91** 187–205

Holmes S M, Cromsigt J P G M, Danell K, Ericsson G, Singh N J and Widemo F 2021 Declining recruitment and mass of Swedish moose calves linked to hot, dry springs and snowy winters *Global Ecology and Conservation* **27** e01594

Hoy S R, Peterson R O and Vucetich J A 2018 Climate warming is associated with smaller body size and shorter lifespans in moose near their southern range limit *Global Change Biology* **24** 2488–97

Jennewein J S, Hebblewhite M, Mahoney P, Gilbert S, Meddens A J H, Boelman N T, Joly K, Jones K, Kellie K A, Brainerd S, Vierling L A and Eitel J U H 2020 Behavioral modifications by a large-northern herbivore to mitigate warming conditions *Mov Ecol* **8** 39

Jin S, Yang L, Danielson P, Homer C, Fry J and Xian G 2013 A comprehensive change detection method for updating the National Land Cover Database to circa 2011 *Remote Sensing of Environment* **132** 159–75

Kautz T M, Belant J L, Beyer D E, Strickland B K and Duquette J F 2020 Influence of body mass and environmental conditions on winter mortality risk of a northern ungulate: Evidence for a late-winter survival bottleneck *Ecology and Evolution* **10** 1666–77

Klappstein N J, Michelot T, Fieberg J, Pedersen E J and Mills Flemming J 2024 Step selection functions with non-linear and random effects *Methods Ecol Evol* 2041-210X.14367

Klappstein N J, Thomas L and Michelot T 2023 Flexible hidden Markov models for behaviour-dependent habitat selection *Mov Ecol* **11** 30

Latifovic R, Pouliot D and Olthof I 2017 Circa 2010 Land Cover of Canada: Local Optimization Methodology and Product Development *Remote Sensing* **9** 1098

Leblond M, Dussault C and Ouellet J 2010 What drives fine-scale movements of large herbivores? A case study using moose *Ecography* **33** 1102–12

Lenarz M S, Nelson M E, Schrage M W and Edwards A J 2009 Temperature Mediated Moose Survival in Northeastern Minnesota *J Wildl Manag* **73** 503–10

Levine R L, Dwinnell S P H, Kroger B, Class C and Monteith K L 2022 Helicopter-based immobilization of moose using butorphanol–azaperone–medetomidine *Wildlife Society Bulletin* **46** e1327

Levine R L, Verzuh T L, Mathewson P D, Porter W P, Kroger B and Monteith K L 2025 Sex-specific trade-offs influence thermoregulation under climate change *Ecology* **106** e70138

Liston G E and Elder K 2006a A Distributed Snow-Evolution Modeling System (SnowModel) *Journal of Hydrometeorology* **7** 1259–76

Liston G E and Elder K 2006b A Meteorological Distribution System for High-Resolution Terrestrial Modeling (MicroMet) *Journal of Hydrometeorology* **7** 217–34

Lundmark C 2008 *Morphological and Behavioural Adaptations of Moose to Climate, Snow, and Forage* PhD Thesis (Umeå, Sweden: Swedish University of Agricultural Sciences)

Lundquist J D, Dickerson-Lange S E, Lutz J A and Cristea N C 2013 Lower forest density enhances snow retention in regions with warmer winters: A global framework developed from plot-scale observations and modeling: Forests and Snow Retention *Water Resour. Res.* **49** 6356–70

Lundquist J D, Dickerson-Lange S, Gutmann E, Jonas T, Lumbrazo C and Reynolds D 2021 Snow interception modelling: Isolated observations have led to many land surface models lacking appropriate temperature sensitivities *Hydrological Processes* **35** Online: https://onlinelibrary.wiley.com/doi/10.1002/hyp.14274

Mahoney P J, Liston G E, LaPoint S, Gurarie E, Mangipane B, Wells A G, Brinkman T J, Eitel J U H, Hebblewhite M, Nolin A W, Boelman N and Prugh L R 2018 Navigating snowscapes: scale-dependent responses of mountain sheep to snowpack properties *Ecol Appl* **28** 1715–29

Massé A and Côté S D 2012 Linking alternative food sources to winter habitat selection of herbivores in overbrowsed landscapes *J Wildl Manag* **76** 544–56

McCann N P, Moen R A and Harris T R 2013 Warm-season heat stress in moose (*Alces alces*) *Can. J. Zool.* **91** 893–8

McClintock B T 2021 Worth the effort? A practical examination of random effects in hidden Markov models for animal telemetry data *Methods Ecol Evol* **12** 1475–97

McClintock B T, Langrock R, Gimenez O, Cam E, Borchers D L, Glennie R and Patterson T A 2020 Uncovering ecological state dynamics with hidden Markov models *Ecology Letters* **23** 1878–903

McClintock B T and Michelot T 2018 momentuHMM: R package for generalized hidden Markov models of animal movement ed S Goslee *Methods Ecol Evol* **9** 1518–30

Melin M, Matala J, Mehtätalo L, Tiilikainen R, Tikkanen O, Maltamo M, Pusenius J and Packalen P 2014 Moose (*Alces alces*) reacts to high summer temperatures by utilizing thermal shelters in boreal forests – an analysis based on airborne laser scanning of the canopy structure at moose locations *Global Change Biology* **20** 1115–25

Menne M J, Durre I, Vose R S, Gleason B E and Houston T G 2012 An Overview of the Global Historical Climatology Network-Daily Database *Journal of Atmospheric and Oceanic Technology* **29** 897–910

Messeri A, Becciolini V, Messeri G, Morabito M, Crisci A, Orlandini S and Ponzetta M P 2019 Wild ungulates and environmental temperature: analysis on the possible utilization of data from sensor placed on GPS collars *Int J Biometeorol* **63** 293–300

Mole M A, Rodrigues DÁraujo S, Van Aarde R J, Mitchell D and Fuller A 2016 Coping with heat: behavioural and physiological responses of savanna elephants in their natural habitat *Conserv Physiol* **4** cow044

Monteith K L, Klaver R W, Hersey K R, Holland A A, Thomas T P and Kauffman M J 2015 Effects of climate and plant phenology on recruitment of moose at the southern extent of their range *Oecologia* **178** 1137–48

Montgomery R A, Redilla K M, Moll R J, Van Moorter B, Rolandsen C M, Millspaugh J J and Solberg E J 2019 Movement modeling reveals the complex nature of the response of moose to ambient temperatures during summer *Journal of Mammalogy* **100** 169–77

Muff S, Signer J and Fieberg J 2020 Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation ed E V Wal *Journal of Animal Ecology* **89** 80–92

Natural Resources Conservation Service 2025 Air & Water Database Reports Online: https://nwcc-apps.sc.egov.usda.gov/awdb/site-plots/POR/WTEQ/WA/Muckamuck.html

Parikh G L, Forbey J S, Robb B, Peterson R O, Vucetich L M and Vucetich J A 2017 The influence of plant defensive chemicals, diet composition, and winter severity on the nutritional condition of a free-ranging, generalist herbivore *Oikos* **126** oik.03359

Parker K L, Barboza P S and Gillingham M P 2009 Nutrition integrates environmental responses of ungulates *Functional Ecology* **23** 57–69

Parker K L, Gillingham M P, Hanley T A and Robbins C T 1999 Energy and Protein Balance of Free-Ranging Black-Tailed Deer in a Natural Forest Environment *Wildlife Monographs* 47

Parker K L, Robbins C T and Hanley T A 1984 Energy Expenditures for Locomotion by Mule Deer and Elk *The Journal of Wildlife Management* **48** 474

Pecl G T, Araújo M B, Bell J D, Blanchard J, Bonebrake T C, Chen I-C, Clark T D, Colwell R K, Danielsen F, Evengård B, Falconi L, Ferrier S, Frusher S, Garcia R A, Griffis R B, Hobday A J, Janion-Scheepers C, Jarzyna M A, Jennings S, Lenoir J, Linnetved H I, Martin V Y, McCormack P C, McDonald J, Mitchell N J, Mustonen T, Pandolfi J M, Pettorelli N, Popova E, Robinson S A, Scheffers B R, Shaw J D, Sorte C J B, Strugnell J

M, Sunday J M, Tuanmu M-N, Vergés A, Villanueva C, Wernberg T, Wapstra E and Williams S E 2017 Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being *Science* **355** eaai9214

Pedersen E J, Miller D L, Simpson G L and Ross N 2019 Hierarchical generalized additive models in ecology: an introduction with mgcv *PeerJ* **7** e6876

Perkins S E, Alexander L V and Nairn J R 2012 Increasing frequency, intensity and duration of observed global heatwaves and warm spells *Geophysical Research Letters* **39** 2012GL053361

Peters W, Hebblewhite M, DeCesare N, Cagnacci F and Musiani M 2013 Resource separation analysis with moose indicates threats to caribou in human altered landscapes *Ecography* **36** 487–98

Poole K G and Stuart-Smith K 2006 Winter habitat selection by female moose in western interior montane forests *Can. J. Zool.* **84** 1823–32

Pouchet C, Fernandez-Prada C, Dussault C, Leclerc M, Tremblay J and Côté S D 2024 Linking weather conditions and winter tick abundance in moose *J Wildl Manag* **88** e22551

Prugh L R, Lundquist J D, Sullender B K, Cunningham C X, Dechow J, Borg B L, Sousanes P J, Stehn S and Durand M T 2024 Landscape heterogeneity buffers the impact of an extreme weather event on wildlife *Commun Biol* **7** 1515

Rantanen M, Karpechko A Yu, Lipponen A, Nordling K, Hyvärinen O, Ruosteenoja K, Vihma T and Laaksonen A 2022 The Arctic has warmed nearly four times faster than the globe since 1979 *Commun Earth Environ* **3** 168

Renecker L A and Hudson R J 1986 Seasonal energy expenditures and thermoregulatory responses of moose *Can. J. Zool.* **64** 322–7

Rickbeil G J M, Merkle J A, Anderson G, Atwood M P, Beckmann J P, Cole E K, Courtemanch A B, Dewey S, Gustine D D, Kauffman M J, McWhirter D E, Mong T, Proffitt K, White P J and Middleton A D 2019 Plasticity in elk migration timing is a response to changing environmental conditions *Global Change Biology* **25** 2368–81

Roever C L, Beyer H L, Chase M J and Van Aarde R J 2014 The pitfalls of ignoring behaviour when quantifying habitat selection *Diversity and Distributions* **20** 322–33

Ruprecht J S, Hersey K R, Hafen K, Monteith K L, DeCesare N J, Kauffman M J and MacNulty D R 2016 Reproduction in moose at their southern range limit *Journal of Mammalogy* **97** 1355–65

Ruprecht J S, Koons D N, Hersey K R, Hobbs N T and MacNulty D R 2020 The effect of climate on population growth in a cold-adapted ungulate at its equatorial range limit *Ecosphere* **11** e03058

Scaff L, Krogh S A, Musselman K, Harpold A, Li Y, Lillo-Saavedra M, Oyarzún R and Rasmussen R 2024 The Impacts of Changing Winter Warm Spells on Snow Ablation Over Western North America *Water Resources Research* **60** e2023WR034492

Schetselaar A, Andersen T and Burn C R 2023 Performance of Climate Projections for Yukon and Adjacent Northwest Territories, 1991 – 2020 *Arctic* **76** 244–64

Schmidt N M, Van Beest F M, Mosbacher J B, Stelvig M, Hansen L H, Nabe-Nielsen J and Gr⊘ndahl C 2016 Ungulate movement in an extreme seasonal environment: year-round movement patterns of high-arctic muskoxen *Wildlife Biology* **22** 253–67

Schrempp T V, Rachlow J L, Johnson T R, Shipley L A, Long R A, Aycrigg J L and Hurley M A 2019 Linking forest management to moose population trends: The role of the nutritional landscape ed A K Fuller *PLoS ONE* **14** e0219128

Schwartz C 1992 Physiological and Nutritional Adaptations of Moose to Northern Environments *Alces* 139–55

Sexstone G A, Fassnacht S R, López-Moreno J I and Hiemstra C A 2016 Subgrid snow depth coefficient of variation within complex mountainous terrain *The Cryosphere* Online: https://tc.copernicus.org/preprints/tc-2016-188/

Shipley L A and Spalinger D E 1992 Mechanics of browsing in dense food patches: effects of plant and animal morphology on intake rate *Can. J. Zool.* **70** 1743–52

Signer J, Fieberg J and Avgar T 2019 Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses *Ecology and Evolution* **9** 880–90

Street G M, Rodgers A R and Fryxell J M 2015 Mid-day temperature variation influences seasonal habitat selection by moose: Temperature Dependent Moose Habitat Selection *Jour. Wild. Mgmt.* **79** 505–12

Studd E K, Landry-Cuerrier M, Menzies A K, Boutin S, McAdam A G, Lane J E and Humphries M M 2019 Behavioral classification of low-frequency acceleration and temperature data from a free-ranging small mammal *Ecology and Evolution* **9** 619–30

Sullender B K, Cunningham C X, Lundquist J D and Prugh L R 2023 Defining the danger zone: critical snow properties for predator–prey interactions *Oikos* **2023** e09925

Tape K D, Gustine D D, Ruess R W, Adams L G and Clark J A 2016 Range Expansion of Moose in Arctic Alaska Linked to Warming and Increased Shrub Habitat ed M S Crowther *PLoS ONE* **11** e0152636

Thieurmel B and Elmarhraoui A 2022 suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase Online: https://CRAN.R-project.org/package=suncalc

Thompson D P, Crouse J A, Jaques S and Barboza P S 2020 Redefining physiological responses of moose (Alces alces) to warm environmental conditions *Journal of Thermal Biology* **90** 102581

Thurfjell H, Ciuti S and Boyce M S 2014 Applications of step-selection functions in ecology and conservation *Mov Ecol* **2** 4

Van Beest F M, Van Moorter B and Milner J M 2012 Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate *Animal Behaviour* **84** 723–35

Verzuh T L, Rogers S A, Mathewson P D, May A, Porter W P, Class C, Knox L, Cufaude T, Hall L E, Long R A and Monteith K L 2023 Behavioural responses of a large, heat-sensitive mammal to climatic variation at multiple spatial scales *Journal of Animal Ecology* **92** 619–34

Viterbi A 1967 Error bounds for convolutional codes and an asymptotically optimum decoding algorithm *IEEE Trans. Inform. Theory* **13** 260–9

Wam H K and Hjeljord O 2010 Moose summer and winter diets along a large scale gradient of forage availability in southern Norway *Eur J Wildl Res* **56** 745–55

Wattles D W, Zeller K A and DeStefano S 2018 Range expansion in unfavorable environments through behavioral responses to microclimatic conditions: Moose (Alces americanus) as the model *Mammalian Biology* **93** 189–97

Weiskopf S R, Ledee O E and Thompson L M 2019 Climate change effects on deer and moose in the Midwest *J Wildl Manag* **83** 769–81

Williamsen L, Pigeon G, Mysterud A, Stien A, Forchhammer M and Loe L E 2019 Keeping cool in the warming Arctic: thermoregulatory behaviour by Svalbard reindeer (*Rangifer tarandus platyrhynchus*) *Can. J. Zool.* **97** 1177–85

Wood S N 2017 *Generalized additive models: an introduction with R* (Chapman and Hall/CRC)

Zhou J, Tape K D, Prugh L, Kofinas G, Carroll G and Kielland K 2020 Enhanced shrub growth in the Arctic increases habitat connectivity for browsing herbivores *Global Change Biology* **26** 3809–20

CHAPTER 5: CLIMATE CHANGE DIMINISHES SNOW-MEDIATED MOVEMENT ADVANTAGE FOR APEX PREDATORS

5.1 Abstract

Climate change is rapidly altering geophysical processes across the planet, with uncertain impacts on species interactions. Snow cover is a critical driver of predator-prey dynamics across much of the Northern Hemisphere, with apex predators gaining an advantage over ungulate prey where and when snow is deep enough to impede animal movement and dense enough to support predators but not their prey. To examine how changing snowpacks will alter these interactions, we applied climate projections to physically based snow modeling across 45,300 km^2 spanning the border between Washington state, USA and British Columbia, Canada. Specifically, we perturbed a historical baseline with seasonally varying adjustments based on a multi-model ensemble for mid-century climate change across two scenarios (SSP2-4.5 and SSP5-8.5) and extracted daily physical snow properties at 30-m resolution. We temporally and spatially tracked the snow-mediated movement advantages of two apex predators (cougars [*Puma concolor*] and wolves [*Canis lupus*]) over their primary prey (white-tailed deer [*Odocoileus virginianus*] and mule deer [*O. hemionus*]), using home ranges from GPS-collared predators to account for seasonally variable habitat use. We found steep declines in snow-mediated predator advantages, both in terms of duration (decline from an average 53 days to 24 days [SSP2-4.5] and 18 days [SSP5-8.5]) and extent (65% and 78% decline in area for SSP2-4.5 and SSP5-8.5, respectively). These declines are greater in magnitude than the physical changes we modeled. Furthermore, current predator home ranges will suffer larger changes in duration of predator-advantaged snow conditions than region-wide trends. Apex predators in snowy ecosystems will bear the impacts of climate change on a scale disproportionate to actual physical changes, requiring large-scale

redistribution, alternate prey sources, or increased ungulate density to counterbalance their dwindling winter edge. Our study indicates that, across much of the Northern Hemisphere, ungulate prey may benefit from declining snowpacks at the expense of their predators.

5.2 Introduction

As climate change reshapes geophysical processes (McCluney et al., 2012; A. C. Wilson et al., 2021), species' distributions are being reshuffled at multiple scales (Pecl et al., 2017; Severson et al., 2021). Consequently, the frequency, magnitude, and direction of species interactions are changing (Blois et al., 2013; Deguines et al., 2017; Romero et al., 2018; Tylianakis et al., 2008), with far-reaching but poorly understood impacts (Gilman et al., 2010; Urban et al., 2016). For example, more severe droughts in Botswana's Okavango Delta have led to greater spatial overlap between the dominant predator (lion, *Panthera leo*) and subordinate competitors such as leopards (*Panthera pardus*; West et al., 2024). Besides increasing lethal interference competition (Balme et al., 2013; Swanson et al., 2016), greater overlap may shift entire food webs as leopards target smaller prey to reduce opportunities for kleptoparasitism (Balme et al., 2017; Stein et al., 2015). Thus, abiotically driven changes to species interactions provide a lens into the broader ecological consequences of our changing climate.

Snow dynamics are among the most rapidly changing geophysical processes (IPCC, 2022; Niittynen et al., 2018) and among the most significant: snow at least periodically covers ~ 48% of the world's land area (Johnston et al., 2023) and influences hydrology across an even greater area (Barnett et al., 2005; Immerzeel et al., 2020). A diverse community of animals have evolved to exploit various aspects of snow: lemmings (*Lemmus* and *Dicrostonyx* spp.) rely on snow that is soft enough to tunnel through (Poirier et al., 2023), ptarmigan (*Lagopus* spp.) benefit from deep snow that permits easy access to browse shrub crowns (St-Georges et al., 1995), and pregnant polar bears (*Ursus maritimus*) seek out snow drifts that provide sufficient insulation for subnivean dens (Durner et al., 2003; R. R. Wilson & Durner, 2020). Beyond influencing animal behavior (Cunningham et al., 2022; Ortega et al., 2024; Poirier et al., 2021;

Prugh et al., 2024) and demography (Borg & Schirokauer, 2022; Rattenbury et al., 2018; Scridel et al., 2018), snow also structures species interactions such as competition (Peers et al., 2020; Verstege et al., 2023), predation (Slettenhaar et al., 2025; Sullender et al., 2025), herbivory (Hansen et al., 2019; Post et al., 1999), and parasitism (Pouchet et al., 2024). Despite its ecological importance, however, the dynamic and heterogeneous nature of snow presents a major challenge for evaluating how wildlife respond to different snow conditions (Reinking et al., 2022). This fundamental challenge of snow ecology is further enhanced by complexities arising from fine-scale snow processes and orographic precipitation patterns that are difficult to resolve in climate projection models (Hammond et al., 2023; Norris et al., 2025).

Generally, global snowpacks are forecasted to decline in extent, duration, and total mass as a consequence of climate change (Gergel et al., 2017; IPCC, 2022). Rising temperatures will result in more midwinter snowmelt and a greater proportion of winter precipitation falling as rain (Barnett et al., 2005; Brown & Mote, 2009), both of which will reduce snow depth and increase snow density (Hill et al., 2019). However, in part because warmer air can hold more moisture (IPCC, 2023), climate change is also forecasted to increase overall precipitation globally, with the strongest effects in winter and in mountainous regions: using multi-model averages of an end-century, severe climate change scenario, a global ~9% increase in year-round precipitation (Rogers & Mauger, 2021) manifests as a ~17% increase in winter precipitation in the northern Alps (Kotlarski et al., 2023) and a ~14% increase in the US Pacific Northwest (Kotlarski et al., 2023). Gains in winter precipitation are projected to fully offset temperature-related decreases to snow accumulation in predominantly colder-climate, tundra-dominated regions like East Siberia (Pulliainen et al., 2020), the Western Himalaya (Smith & Bookhagen, 2020), and Arctic Alaska (Newman et al., 2021).

These spatially and temporally variable changes to snowpack have the potential to dramatically shift species interactions (Aryal et al., 2016; Felton et al., 2024). For large carnivores like wolves (*Canis lupus*) and cougars (*Puma concolor*), snow provides an opportunity to exploit an advantage in locomotion: compared with deer (*Odocoileus* spp.) and other ungulate prey, carnivores have greater foot surface area relative to body mass (i.e., foot loading; Telfer & Kelsall, 1984; Sullender et al., 2023). This lower foot loading causes predators to sink into the snow less than their prey, creating a "danger zone" as prey are slowed down, expend more energy, and ultimately are more vulnerable to predation (Nelson & Mech, 1986; Parker et al., 1984; Sivy et al., 2018; Sullender et al., 2023). Easier hunting conditions combine with seasonal declines in ungulate body condition to produce demographic and population-scale effects: winters with deeper snow increase overall ungulate mortality (Horne et al., 2019), can triple predator kill rates (Nelson & Mech, 1986; Post et al., 1999), and increase predator survival and birth rates (Borg & Schirokauer, 2022; Post et al., 1999). Well-established connections between snow and wolf predation patterns (Mech & Peterson, 2003) have recently been extended to include cougars, which are more likely to make deer kills in areas with advantageous snow (i.e., moderately deep and dense; Sullender et al., 2025). As winter conditions diverge from historical baselines, the extent to which danger zones will be conserved or transformed remains unknown yet is of fundamental concern to ecosystem function.

In this study, we simulate changes to snowpack in the Pacific Northwest region of North America to investigate our central question of how climate change will alter snow-mediated predator movement advantages. This region supports abundant populations of two predator-prey pairs (deer-wolves and deer-cougars) whose winter interactions are structured by snow properties (Sullender et al., 2025), and serves as an ideal proxy to assess the diverse impacts of climate change given its complex topography, highly variable snowfall patterns, and representation of all known global snow-climate classes (Sturm & Liston, 2021). To quantify snow properties, we couple physically based snow modeling (SnowModel; Liston & Elder, 2006a; Mower et al., 2024) with a multi-model ensemble of climate projections (Coupled Model Intercomparison Project Phase 6; Eyring et al., 2016; Chen et al., 2021). Next, we extract specific snow properties that delineate conditions that provide predators with a movement advantage, based on a mechanistic, field-validated definition of how snow affects mammal movement (Penczykowski et al., 2017; Sivy et al., 2018; Sullender et al., 2023). Finally, we generate home ranges for GPS-collared cougars and wolves to account for seasonally variable habitat use and track how future snowpacks may shift danger zones for the primary prey (white-tailed deer [*O. virginianus*] and mule deer [*O. hemionus*]) of cougars and wolves. These apex predators strongly avoid human settlements that are widely distributed at lower elevations (Prugh et al., 2023) whereas projected increases in precipitation may increase snow depth at higher elevations (Norris et al., 2025). Thus, we hypothesize that (*H1*) on a regional scale, cougars' and wolves' seasonal advantages over deer will decline in both duration and spatial extent, but that (*H2*) current predator home ranges will be largely resilient to changes in snowpack and maintain a similar duration and extent of danger zones across baseline and climate change scenarios. By quantifying how a changing snowpack will affect these globally distributed species, we provide broadly applicable insight into how climate change will alter large mammal predator-prey interactions across seasonally snow-covered ecosystems.

5.3 Methods

5.3.1 Study Area

Our study took place in two large areas within the Pacific Northwest, including portions of the states of Washington and Idaho, USA, and the province of British Columbia, Canada (Figure 5.1). The Northeast study area covers about 19,300 km^2 (approx. 47.5-49°N, 116.5-118.5°W) and our Okanogan study area covers about 26,000 km^2 (approx. 47.5-49.5°N, 119-121°W). Collectively, our study areas include portions of all six recognized global snow classes (Figure 5.1): tundra, boreal forest, maritime, ephemeral, prairie, and montane forest (Sturm et al. 1995; Sturm & Liston 2021). Depending on prevailing environmental conditions, these snow classes vary from deep and wet (maritime) to shallow, cold, and windblown (tundra) and effectively bound the full range of snow conditions an animal might encounter anywhere in the world (Sturm et al. 1995).

In both of our study areas, upper elevations (i.e., >1200m) are typically snow-covered from mid-Nov until early May (Natural Resources Conservation Service, 2025). Lower elevations (~400m) have less persistent snow and are home to a greater human footprint, with communities, roads, and agriculture. Vegetation varies from dense stands of hemlock (*Tsuga* spp.) and Douglas-fir (*Pseudotsuga menziesii*) trees, open slopes with ponderosa pines (*Pinus ponderosa*) and sagebrush (*Artemisia* spp.), and alpine meadows. Aside from our focal predator-prey pairs (cougars, wolves, mule deer, and white-tailed deer), alternate prey such as elk (*Cervus canadensis*) and moose (*Alces alces*) are also present but much less frequently targeted by cougars and wolves (A. Wirsing, pers. comm.).

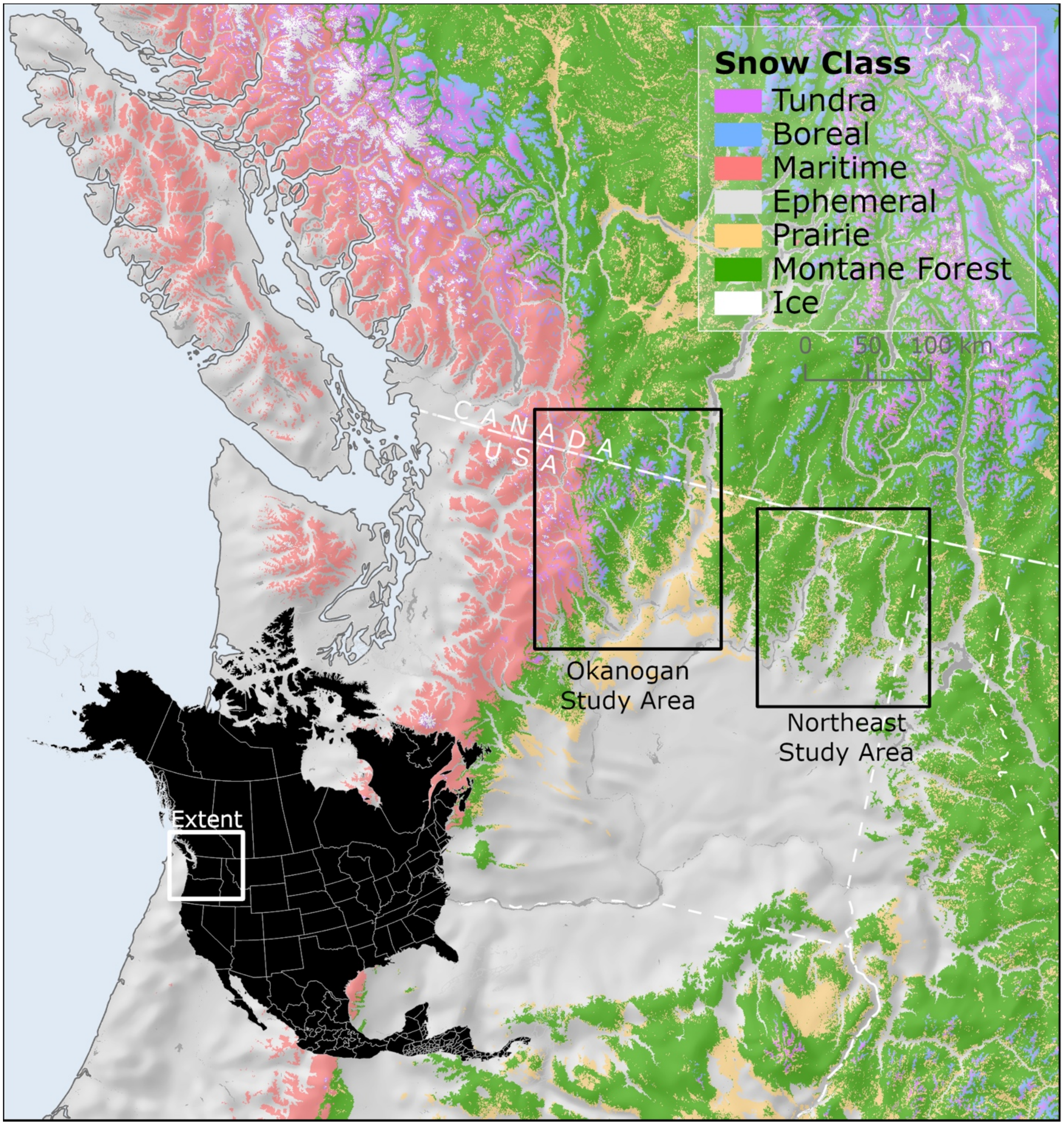

Figure 5.1. Study areas within the Pacific Northwest of North America. Colors represent the spatial extent of the six recognized classes of snow and ice/glaciated features (Sturm & Liston, 2021).

5.3.2 Baseline Snow Conditions

We used SnowModel, a distributed snow-evolution modeling system, to model wildlife-relevant snow properties (Liston & Elder, 2006a). SnowModel combines spatially and temporally distributed meteorological variables with topography and land-cover type, numerically solving physical processes such as blowing-snow redistribution, canopy interception, and snow density evolution at user-specified spatial and temporal steps (Liston & Elder, 2006a). We used NASA's Center for Climate Simulation Discover supercomputer to run a parallelized version of SnowModel (Mower et al., 2024) at a 30-m grid increment with a 3-hour forcing time step, and daily aggregated output snow depth (m) and snow density (kg/m^3).

We ran SnowModel simulations for water years 2018-2022 for the Okanogan and Northeast study areas using a water percolation scheme (Pflug et al., 2019) that provides realistic model representations of rain-on-snow and midseason melt, common in maritime snowpacks. A water year begins on October 1 and concludes the following September 30, with the year assigned based on spring (i.e., October 1, 2017 and September 30, 2018 are both water year 2018). We used the USGS National Elevation Dataset (NED) for topography on a 30-m grid (Gesch et al., 2018), the North American Land Change Monitoring System (NALCMS) Land Cover 2015 map for vegetation on a 30-m grid (Latifovic et al., 2016), and forcing variables from a Weather Research Forecast (WRF) model from the National Center for Atmospheric Research (NCAR) on approximately a 4-km grid (Rasmussen et al., 2023). We evaluated snow output with snow telemetry observations (SNOTEL; Natural Resources Conservation Service, 2025) at 7 stations within the Okanogan and 4 stations within the Northeast study areas (see Supplement).

5.3.3 Climate Change Projections

We selected two climate-change scenarios, SSP 2-4.5 and SSP 5-8.5, to represent moderate and severe warming, respectively. SSP 2-4.5 represents a “middle-of-the-road” scenario, characterized by radiative forcing of 4.5 W/m^2 in 2100, a 2.0°C increase in global temperatures by mid-century, and a 2.7°C increase by 2100 (Intergovernmental Panel on Climate Change, 2023). The more carbon-intensive SSP 5-8.5, known as the “fossil-fueled development” scenario, has radiative forcing of 8.5 W/m^2 in 2100, corresponding to global temperature increases of 2.4°C by midcentury and 4.4°C by 2100 (Intergovernmental Panel on Climate Change, 2023).

We used the University of Washington Climate Impacts Group’s Pacific Northwest Climate Projection Tool (Rogers & Mauger, 2021) to extract output from 15 global climate models (GCMs) indexed in the Coupled Model Intercomparison Project Phase 6 (CMIP6; full list in Supplement; Eyring et al. 2019). Rather than directly analyze GCM output, which is highly sensitive to boundary conditions (Rasmussen et al., 2011) and poorly represents regional processes critical for snow physics (Kawase et al., 2020; Norris et al., 2025), we used a pseudo-global warming approach to better discern local conditions (Brogli et al., 2023; Liu et al., 2017; Schär et al., 1996). Thus, our approach took a basic form of

$$PGW_x = CTRL + \Delta CMIP6_x, \quad (1)$$

where *PGW* represents pseudo-global warming boundary conditions for SSP *x* and *CTRL* refers to baseline conditions (Brogli et al., 2023). $\Delta CMIP6_x$ represents future changes to meteorological variables based on SSP *x* and is defined as

$$\Delta CMIP6_x = CMIP6_x - HIST, \quad (2)$$

where $CMIP6_x$ is a future time slice for SSP x and $HIST$ is a corresponding historical time slice, again following Brogli et al. (2023).

We used a baseline period of 2018-2022 (i.e., *CTRL*), with meteorological variables derived from NCAR's 4-km WRF model (Rasmussen et al., 2023). We calculated $\Delta CMIP6x$ using a multi-model mean of projected changes in temperature and precipitation for mid-century (2040-2069) within the Pacific Northwest region (41.5-49.5°N, 125-111°W), calculated relative to a baseline of 1950-1999 (Rogers & Mauger, 2021).

In our approach, we perturbed baseline conditions for temperature and precipitation at a seasonal timestep (i.e., summer, fall, winter, or spring; (Norris et al., 2025) 5-1) to better capture the large intra-annual variation in warming and precipitation patterns within our study region (Rupp et al., 2017; Taylor et al., 2023), applied at a 4-km baseline (i.e., *CTRL*) resolution. We used SnowModel's MicroMet submodule (Liston & Elder, 2006b) to downscale these perturbations to a 30-m resolution within our study area and used Parallel SnowModel (Liston & Elder, 2006a; Mower et al., 2024) to simulate future snowpacks under SSPs 2-4.5 and 5-8.5. For each scenario, this approach generated five years of daily snowpack data under pseudo-global warming conditions to compare with our baseline five years of daily snowpack data.

5.3.4 Danger Zones

We extracted the modeled physical properties of snow for each 30-m cell across our study areas at a daily time step to quantify the times and places when cougars and wolves would gain a movement advantage over deer (i.e., "danger zones"). We filtered cells to only include those with sufficiently deep snow and with densities shown to define danger zones for these predator-prey pairs (Sullender et al., 2023). Cougars have an advantage over deer at snow densities between 210 – 450 kg/m^3, and wolves have a slightly broader advantage range, at densities between 110 – 460 kg/m^3 (Sullender et al., 2023).

We defined the minimum snow depth that would impede ungulate mobility as half the chest height of deer (>30 cm; average chest height of 61.7 cm and 59.2 cm for adult white-tailed and mule deer, respectively; Parker et al., 1984; Telfer & Kelsall, 1984). This snow depth is recognized as a threshold for deer above which nutritional stress, energy expenditure, and predation risk all increase dramatically (Ganz et al., 2022; Telfer, 1970; White et al., 2009). In addition to driving general shifts in ungulate movement and habitat use (DelGiudice et al., 2013; Morrison et al., 2003; Sabine et al., 2002), snow deeper than 30 cm doubles the energetic costs of locomotion (Hobbs, 1989; Parker et al., 1984) and increases predation rates as much as threefold (DeLgiudice et al., 2002; Fuller, 1991; Nelson & Mech, 1986).

In the context of our modeled snow properties, we categorized each 30-m daily cell for baseline, SSP2-4.5, and SSP5-8.5 snow conditions into whether that cell, on that day, had sufficient snow depth and density to provide a movement advantage for predators over prey (i.e., a "danger zone day"). We aggregated these data by cumulative extent (for a given day, the sum of 30m cells classified as danger zones) and by cumulative duration (for a given 30m cell, how many days would be classified as danger zones). We defined seasons as autumn from September to November, winter from December to February, spring from March to May, and summer from June to August. We excluded summer from our analyses due to lack of snow cover. We computed daily statistics from the five-year runs of each of our three climate simulations (historic, SSP 2-4.5, and SSP 5-8.5).

5.3.5 Predator Home Ranges

We used GPS-collared animals to determine predator home ranges, based on wildlife telemetry data from the Washington Predator-Prey Project (described in Bassing et al. [2023]) Location fix rates varied between 2 and 12 hours, depending on the species, year, and collar model. After excluding dispersing animals, erroneous locations, and individuals with fewer than 50 locations in a given season, we analyzed GPS collar data from 49 cougars (99 animal-years) and 53 wolves (98 animal-years), resulting in a total of 195,758 predator locations between 2017 and 2022. We generated kernel density estimates for each individual animal, each year, and each season. We then extracted the 95% isopleth for each kernel density estimate to approximate seasonal predator home ranges (Prugh et al., 2023). We used the *amt* (Signer et al., 2019) and *terra* (Hijmans, 2024) packages in R for all home range analyses. We followed the same methods described above to extract the mean number of danger zone days within each individual's home range. We used Kruskal-Wallis tests and subsequent Dunn's tests to examine differences in danger zone durations between species, regions, and seasons. To compare single-species home ranges with region-wide patterns, we used the Wilcoxon signed-rank test as a non-parametric single-sample test.

5.4 Results

5.4.1 Baseline and Projected Snow Conditions

Our SnowModel simulations reasonably captured snow dynamics during our baseline period of 2018-2022, using daily observations from 11 SNOTEL stations across our study areas. There was good agreement between modeled and observed peak snow water equivalent (SWE;

Pearson's *r* = 0.81) and melt rates (Pearson's *r* = 0.67; details in Supplement), two key components of snow physical processes (Besso et al., 2024; Clark et al., 2015; Raleigh & Lundquist, 2012). Our five-year baseline encompassed enormous variability in snow conditions (Figure 5.2a), including record-high snow water equivalent (2018 at Sentinel Butte SNOTEL station) as well as 2019's low snowpack that remained below the 10th percentile of the long-term record (Rainy Pass SNOTEL station; Natural Resources Conservation Service, 2025).

Our climate perturbations (Table 5-1) significantly reduced snowpacks across the majority of both study areas. Annual peak SWE at the 11 SNOTEL stations used in validation declined by 14.0% and 27.4% in our 2050s SSP2-4.5 simulation compared to the 2018-2022 baseline for the Northeast and the Okanogan study areas, respectively. Under SSP5-8.5, these declines in peak SWE reach 27.3% for Northeast and 35.2% for Okanogan. Snowpack losses were most dramatic on valley floors and south-facing slopes (Figure 5.3a-b). However, some high-elevation terrain accumulated more snow under climate-change scenarios, including alpine areas immediately surrounding Castle Peak (2543m; 48.98N, 120.86W) and Eldorado Peak (2703m; 48.54N, 121.13W) in the Okanogan study area and the northern slopes of Taylor Ridge (1880m; 48.8N, 118.38W) and Jackknife Mountain (1549m; 48.72N, 118.26W) in the Northeast study area (Figure 5.3a-b).

Table 5.1. Seasonal perturbations used in climate change projections. We adjusted input forcing parameters based on these values, then used SnowModel's MicroMet submodule (Liston & Elder 2006) to downscale the modified forcing data into 30m-compatible meteorological variables.

Scenario	Season	Months	Temperature Change (°C)	Precipitation Change (%)
SSP 2-4.5	Fall	Sep, Oct, Nov	2.91	3.55
SSP 2-4.5	Winter	Dec, Jan, Feb	2.47	7.05
SSP 2-4.5	Spring	Mar, Apr, May	2.43	6.77
SSP 2-4.5	Summer	Jun, Jul, Aug	3.29	-4.11
SSP 5-8.5	Fall	Sep, Oct, Nov	3.67	3.48
SSP 5-8.5	Winter	Dec, Jan, Feb	3.29	9.63
SSP 5-8.5	Spring	Mar, Apr, May	3.02	6.36
SSP 5-8.5	Summer	Jun, Jul, Aug	4.27	-4.95

5.4.2 Danger Zones

Climate change simulations dramatically reduced both the extent and duration of snow conditions that provided an advantage to predators over prey (danger zones). As defined by 1) snow densities that support large carnivores on the snow surface while ungulate prey sink deep into the snowpack, and 2) snow depths sufficient to impede prey movements, danger zones were widespread across both our study areas during the historic period (2018-2022). This snow-based advantage reached a maximum in mid-winter: on Feb 18, a baseline-period average of 56% and 59% of our combined study areas (45,304 km^2) provided an advantage to cougars and wolves, respectively. For most of the year, however, danger zones typically covered far less area. From

Oct 1 - April 30, baseline conditions in a median of 15.8% (7,151 km^2) of the study area provided an advantage for cougars over deer (Figure 5.2b) and 17.5% (7,917 km^2) for wolves (Figure 5.2c). The mid-winter danger zone maximum declined to 26% of our combined study areas (cougars) and 28% (wolves) with SSP2-4.5 and 18% (cougars) and 20% (wolves) with SSP5-8.5. Mid-century, moderate climate change (SSP2-4.5 2050s) led to a three-fold reduction in danger zone extent for both predators (median cougar danger zone extent = 2,374 km^2; median wolf danger zone extent = 2,980 km^2). Severe climate change (SSP5-8.5) reduced the median danger zone extent even more dramatically (Figure 5.2b-c), resulting in an approximately five-fold reduction by mid-century (median cougar danger zone extent = 1,468 km^2; median wolf danger zone extent = 1,931 km^2).

Throughout our baseline 2018-2022 conditions, a cumulative 39 days per year (standard deviation = 28 days) provided a snow-mediated movement advantage for predators in the Northeast study area and 67 days/year (SD = 43 days) in our Okanogan study area (Figure 5.3a). The moderate climate-change scenario decreased these region-wide durations to 11 days/year (SD = 19 days) and 37 days/year (SD = 35 days) in Northeast and Okanogan, with severe climate change further reducing these durations to 6 days/year (SD = 14 days; Northeast) and 29 days/year (SD = 31 days; Okanogan). Across both regions, winters (Dec-Feb) had far more days (39 days/year on average) during which predators gained an advantage compared to the autumn (Sept-Nov; 5 days/year) or spring (Mar-May; 8 days/year; Figure 5.3a).

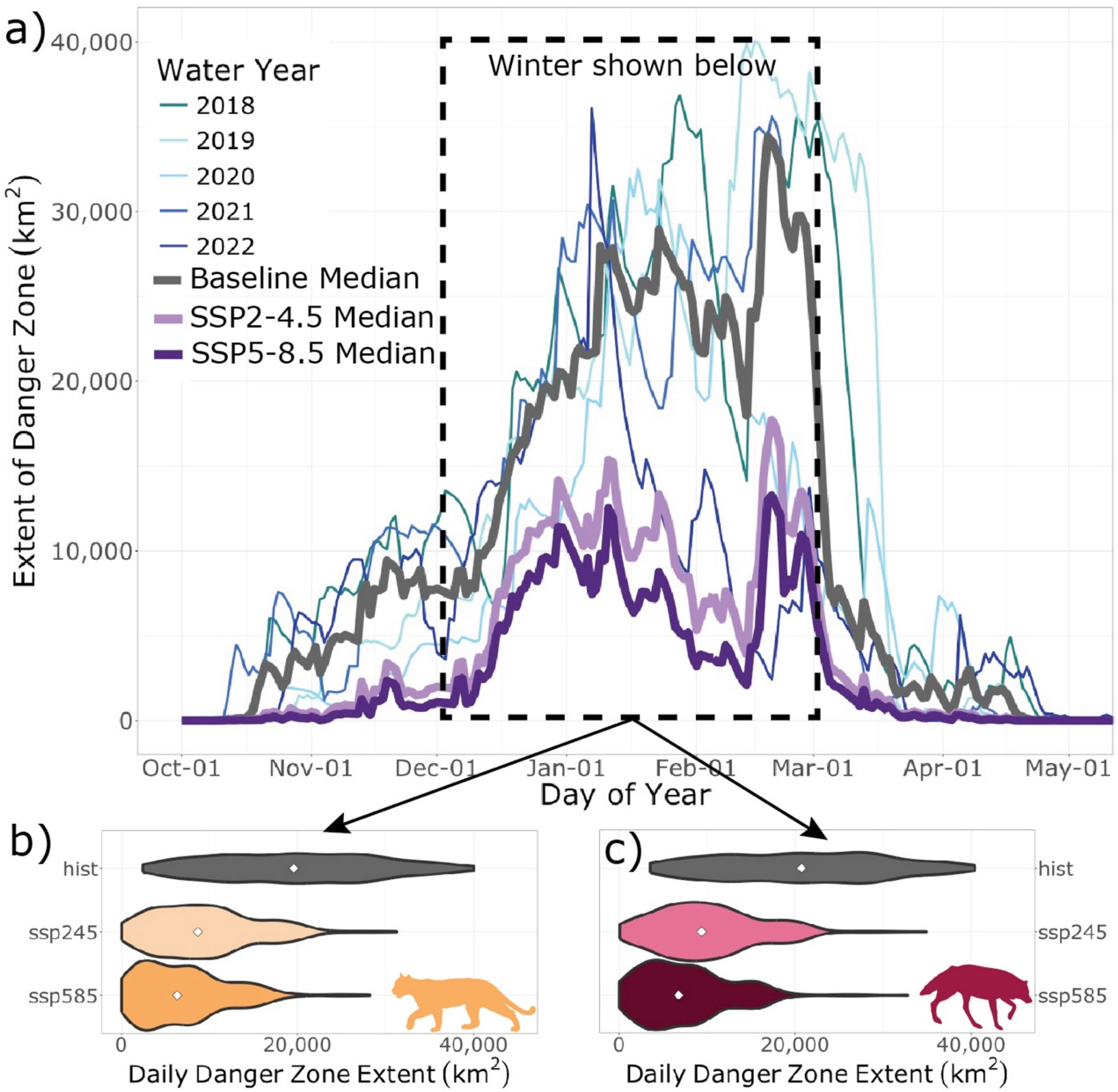

Figure 5.2. Total cumulative extent of snow conditions that provide an advantage to predators over deer ("danger zone"). (a) shows annual time series of total danger zone extent, Oct 1 - May 1, across both study areas for individual years used in baseline (blue), as well as baseline median (gray), SSP2-4.5 median (moderate climate change scenario; lavender), and SSP5-8.5 median (severe climate change scenario; purple). Although (a) shows results for cougars-deer, results are nearly identical for wolves-deer because of the substantial overlap between danger zone definitions for these two predators. (b) and (c) show winter only (Dec 1-Feb 28/29) cumulative

extent of danger zones across baseline, SSP2-4.5, and SSP5-8.5 scenarios for (b) cougars and (c) wolves. Dots indicate median cumulative extent of danger zones for each scenario. Under climate-change projections, both predators will suffer a reduced extent of areas in which to exploit a snow-mediated advantage over ungulate prey, with the most marked reduction during midwinter.

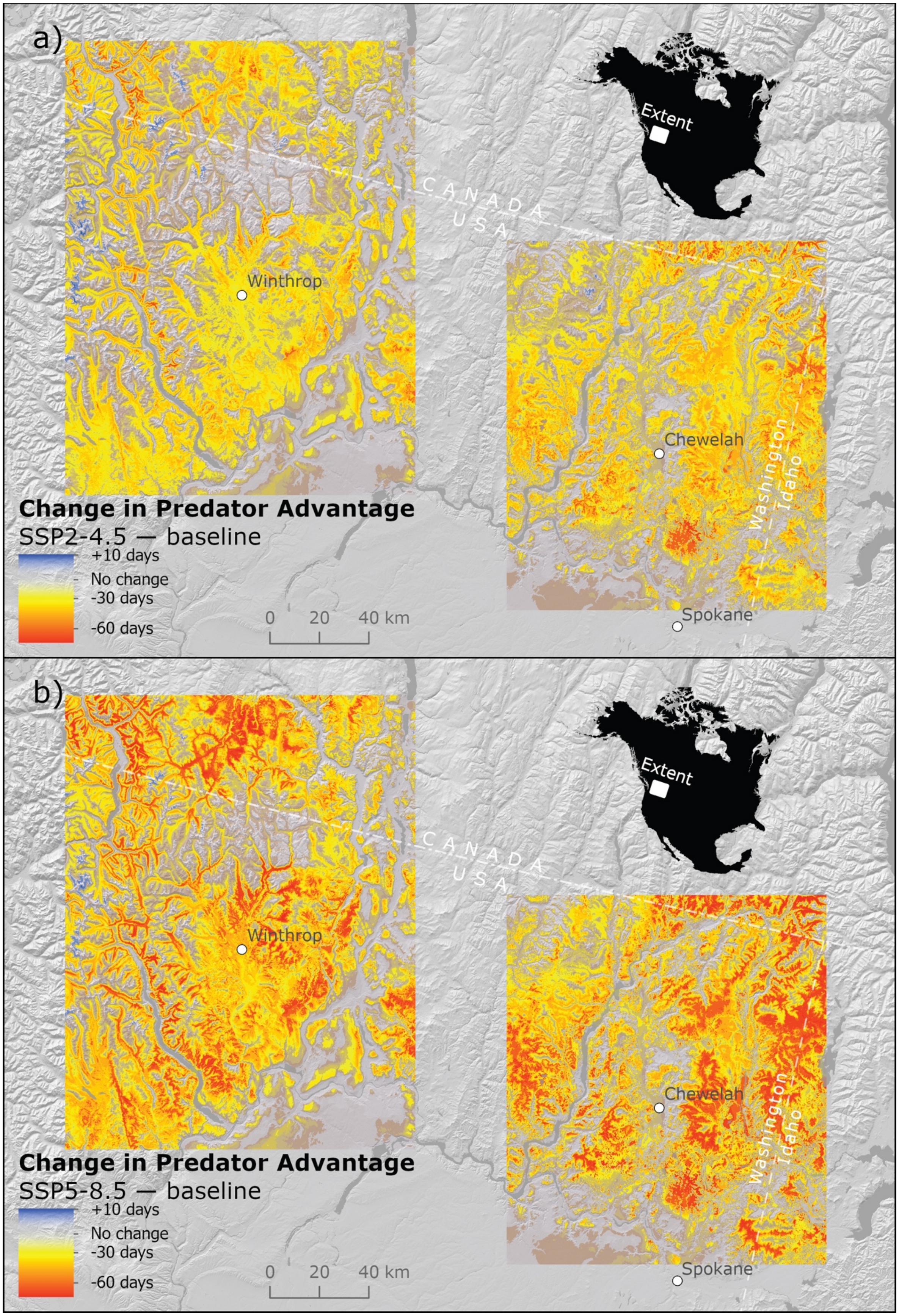
a)
Extent
CANADA
USA
Winthrop
Chewelah
Washington
Idaho
Spokane
Change in Predator Advantage
SSP2-4.5 — baseline
+10 days
No change
-30 days
-60 days
0 20 40 km
b)
Extent
CANADA
USA
Winthrop
Chewelah
Washington
Idaho
Spokane
Change in Predator Advantage
SSP5-8.5 — baseline
+10 days
No change
-30 days
-60 days
0 20 40 km

Figure 5.3. Change in mid-winter snow conditions that provide an advantage to predators over ungulate prey, for projections of (a) moderate climate change (SSP2-4.5) and (b) severe climate change (SSP5-8.5). Both panels use an identical color ramp to show the change in number of days from Dec 1 - Feb 28/29 when snow conditions are advantageous relative to a baseline of 2018-2022. Negative values highlight declining danger zones, with the darkest red areas (-60 days) showing areas where predator-advantage snow conditions have entirely disappeared from a baseline that previously lasted two entire months. Base data derived from NASA SRTM (2013).

5.4.3 Predator Home Ranges

From 2018-2022, cougar and wolf seasonal home ranges had similar overall durations of danger zones to the region-wide average (Table 5.2; Figure 5.4a), although in the Okanogan study area, home ranges of both cougars and wolves had significantly more danger zone days in winter than regional averages (cougars: n=23, V=255, P<0.001; wolves: n=30, V=354, P<0.05). Across both regions and across all seasons, wolves had two more days of danger zones within their home ranges than cougars ($\chi^2 = 30.41$, $P < 0.001$). The only exception to this broader pattern was Okanogan cougars, which averaged four more days of danger zones than wolves ($\chi^2 = 15.03$, $P < 0.001$).

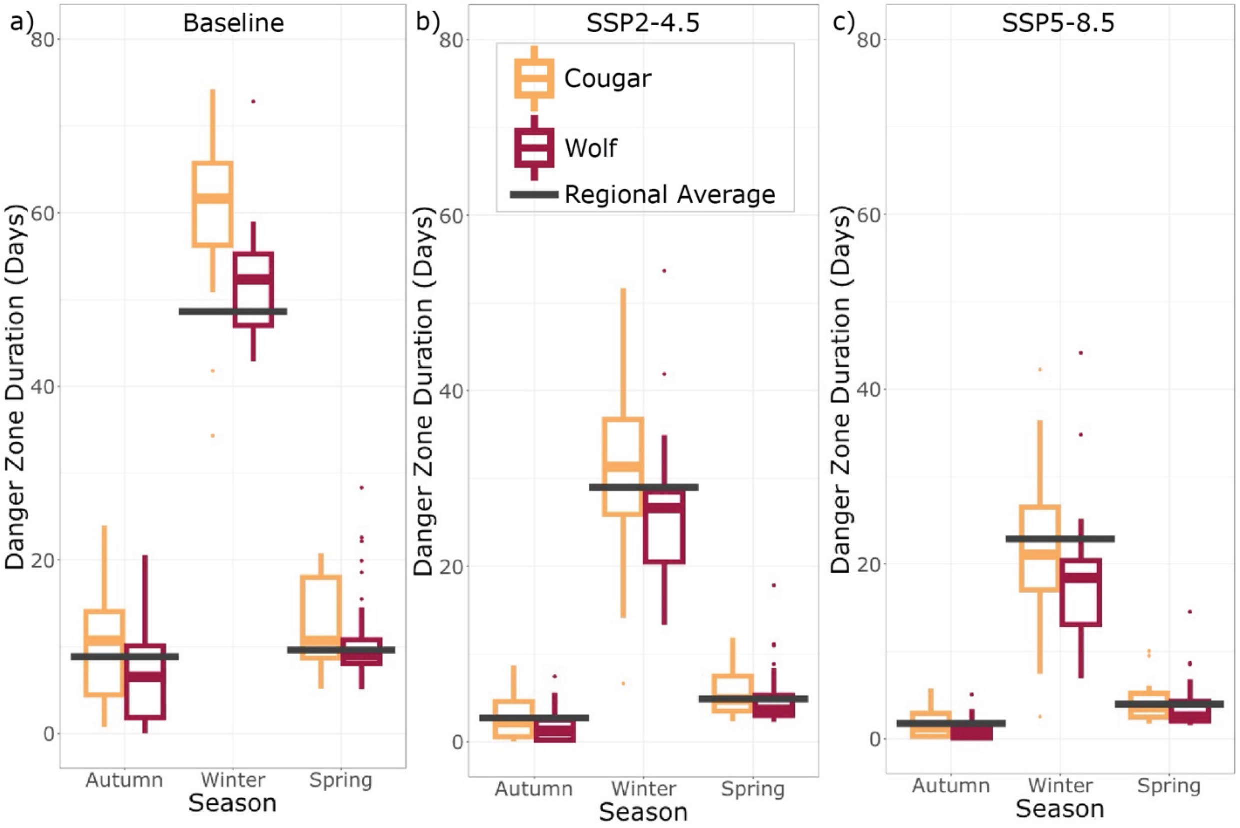

Figure 5.4. Seasonal comparison of average duration of predator-advantaged snow conditions (danger zones) within each individual predator's home range within the Okanogan study area. Durations calculated for (a) baseline snow conditions (2018-2022), (b) moderate climate-change scenario (SSP2-4.5), and (c) severe climate-change scenario (SSP5-8.5). Predator home ranges defined as the isopleth bounding the 95% kernel density estimate for GPS-collared animals, computed for each year, each season, and each individual. Seasons defined as autumn including Sep-Nov, winter Dec-Feb, and spring Mar-May.

Table 5.2. Comparison of snow conditions within apex predator seasonal home ranges to conditions within broader regions. Cells with a single * have significantly shorter duration of danger zones (snow conditions that provide an advantage to predators over ungulate prey) than regional average, and cells with a double ** have significantly longer duration (significance defined as $P<0.05$ with Wilcoxon signed-rank test). Seasons defined as autumn = Sep-Nov, winter = Dec-Feb, and spring = Mar-May.

Species	Region	Season	*n* Individual-Years	Mean Baseline Danger Zone Duration (days)	Mean SSP2-4.5 Danger Zone Duration (days)	Mean SSP5-8.5 Danger Zone Duration (days)
Cougar	Northeast	Autumn	54	0.0*	0.0*	0.0*
Cougar	Northeast	Winter	48	28.3*	4.7*	2.3*
Cougar	Northeast	Spring	55	5.5*	0.0*	1.1
Cougar	Okanogan	Autumn	23	10.1	2.7	1.7
Cougar	Okanogan	Winter	23	60.0**	31.1	21.8
Cougar	Okanogan	Spring	22	12.5**	5.6	4.2
Wolf	Northeast	Autumn	45	0.2*	0.0*	0.0*
Wolf	Northeast	Winter	49	33.4	8.5	4.6*
Wolf	Northeast	Spring	42	7.2	2.1	0.0*
Wolf	Okanogan	Autumn	32	6.9	1.8*	1.1*
Wolf	Okanogan	Winter	30	51.6**	25.7*	18.0*
Wolf	Okanogan	Spring	29	11.1	5.1	3.8

5.5 Discussion

Across the northern hemisphere, the physical properties of snow strongly shape habitat, distribution, and interactions of a wide range of wildlife species. We quantified likely changes to snowpack in mid-century under two different climate-change scenarios and translated these hydrological changes into ecological impacts by extracting physical properties important to ungulate-carnivore interactions. As hypothesized (*H1*), region-wide snow conditions (i.e., minimum depth and range of densities) that provide a movement advantage to large carnivores over ungulate prey will decrease dramatically in both spatial extent and in duration under scenarios of climate change. Crucially, these ecologically relevant declines (65% decline in extent and 55% decline in duration for SSP2-4.5) are more than double the magnitude of the general hydrological declines we estimated (21% decline in maximum snow water equivalent for SSP2-4.5). Thus, our results indicate that apex predators in snowy ecosystems will bear the impacts of climate change on a scale disproportionate to actual physical changes.

Although there is high variability in snowpack predictions due in part to complex underlying physical processes (Newman et al., 2021; Rasmussen et al., 2011), we found declines in snowpack similar in magnitude to those estimated by other recent studies (Gergel et al., 2017; Siirila-Woodburn et al., 2021). Our estimates of overall peak SWE decline in the Okanogan region (27.4% for SSP2-4.5 and 35.2% for SSP5-8.5) correspond to similar estimates of 33.6% and 41.3% for a similar region in Gergel et al. (2017) and a 36% decline in SWE over the entire western United States (Siirila-Woodburn et al., 2021).

Our prediction that climate change will reduce winter movement advantages of cougars and wolves over deer is likely relevant to other predator-prey pairs as well. Snow conditions have been linked with habitat use, seasonal distribution, and hunting success rates for a wide variety of predators: Arctic foxes (*Vulpes lagopus*; Bilodeau et al., 2013), bobcats (*Lynx rufus*; Koehler & Hornocker, 1991), cougars (Sullender et al., 2025), coyotes (*Canis latrans*; Peers et al. 2020), Canada lynx (*L. canadensis*; Stenseth et al., 2004), stoats (*Mustela erminea*; Bilodeau et al., 2013), wolverines (*Gulo gulo*; Glass et al., 2021), and wolves (Nelson & Mech, 1986) all benefit to some extent from different combinations of snow properties. As noted in this study, our results are surprisingly species agnostic - despite different ranges of snow densities that provide a movement advantage (Sullender et al., 2023), both cougars and wolves are likely to be affected similarly by projected snow loss associated with the two climate-change scenarios (Figure 5.2b-c). Similarly, because all cervids share the general morphological characteristics of comparatively higher foot-loads than their mammalian predators (Penczykowski et al., 2017; Telfer & Kelsall, 1984), the danger zones we identify are likely to be conserved for ungulate prey species not analyzed here. Besides the two species of deer (*Odocoileus* spp.) analyzed here, snow-mediated vulnerability to predation has also been observed in moose (*Alces alces*; Dussault et al., 2005), roe deer (*Caproeolus* spp.; Jędrzejewski et al., 2002; Mysterud & Østbye, 2006), elk (*Cervus canadensis*; Horne et al., 2019; Kittle et al., 2008), and red deer (*Cervus elaphus;* Gervasi et al., 2013). The regional exceptions to our snow projections have similar directional conclusions: the high Arctic is one of very few ecosystems predicted to have increased snow accumulation with climate change (Newman et al., 2021). Although greater snow depth might be expected to benefit Arctic wolves, the primary ungulate prey (caribou/reindeer; *Rangifer tarandus*) have much lower foot-loads than temperate-latitude deer (Telfer & Kelsall, 1984) and therefore do not share the same vulnerabilities to deep, low-density snow (Sullender et al., 2023). Thus, in winter, climate change is likely to tilt movement advantages away from predators and towards prey during winter across many large mammal communities worldwide.

As components of suitable habitat shift – including advantageous snow conditions – wildlife are expected to shift distribution to track their preferred niches (Berg et al., 2010; Pecl et al., 2017). We show that, counter to our expectations (*H2*), snow conditions should become worse for cougars and wolves within current predator home ranges than on average across our study regions (Table 5.2). A handful of high-elevation climate strongholds will stay snowier for longer and extend predator advantage into mid-century, but the extent of these areas is far more limited than hypothesized. Furthermore, apex predator home ranges include both mountainsides and valley floors, which will be more strongly affected by climate change than alpine areas (Figure 5.3). It is possible that predators will track snow conditions upslope, but if prey remain at low elevations, this redistribution may prove counterproductive as hunting opportunities become less frequent. In addition to reducing predation risk, diminishing snow depths will increase food availability and thus enhance suitable winter foraging habitat for ungulates such as Sitka black-tailed deer (*O. hemionus sitkensis*; Gilbert et al., 2017), white-tailed deer (Garroway & Broders, 2005), moose (Leblond et al., 2010), and roe deer (Mysterud & Østbye, 2006). Robust ecological evidence suggests that ungulates strongly select habitat that minimizes exposure to predation (Bassing et al., 2024; Ganz et al., 2022; Ganz, DeVivo, et al., 2024; Penczykowski et al., 2017), so with both improved foraging and reduced predation risk, ungulates are likely to stay at lower elevations in winter. However, snow is also a strong migration cue in ungulates (Ortega et al., 2024; Rivrud et al., 2016), with later frost and later snowfall resulting in delays in autumn migration for elk of nearly 50 days, for example (Rickbeil et al., 2019). The changing seasonal signals – such as the region-wide reduction in autumn snow that our scenarios predict (Figure 5.4) – might offset some of the effects of wildlife redistribution, as ungulates may move through predator-inhabited areas later in the season, when snow is more likely to be sufficiently deep to provide a “danger zone” advantage. The influence of projected declines and delays in snowfall on ungulate migration remains a critical, unanswered question, with direct bearing on the future of predator-prey interactions in a changing climate.

Although we do not directly quantify migratory movements, our results do include both autumn and spring migratory seasons. Already-marginal snow conditions during these shoulder seasons will become even poorer for predators under scenarios of climate change (Figure 5.4). Autumns during our baseline period had too little snow accumulation for prey to be significantly slowed, and the forecasted 2.9°C (SSP2-4.5) and 3.7°C (SSP5-8.5) autumn temperature increase further reduced snow persistence. Spring, by contrast, typically had sufficient snow depth to affect predator-prey interactions, but quickly became dense enough to support predators and prey alike (Figure 5.4). During the melt period (typically, Apr-May; Figure 5.2a), snow becomes saturated with liquid water during daytime and structurally hardens during overnight re-freeze or consolidation periods (Bormann et al., 2013; Breen, 2024). Mid-century scenarios of climate change advance the initiation of these melt periods (Figure 5.2a), in which snow becomes too dense for predators to effectively exploit. Given that longer-lasting and greater coverage of snow in these shoulder seasons have been linked with major negative impacts on ungulate body condition, mortality, and population trends (Loe et al., 2021; Rattenbury et al., 2018; van de Kerk et al., 2018), the seasonally reduced extent and duration of danger zones will likely benefit herbivores.

Together with these milder autumns and springs, ungulates within our study area should also benefit from changes in winter conditions. Climate-driven reductions in winter severity, typically defined as a combination of increased snow depth and lower temperatures (Ganz, Bassing, et al., 2024), will result in all endothermic mammals expending less energy on locomotion and homeostasis (Bryce et al., 2022; Crête & Larivière, 2003; Long et al., 2014). When combined with predation, winter severity has been identified as the leading driver of juvenile and female mortality in ungulate populations across the Northern Hemisphere (DeLgiudice et al., 2002; Forrester & Wittmer, 2013; Griffin et al., 2011; Holmes et al., 2021). With these mid-winter environmental constraints lifted by a warmer, less snowy climate (Felton et al., 2024), we expect ungulate survival and recruitment to increase as a function of superior habitat quality (Rivrud et al., 2019), reduced energetic demands (Long et al., 2014), and a projected decrease in predation success rates (Figure 5.2). This may lead to an indirect, time-lagged benefit for carnivores: foundational theories of multi-species dynamics – i.e., Lotka-Volterra predator-prey models (Lotka, 1920; Volterra, 1927) – indicate that predators benefit from increasing prey density as more young, old, and infirm individuals become available (Post et al., 1999). This indirect pathway could buffer against potential predator population declines as result of the dramatic decrease in winter hunting quality that we quantify here.

As climate science advances, there has been a proliferation of potential approaches to translate between projections from global climate models (GCMs) into regional or local ecological impacts. Despite significant improvements in each generation of CMIP (Mudryk et al., 2020; Taylor et al., 2023; Tittensor et al., 2021), GCM performance still varies widely across different regions, timescales, and output parameters (Deser, Phillips, et al., 2012; Lybarger et al., 2024), making computationally demanding ensemble approaches critical to reducing bias (Ahmed et al., 2019; Deser et al., 2020; Pierce et al., 2009). Furthermore, the coarse scale of GCMs poorly captures influential regional-scale phenomena such as orographic uplift or lake effect snow (Maraun et al., 2010; Rahimi, Huang, Norris, Hall, Goldenson, Krantz, et al., 2024; Strong et al., 2014), requiring yet more investment in statistical or dynamical downscaling to resolve these processes. Even with all these complex modifications of GCM projections, natural climate variability remains the primary source of uncertainty in model output and cannot be entirely eliminated through these approaches (Deser, Phillips, et al., 2012; Liu et al., 2017; Rahimi, Huang, Norris, Hall, Goldenson, Risser, et al., 2024). This natural variability is especially heightened for winter at mid- and high-latitudes (Deser, Knutti, et al., 2012; Gutmann et al., 2012) – i.e., areas with seasonal snowcover, which makes selection of an appropriate methodology especially challenging for snow-related applications such as ours (Mortezapour et al., 2022; Norris et al., 2025). In this study, our comparatively simple pseudo-global warming approach isolates two high-confidence features of climate change (increasing temperatures and seasonally varying precipitation) and, by using a multi-year baseline capturing much of our region's natural variability, avoids pitfalls common to GCMs (Deser et al., 2014; Liu et al., 2017; Rasmussen et al., 2011; Scalzitti et al., 2016). GCMs and myriad downscaling approaches hold promise but, in addition to the non-trivial internal variability issues described above, also require significant computational resources and storage space (Rahimi, Huang, Norris, Hall, Goldenson, Krantz, et al., 2024). We suggest that the pseudo-global warming approach is an underused yet valuable tool for quantifying the ecological implications of climate change when accurately capturing local physical processes is of primary importance.

Our results indicate that predators may have less time and less area over which to exploit movement advantages, which should increase overwinter survival rates of ungulates. Thus, natural resource managers may need to adjust harvest quotas to account for more limited mid-winter predation and milder winter conditions. Additionally, our spatially and temporally explicit analysis predicts where and when predators should have the most success in attacking prey, and areas that are most likely to remain important for sustaining predator populations in the future, guiding conservation efforts and management actions. As wildlife managers, policy makers, and the general public alike grapple with how our planet is changing, our study provides insight into how predator-prey interactions might shift, as well as when and where predator-preferred snow will endure.

5.6 References

Ahmed, K., Sachindra, D. A., Shahid, S., Demirel, M. C., & Chung, E.-S. (2019). Selection of multi-model ensemble of general circulation models for the simulation of precipitation and maximum and minimum temperature based on spatial assessment metrics. *Hydrology and Earth System Sciences*, *23*(11), 4803–4824. https://doi.org/10.5194/hess-23-4803-2019

Aryal, A., Shrestha, U. B., Ji, W., Ale, S. B., Shrestha, S., Ingty, T., Maraseni, T., Cockfield, G., & Raubenheimer, D. (2016). Predicting the distributions of predator (snow leopard) and prey (blue sheep) under climate change in the Himalaya. *Ecology and Evolution*, *6*(12), 4065–4075. https://doi.org/10.1002/ece3.2196

Balme, G. A., Batchelor, A., De Woronin Britz, N., Seymour, G., Grover, M., Hes, L., Macdonald, D. W., & Hunter, L. T. B. (2013). Reproductive success of female leopards *P anthera pardus* : The importance of top-down processes. *Mammal Review*, *43*(3), 221–237. https://doi.org/10.1111/j.1365-2907.2012.00219.x

Balme, G. A., Miller, J. R. B., Pitman, R. T., & Hunter, L. T. B. (2017). Caching reduces kleptoparasitism in a solitary, large felid. *Journal of Animal Ecology*, *86*(3), 634–644. https://doi.org/10.1111/1365-2656.12654

Barnett, T. P., Adam, J. C., & Lettenmaier, D. P. (2005). Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature*, *438*(7066), 303–309. https://doi.org/10.1038/nature04141

Bassing, S. B., DeVivo, M., Ganz, T. R., Kertson, B. N., Prugh, L. R., Roussin, T., Satterfield, L., Windell, R. M., Wirsing, A. J., & Gardner, B. (2023). Are we telling the same story?

Comparing inferences made from camera trap and telemetry data for wildlife monitoring. *Ecological Applications*, *33*(1), e2745. https://doi.org/10.1002/eap.2745

Bassing, S. B., Satterfield, L., Ganz, T. R., DeVivo, M., Kertson, B. N., Roussin, T., Wirsing, A. J., & Gardner, B. (2024). Predator–prey space use and landscape features influence movement behaviors in a large-mammal community. *Ecology*, *105*(11), e4448. https://doi.org/10.1002/ecy.4448

Berg, M. P., Kiers, E. T., Driessen, G., Van Der Heijden, M., Kooi, B. W., Kuenen, F., Liefting, M., Verhoef, H. A., & Ellers, J. (2010). Adapt or disperse: Understanding species persistence in a changing world. *Global Change Biology*, *16*(2), 587–598. https://doi.org/10.1111/j.1365-2486.2009.02014.x

Besso, H., Shean, D., & Lundquist, J. D. (2024). Mountain snow depth retrievals from customized processing of ICESat-2 satellite laser altimetry. *Remote Sensing of Environment*, *300*, 113843. https://doi.org/10.1016/j.rse.2023.113843

Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., & Finnegan, S. (2013). Climate Change and the Past, Present, and Future of Biotic Interactions. *Science*, *341*(6145), 499–504. https://doi.org/10.1126/science.1237184

Borg, B. L., & Schirokauer, D. W. (2022). The Role of Weather and Long-Term Prey Dynamics as Drivers of Wolf Population Dynamics in a Multi-Prey System. *Frontiers in Ecology and Evolution*, *10*, 791161. https://doi.org/10.3389/fevo.2022.791161

Bormann, K. J., Westra, S., Evans, J. P., & McCabe, M. F. (2013). Spatial and temporal variability in seasonal snow density. *Journal of Hydrology*, *484*, 63–73. https://doi.org/10.1016/j.jhydrol.2013.01.032

Breen, C. M. (2024). *Evaluating Camera Traps as Ground-Based Remote Sensing Networks, Linking Snow and Wildlife* [PhD Thesis]. University of Washington.

Brogli, R., Heim, C., Mensch, J., Sørland, S. L., & Schär, C. (2023). The pseudo-global-warming (PGW) approach: Methodology, software package PGW4ERA5 v1.1, validation, and sensitivity analyses. *Geoscientific Model Development*, *16*(3), 907–926. https://doi.org/10.5194/gmd-16-907-2023

Brown, R. D., & Mote, P. W. (2009). The Response of Northern Hemisphere Snow Cover to a Changing Climate*. *Journal of Climate*, *22*(8), 2124–2145. https://doi.org/10.1175/2008JCLI2665.1

Bryce, C. M., Dunford, C. E., Pagano, A. M., Wang, Y., Borg, B. L., Arthur, S. M., & Williams, T. M. (2022). Environmental correlates of activity and energetics in a wide-ranging social carnivore. *Animal Biotelemetry*, *10*(1), 1. https://doi.org/10.1186/s40317-021-00272-w

Chen, D., Rojas, M., Samset, B. H., Cobb, K., Diongue Niang, A., Edwards, P., Emori, S., Faria, S. H., Hawkins, E., Hope, P., Huybrechts, P., Meinshausen, M., Mustafa, S. K., Plattner, G.-K., & Tréguier, A.-M. (2021). Framing, Context, and Methods. In *Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 147–286). Cambridge University Press.

Clark, M. P., Nijssen, B., Lundquist, J. D., Kavetski, D., Rupp, D. E., Woods, R. A., Freer, J. E., Gutmann, E. D., Wood, A. W., Gochis, D. J., Rasmussen, R. M., Tarboton, D. G., Mahat, V., Flerchinger, G. N., & Marks, D. G. (2015). A unified approach for process-based hydrologic modeling: 2. Model implementation and case studies. *Water Resources Research*, *51*(4), 2515–2542. https://doi.org/10.1002/2015WR017200

Crête, M., & Larivière, S. (2003). Estimating the costs of locomotion in snow for coyotes. *Canadian Journal of Zoology*, *81*(11), 1808–1814. https://doi.org/10.1139/z03-182

Cunningham, C. X., Liston, G. E., Reinking, A. K., Boelman, N. T., Brinkman, T. J., Joly, K., Hebblewhite, M., Boutin, S., Czetwertynski, S., Sielecki, L. E., & Prugh, L. R. (2022). Human and animal movements combine with snow to increase moose-vehicle collisions in winter. *Environmental Research Letters*, *17*(12), 125007. https://doi.org/10.1088/1748-9326/aca8bf

Deguines, N., Brashares, J. S., & Prugh, L. R. (2017). Precipitation alters interactions in a grassland ecological community. *Journal of Animal Ecology*, *86*(2), 262–272. https://doi.org/10.1111/1365-2656.12614

DelGiudice, G. D., Fieberg, J. R., & Sampson, B. A. (2013). A Long-Term Assessment of the Variability in Winter Use of Dense Conifer Cover by Female White-Tailed Deer. *PLoS ONE*, *8*(6), e65368. https://doi.org/10.1371/journal.pone.0065368

DeLgiudice, G. D., Riggs, M. R., Joly, P., & Pan, W. (2002). Winter Severity, Survival, and Cause-Specific Mortality of Female White-Tailed Deer in North-Central Minnesota. *The Journal of Wildlife Management*, *66*(3), 698. https://doi.org/10.2307/3803136

Deser, C., Knutti, R., Solomon, S., & Phillips, A. S. (2012). Communication of the role of natural variability in future North American climate. *Nature Climate Change*, *2*(11), 775–779. https://doi.org/10.1038/nclimate1562

Deser, C., Lehner, F., Rodgers, K. B., Ault, T., Delworth, T. L., DiNezio, P. N., Fiore, A., Frankignoul, C., Fyfe, J. C., Horton, D. E., Kay, J. E., Knutti, R., Lovenduski, N. S., Marotzke, J., McKinnon, K. A., Minobe, S., Randerson, J., Screen, J. A., Simpson, I. R., & Ting, M. (2020). Insights from Earth system model initial-condition large ensembles and future prospects. *Nature Climate Change*, *10*(4), 277–286. https://doi.org/10.1038/s41558-020-0731-2

Deser, C., Phillips, A., Bourdette, V., & Teng, H. (2012). Uncertainty in climate change projections: The role of internal variability. *Climate Dynamics*, *38*(3–4), 527–546. https://doi.org/10.1007/s00382-010-0977-x

Deser, C., Phillips, A. S., Alexander, M. A., & Smoliak, B. V. (2014). Projecting North American Climate over the Next 50 Years: Uncertainty due to Internal Variability*. *Journal of Climate*, *27*(6), 2271–2296. https://doi.org/10.1175/JCLI-D-13-00451.1

Durner, G. M., Amstrup, S. C., & Fischbach, A. S. (2003). Habitat Characteristics of Polar Bear Terrestrial Maternal Den Sites in Northern Alaska. *ARCTIC*, *56*(1), 55–62. https://doi.org/10.14430/arctic602

Dussault, C., Ouellet, J., Courtois, R., Huot, J., Breton, L., & Jolicoeur, H. (2005). Linking moose habitat selection to limiting factors. *Ecography*, *28*(5), 619–628. https://doi.org/10.1111/j.2005.0906-7590.04263.x

Eyring, V., Bony, S., Meehl, G. A., Senior, C. A., Stevens, B., Stouffer, R. J., & Taylor, K. E. (2016). Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization. *Geoscientific Model Development*, *9*(5), 1937–1958. https://doi.org/10.5194/gmd-9-1937-2016

Felton, A. M., Wam, H. K., Borowski, Z., Granhus, A., Juvany, L., Matala, J., Melin, M., Wallgren, M., & Mårell, A. (2024). Climate change and deer in boreal and temperate regions: From physiology to population dynamics and species distributions. *Global Change Biology*, *30*(9), e17505. https://doi.org/10.1111/gcb.17505

Forrester, T. D., & Wittmer, H. U. (2013). A review of the population dynamics of mule deer and black-tailed deer *O docoileus hemionus* in N orth A merica. *Mammal Review*, *43*(4), 292–308. https://doi.org/10.1111/mam.12002

Fuller, T. K. (1991). Effect of snow depth on wolf activity and prey selection in north central Minnesota. *Canadian Journal of Zoology*, *69*(2), 283–287. https://doi.org/10.1139/z91-044

Ganz, T. R., Bassing, S. B., DeVivo, M. T., Gardner, B., Kertson, B. N., Satterfield, L. C., Shipley, L. A., Turnock, B. Y., Walker, S. L., Abrahamson, D., Wirsing, A. J., & Prugh, L. R. (2024). White-tailed deer population dynamics in a multipredator landscape shaped by humans. *Ecological Applications*, *34*(5), e3003. https://doi.org/10.1002/eap.3003

Ganz, T. R., DeVivo, M. T., Kertson, B. N., Roussin, T., Satterfield, L., Wirsing, A. J., & Prugh, L. R. (2022). Interactive effects of wildfires, season and predator activity shape mule deer movements. *Journal of Animal Ecology*, *91*(11), 2273–2288. https://doi.org/10.1111/1365-2656.13810

Ganz, T. R., DeVivo, M. T., Wirsing, A. J., Bassing, S. B., Kertson, B. N., Walker, S. L., & Prugh, L. R. (2024). Cougars, wolves, and humans drive a dynamic landscape of fear for elk. *Ecology*, *105*(4), e4255. https://doi.org/10.1002/ecy.4255

Garroway, C. J., & Broders, H. G. (2005). The quantitative effects of population density and winter weather on the body condition of white-tailed deer (*Odocoileus virginianus*) in Nova Scotia, Canada. *Canadian Journal of Zoology*, *83*(9), 1246–1256. https://doi.org/10.1139/z05-118

Gergel, D. R., Nijssen, B., Abatzoglou, J. T., Lettenmaier, D. P., & Stumbaugh, M. R. (2017). Effects of climate change on snowpack and fire potential in the western USA. *Climatic Change*, *141*(2), 287–299. https://doi.org/10.1007/s10584-017-1899-y

Gervasi, V., Sand, H., Zimmermann, B., Mattisson, J., Wabakken, P., & Linnell, J. D. C. (2013). Decomposing risk: Landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. *Ecological Applications*, *23*(7), 1722–1734. https://doi.org/10.1890/12-1615.1

Gesch, D. B., Evans, G. A., Oimoen, M. J., & Arundel, S. (2018). *The National Elevation Dataset* (pp. 83–110). American Society for Photogrammetry and Remote Sensing; USGS Publications Warehouse. https://pubs.usgs.gov/publication/70201572

Gilbert, S. L., Hundertmark, K. J., Person, D. K., Lindberg, M. S., & Boyce, M. S. (2017). Behavioral plasticity in a variable environment: Snow depth and habitat interactions drive deer movement in winter. *Journal of Mammalogy*, *98*(1), 246–259. https://doi.org/10.1093/jmammal/gyw167

Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution*, *25*(6), 325–331. https://doi.org/10.1016/j.tree.2010.03.002

Griffin, K. A., Hebblewhite, M., Robinson, H. S., Zager, P., Barber-Meyer, S. M., Christianson, D., Creel, S., Harris, N. C., Hurley, M. A., Jackson, D. H., Johnson, B. K., Myers, W. L., Raithel, J. D., Schlegel, M., Smith, B. L., White, C., & White, P. J. (2011). Neonatal mortality of elk driven by climate, predator phenology and predator community composition: Neonate elk calf survival across the north-western USA. *Journal of Animal Ecology*, *80*(6), 1246–1257. https://doi.org/10.1111/j.1365-2656.2011.01856.x

Gutmann, E. D., Rasmussen, R. M., Liu, C., Ikeda, K., Gochis, D. J., Clark, M. P., Dudhia, J., & Thompson, G. (2012). A Comparison of Statistical and Dynamical Downscaling of Winter Precipitation over Complex Terrain. *Journal of Climate*, *25*(1), 262–281. https://doi.org/10.1175/2011JCLI4109.1

Hammond, J. C., Sexstone, G. A., Putman, A. L., Barnhart, T. B., Rey, D. M., Driscoll, J. M., Liston, G. E., Rasmussen, K. L., McGrath, D., Fassnacht, S. R., & Kampf, S. K. (2023). High Resolution SnowModel Simulations Reveal Future Elevation-Dependent Snow Loss and Earlier, Flashier Surface Water Input for the Upper Colorado River Basin. *Earth's Future*, *11*(2), e2022EF003092. https://doi.org/10.1029/2022EF003092

Hansen, B. B., Lorentzen, J. R., Welker, J. M., Varpe, Ø., Aanes, R., Beumer, L. T., & Pedersen, Å. Ø. (2019). Reindeer turning maritime: Ice-locked tundra triggers changes in dietary niche utilization. *Ecosphere*, *10*(4), e02672. https://doi.org/10.1002/ecs2.2672

Hijmans, R. J. (2024). *terra: Spatial Data Analysis* (Version R package version 1.7-78) [Computer software]. https://CRAN.R-project.org/package=terra

Hill, D. F., Burakowski, E. A., Crumley, R. L., Keon, J., Hu, J. M., Arendt, A. A., Wikstrom Jones, K., & Wolken, G. J. (2019). Converting snow depth to snow water equivalent using climatological variables. *The Cryosphere*, *13*(7), 1767–1784. https://doi.org/10.5194/tc-13-1767-2019

Hobbs, N. T. (1989). Linking Energy Balance to Survival in Mule Deer: Development and Test of a Simulation Model. *Wildlife Monographs*, *101*, 1–39.

Holmes, S. M., Cromsigt, J. P. G. M., Danell, K., Ericsson, G., Singh, N. J., & Widemo, F. (2021). Declining recruitment and mass of Swedish moose calves linked to hot, dry springs and snowy winters. *Global Ecology and Conservation*, *27*, e01594. https://doi.org/10.1016/j.gecco.2021.e01594

Horne, J. S., Hurley, M. A., White, C. G., & Rachael, J. (2019). Effects of wolf pack size and winter conditions on elk mortality. *The Journal of Wildlife Management*, *83*(5), 1103–1116. https://doi.org/10.1002/jwmg.21689

Immerzeel, W. W., Lutz, A. F., Andrade, M., Bahl, A., Biemans, H., Bolch, T., Hyde, S., Brumby, S., Davies, B. J., Elmore, A. C., Emmer, A., Feng, M., Fernández, A., Haritashya, U., Kargel, J. S., Koppes, M., Kraaijenbrink, P. D. A., Kulkarni, A. V., Mayewski, P. A., … Baillie, J. E. M. (2020). Importance and vulnerability of the world's water towers. *Nature*, *577*(7790), 364–369. https://doi.org/10.1038/s41586-019-1822-y

Intergovernmental Panel on Climate Change (Ed.). (2023). Summary for Policymakers. In *Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 3–32). Cambridge University Press; Cambridge Core. https://doi.org/10.1017/9781009157896.001

IPCC. (2022). *The Ocean and Cryosphere in a Changing Climate: Special Report of the Intergovernmental Panel on Climate Change* (1st ed.). Cambridge University Press. https://doi.org/10.1017/9781009157964

IPCC. (2023). *Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (1st ed.). Cambridge University Press. https://doi.org/10.1017/9781009157896

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B., Selva, N., Zub, K., & Szymura, L. (2002). Kill rates and predation by wolves on ungulate populations in Bialowieza

Primeval Forest (Poland). *Ecology*, *83*(5), 1341–1356. https://doi.org/10.1890/0012-9658(2002)083%255B1341:KRAPBW%255D2.0.CO;2

Johnston, J., Jacobs, J. M., & Cho, E. (2023). Global Snow Seasonality Regimes from Satellite Records of Snow Cover. *Journal of Hydrometeorology*.

Kawase, H., Yamazaki, T., Sugimoto, S., Sasai, T., Ito, R., Hamada, T., Kuribayashi, M., Fujita, M., Murata, A., Nosaka, M., & Sasaki, H. (2020). Changes in extremely heavy and light snow-cover winters due to global warming over high mountainous areas in central Japan. *Progress in Earth and Planetary Science*, *7*(1), 10. https://doi.org/10.1186/s40645-020-0322-x

Kittle, A. M., Fryxell, J. M., Desy, G. E., & Hamr, J. (2008). The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia*, *157*(1), 163–175. https://doi.org/10.1007/s00442-008-1051-9

Kotlarski, S., Gobiet, A., Morin, S., Olefs, M., Rajczak, J., & Samacoïts, R. (2023). 21st Century alpine climate change. *Climate Dynamics*, *60*(1–2), 65–86. https://doi.org/10.1007/s00382-022-06303-3

Latifovic, R., Homer, C., Ressl, R., Pouliot, D., Hossain, S. N., Colditz, R. R., Olthof, I., Giri, C. P., & Victoria, A. (2016). 20 North American land-change monitoring system. *Remote Sensing of Land Use and Land Cover: Principles and Applications*, 303.

Leblond, M., Dussault, C., & Ouellet, J. (2010). What drives fine-scale movements of large herbivores? A case study using moose. *Ecography*, *33*(6), 1102–1112. https://doi.org/10.1111/j.1600-0587.2009.06104.x

Liston, G. E., & Elder, K. (2006a). A Distributed Snow-Evolution Modeling System (SnowModel). *Journal of Hydrometeorology*, *7*(6), 1259–1276. https://doi.org/10.1175/JHM548.1

Liston, G. E., & Elder, K. (2006b). A Meteorological Distribution System for High-Resolution Terrestrial Modeling (MicroMet). *Journal of Hydrometeorology*, *7*(2), 217–234. https://doi.org/10.1175/JHM486.1

Liu, C., Ikeda, K., Rasmussen, R., Barlage, M., Newman, A. J., Prein, A. F., Chen, F., Chen, L., Clark, M., Dai, A., Dudhia, J., Eidhammer, T., Gochis, D., Gutmann, E., Kurkute, S., Li, Y., Thompson, G., & Yates, D. (2017). Continental-scale convection-permitting modeling of the current and future climate of North America. *Climate Dynamics*, *49*(1–2), 71–95. https://doi.org/10.1007/s00382-016-3327-9

Loe, L. E., Liston, G. E., Pigeon, G., Barker, K., Horvitz, N., Stien, A., Forchhammer, M., Getz, W. M., Irvine, R. J., Lee, A., Movik, L. K., Mysterud, A., Pedersen, Å. Ø., Reinking, A. K., Ropstad, E., Trondrud, L. M., Tveraa, T., Veiberg, V., Hansen, B. B., & Albon, S. D. (2021). The neglected season: Warmer autumns counteract harsher winters and promote population growth in Arctic reindeer. *Global Change Biology*, *27*(5), 993–1002. https://doi.org/10.1111/gcb.15458

Long, R. A., Bowyer, R. T., Porter, W. P., Mathewson, P., Monteith, K. L., & Kie, J. G. (2014). Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. *Ecological Monographs*, *84*(3), 513–532. https://doi.org/10.1890/13-1273.1

Lotka, A. J. (1920). Analytical Note on Certain Rhythmic Relations in Organic Systems. *Proceedings of the National Academy of Sciences*, *6*(7), 410–415. https://doi.org/10.1073/pnas.6.7.410

Lybarger, N. D., Smith, A., Newman, A. J., Gutmann, E. D., Wood, A. W., Frans, C. D., Warner, M. D., & Arnold, J. R. (2024). Improving Earth System Model Selection Methodologies for Projecting Hydroclimatic Change: Case Study in the Pacific Northwest. *Journal of Geophysical Research: Atmospheres*, *129*(7), e2023JD039774. https://doi.org/10.1029/2023JD039774

Maraun, D., Wetterhall, F., Ireson, A. M., Chandler, R. E., Kendon, E. J., Widmann, M., Brienen, S., Rust, H. W., Sauter, T., Themeßl, M., Venema, V. K. C., Chun, K. P., Goodess, C. M., Jones, R. G., Onof, C., Vrac, M., & Thiele-Eich, I. (2010). Precipitation downscaling under climate change: Recent developments to bridge the gap between dynamical models and the end user. *Reviews of Geophysics*, *48*(3), RG3003. https://doi.org/10.1029/2009RG000314

McCluney, K. E., Belnap, J., Collins, S. L., González, A. L., Hagen, E. M., Nathaniel Holland, J., Kotler, B. P., Maestre, F. T., Smith, S. D., & Wolf, B. O. (2012). Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change. *Biological Reviews*, *87*(3), 563–582. https://doi.org/10.1111/j.1469-185X.2011.00209.x

Mech, L. D., & Peterson, R. O. (2003). *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press.

Morrison, S. F., Forbes, G. J., Young, S. J., & Lusk, S. (2003). Within-yard habitat use by white-tailed deer at varying winter severity. *Forest Ecology and Management*, *172*(2–3), 173–182. https://doi.org/10.1016/S0378-1127(01)00809-X

Mortezapour, M., Menounos, B., Jackson, P. L., & Erler, A. R. (2022). Future Snow Changes over the Columbia Mountains, Canada, using a Distributed Snow Model. *Climatic Change*, *172*(1–2), 6. https://doi.org/10.1007/s10584-022-03360-9

Mower, R., Gutmann, E. D., Liston, G. E., Lundquist, J., & Rasmussen, S. (2024). Parallel SnowModel (v1.0): A parallel implementation of a distributed snow-evolution modeling system (SnowModel). *Geoscientific Model Development*, *17*(10), 4135–4154. https://doi.org/10.5194/gmd-17-4135-2024

Mudryk, L., Santolaria-Otín, M., Krinner, G., Ménégoz, M., Derksen, C., Brutel-Vuilmet, C., Brady, M., & Essery, R. (2020). Historical Northern Hemisphere snow cover trends and projected changes in the CMIP6 multi-model ensemble. *The Cryosphere*, *14*(7), 2495–2514. https://doi.org/10.5194/tc-14-2495-2020

Mysterud, A., & Østbye, E. (2006). Effect of climate and density on individual and population growth of roe deer Capreolus capreolus at northern latitudes: The Lier valley, Norway. *Wildlife Biology*, *12*(3), 321–329. https://doi.org/10.2981/0909-6396(2006)12%255B321:EOCADO%255D2.0.CO;2

Natural Resources Conservation Service. (2025). *Air & Water Database Reports* [Dataset]. National Water & Climate Center. https://nwcc-apps.sc.egov.usda.gov/awdb/site-plots/POR/WTEQ/WA/Muckamuck.html

Nelson, M. E., & Mech, L. D. (1986). Relationship between Snow Depth and Gray Wolf Predation on White-Tailed Deer. *The Journal of Wildlife Management*, *50*(3), 471. https://doi.org/10.2307/3801108

Newman, A. J., Monaghan, A. J., Clark, M. P., Ikeda, K., Xue, L., Gutmann, E. D., & Arnold, J. R. (2021). Hydroclimatic changes in Alaska portrayed by a high-resolution regional climate simulation. *Climatic Change*, *164*(1–2), 17. https://doi.org/10.1007/s10584-021-02956-x

Niittynen, P., Heikkinen, R. K., & Luoto, M. (2018). Snow cover is a neglected driver of Arctic biodiversity loss. *Nature Climate Change*, *8*(11), 997–1001. https://doi.org/10.1038/s41558-018-0311-x

Norris, J., Rahimi, S., Huang, L., Bass, B., Thackeray, C. W., & Hall, A. (2025). Uncertainty of 21st Century western U.S. snowfall loss derived from regional climate model large ensemble. *Npj Climate and Atmospheric Science*, *8*(1), 134. https://doi.org/10.1038/s41612-025-01002-2

Ortega, A. C., Merkle, J. A., Sawyer, H., Monteith, K. L., Lionberger, P., Valdez, M., & Kauffman, M. J. (2024). A test of the frost wave hypothesis in a temperate ungulate. *Ecology*, e4238. https://doi.org/10.1002/ecy.4238

Parker, K. L., Robbins, C. T., & Hanley, T. A. (1984). Energy Expenditures for Locomotion by Mule Deer and Elk. *The Journal of Wildlife Management*, *48*(2), 474. https://doi.org/10.2307/3801180

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S.,

… Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214. https://doi.org/10.1126/science.aai9214

Peers, M. J. L., Majchrzak, Y. N., Menzies, A. K., Studd, E. K., Bastille-Rousseau, G., Boonstra, R., Humphries, M., Jung, T. S., Kenney, A. J., Krebs, C. J., Murray, D. L., & Boutin, S. (2020). Climate change increases predation risk for a keystone species of the boreal forest. *Nature Climate Change*, *10*(12), 1149–1153. https://doi.org/10.1038/s41558-020-00908-4

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

Pflug, J. M., Liston, G. E., Nijssen, B., & Lundquist, J. D. (2019). Testing model representations of snowpack liquid water percolation across multiple climates. *Water Resources Research*, *55*(6), 4820–4838.

Pierce, D. W., Barnett, T. P., Santer, B. D., & Gleckler, P. J. (2009). Selecting global climate models for regional climate change studies. *Proceedings of the National Academy of Sciences*, *106*(21), 8441–8446. https://doi.org/10.1073/pnas.0900094106

Poirier, M., Fauteux, D., Gauthier, G., Domine, F., & Lamarre, J. (2021). Snow hardness impacts intranivean locomotion of arctic small mammals. *Ecosphere*, *12*(11), e03835. https://doi.org/10.1002/ecs2.3835

Poirier, M., Gauthier, G., Domine, F., & Fauteux, D. (2023). Lemming winter habitat: The quest for warm and soft snow. *Oecologia*, *202*(2), 211–225. https://doi.org/10.1007/s00442-023-05385-y

Post, E., Peterson, R. O., Stenseth, N. Chr., & McLaren, B. E. (1999). Ecosystem consequences of wolf behavioural response to climate. *Nature*, *401*(6756), 905–907. https://doi.org/10.1038/44814

Pouchet, C., Fernandez-Prada, C., Dussault, C., Leclerc, M., Tremblay, J., & Côté, S. D. (2024). Linking weather conditions and winter tick abundance in moose. *The Journal of Wildlife Management*, *88*(3), e22551. https://doi.org/10.1002/jwmg.22551

Prugh, L. R., Cunningham, C. X., Windell, R. M., Kertson, B. N., Ganz, T. R., Walker, S. L., & Wirsing, A. J. (2023). Fear of large carnivores amplifies human-caused mortality for mesopredators. *Science*, *380*(6646), 754–758. https://doi.org/10.1126/science.adf2472

Prugh, L. R., Lundquist, J. D., Sullender, B. K., Cunningham, C. X., Dechow, J., Borg, B. L., Sousanes, P. J., Stehn, S., & Durand, M. T. (2024). Landscape heterogeneity buffers the impact of an extreme weather event on wildlife. *Communications Biology*, *7*(1), 1515. https://doi.org/10.1038/s42003-024-07195-1

Pulliainen, J., Luojus, K., Derksen, C., Mudryk, L., Lemmetyinen, J., Salminen, M., Ikonen, J., Takala, M., Cohen, J., Smolander, T., & Norberg, J. (2020). Patterns and trends of Northern Hemisphere snow mass from 1980 to 2018. *Nature*, *581*(7808), 294–298. https://doi.org/10.1038/s41586-020-2258-0

Rahimi, S., Huang, L., Norris, J., Hall, A., Goldenson, N., Krantz, W., Bass, B., Thackeray, C., Lin, H., Chen, D., Dennis, E., Collins, E., Lebo, Z. J., Slinskey, E., Graves, S., Biyani, S., Wang, B., Cropper, S., & the UCLA Center for Climate Science Team. (2024). An overview of the Western United States Dynamically Downscaled Dataset (WUS-D3). *Geoscientific Model Development*, *17*(6), 2265–2286. https://doi.org/10.5194/gmd-17-2265-2024

Rahimi, S., Huang, L., Norris, J., Hall, A., Goldenson, N., Risser, M., Feldman, D. R., Lebo, Z. J., Dennis, E., & Thackeray, C. (2024). Understanding the Cascade: Removing GCM Biases Improves Dynamically Downscaled Climate Projections. *Geophysical Research Letters*, *51*(9), e2023GL106264. https://doi.org/10.1029/2023GL106264

Raleigh, M. S., & Lundquist, J. D. (2012). Comparing and combining SWE estimates from the SNOW-17 model using PRISM and SWE reconstruction. *Water Resources Research*, *48*(1), 2011WR010542. https://doi.org/10.1029/2011WR010542

Rasmussen, R., Liu, C., Ikeda, K., Chen, F., Kim, J.-H., Schneider, T., Gochis, D., Dugger, A., & Viger, R. (2023). *Four-kilometer long-term regional hydroclimate reanalysis over the conterminous United States (CONUS)*.

Rasmussen, R., Liu, C., Ikeda, K., Gochis, D., Yates, D., Chen, F., Tewari, M., Barlage, M., Dudhia, J., Yu, W., Miller, K., Arsenault, K., Grubišić, V., Thompson, G., & Gutmann, E. (2011). High-Resolution Coupled Climate Runoff Simulations of Seasonal Snowfall over Colorado: A Process Study of Current and Warmer Climate. *Journal of Climate*, *24*(12), 3015–3048. https://doi.org/10.1175/2010JCLI3985.1

Rattenbury, K. L., Schmidt, J. H., Swanson, D. K., Borg, B. L., Mangipane, B. A., & Sousanes, P. J. (2018). Delayed spring onset drives declines in abundance and recruitment in a mountain ungulate. *Ecosphere*, *9*(11), e02513. https://doi.org/10.1002/ecs2.2513

Reinking, A. K., Højlund Pedersen, S., Elder, K., Boelman, N. T., Glass, T. W., Oates, B. A., Bergen, S., Roberts, S., Prugh, L. R., Brinkman, T. J., Coughenour, M. B., Feltner, J. A., Barker, K. J., Bentzen, T. W., Pedersen, Å. Ø., Schmidt, N. M., & Liston, G. E. (2022). Collaborative wildlife–snow science: Integrating wildlife and snow expertise to improve research and management. *Ecosphere*, *13*(6). https://doi.org/10.1002/ecs2.4094

Rickbeil, G. J. M., Merkle, J. A., Anderson, G., Atwood, M. P., Beckmann, J. P., Cole, E. K., Courtemanch, A. B., Dewey, S., Gustine, D. D., Kauffman, M. J., McWhirter, D. E., Mong, T., Proffitt, K., White, P. J., & Middleton, A. D. (2019). Plasticity in elk migration timing is a response to changing environmental conditions. *Global Change Biology*, *25*(7), 2368–2381. https://doi.org/10.1111/gcb.14629

Rivrud, I. M., Bischof, R., Meisingset, E. L., Zimmermann, B., Loe, L. E., & Mysterud, A. (2016). Leave before it's too late: Anthropogenic and environmental triggers of autumn migration in a hunted ungulate population. *Ecology*, *97*(4), 1058–1068. https://doi.org/10.1890/15-1191.1

Rivrud, I. M., Meisingset, E. L., Loe, L. E., & Mysterud, A. (2019). Future suitability of habitat in a migratory ungulate under climate change. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1899), 20190442. https://doi.org/10.1098/rspb.2019.0442

Rogers, M., & Mauger, G. S. (2021). *Pacific Northwest Climate Projection Tool* [Dataset]. https://cig.uw.edu/resources/analysis-tools/pacific-northwest-climate-projection-tool/

Romero, G. Q., Gonçalves-Souza, T., Kratina, P., Marino, N. A. C., Petry, W. K., Sobral-Souza, T., & Roslin, T. (2018). Global predation pressure redistribution under future climate change. *Nature Climate Change*, *8*(12), 1087–1091. https://doi.org/10.1038/s41558-018-0347-y

Rupp, D. E., Abatzoglou, J. T., & Mote, P. W. (2017). Projections of 21st century climate of the Columbia River Basin. *Climate Dynamics*, *49*(5–6), 1783–1799. https://doi.org/10.1007/s00382-016-3418-7

Sabine, D. L., Morrison, S. F., Whitlaw, H. A., Ballard, W. B., Forbes, G. J., & Bowman, J. (2002). Migration Behavior of White-Tailed Deer under Varying Winter Climate

Regimes in New Brunswick. *The Journal of Wildlife Management*, *66*(3), 718. https://doi.org/10.2307/3803137

Scalzitti, J., Strong, C., & Kochanski, A. (2016). Climate change impact on the roles of temperature and precipitation in western U.S. snowpack variability. *Geophysical Research Letters*, *43*(10), 5361–5369. https://doi.org/10.1002/2016GL068798

Schär, C., Frei, C., Lüthi, D., & Davies, H. C. (1996). Surrogate climate-change scenarios for regional climate models. *Geophysical Research Letters*, *23*(6), 669–672. https://doi.org/10.1029/96GL00265

Scridel, D., Brambilla, M., Martin, K., Lehikoinen, A., Iemma, A., Matteo, A., Jähnig, S., Caprio, E., Bogliani, G., Pedrini, P., Rolando, A., Arlettaz, R., & Chamberlain, D. (2018). A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations. *Ibis*, *160*(3), 489–515. https://doi.org/10.1111/ibi.12585

Severson, J. P., Johnson, H. E., Arthur, S. M., Leacock, W. B., & Suitor, M. J. (2021). Spring phenology drives range shifts in a migratory Arctic ungulate with key implications for the future. *Global Change Biology*, *27*(19), 4546–4563. https://doi.org/10.1111/gcb.15682

Signer, J., Fieberg, J., & Avgar, T. (2019). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and Evolution*, *9*(2), 880–890. https://doi.org/10.1002/ece3.4823

Siirila-Woodburn, E. R., Rhoades, A. M., Hatchett, B. J., Huning, L. S., Szinai, J., Tague, C., Nico, P. S., Feldman, D. R., Jones, A. D., Collins, W. D., & Kaatz, L. (2021). A low-to-no snow future and its impacts on water resources in the western United States. *Nature*

Reviews Earth & Environment, *2*(11), 800–819. https://doi.org/10.1038/s43017-021-00219-y

Sivy, K. J., Nolin, A. W., Cosgrove, C. L., & Prugh, L. R. (2018). Critical snow density threshold for Dall's sheep (*Ovis dalli dalli*). *Canadian Journal of Zoology*, *96*(10), 1170–1177. https://doi.org/10.1139/cjz-2017-0259

Slettenhaar, A. J., Østnes, J. E., Moen, B. C., Kroglund, R. T., Nygård, T., & Nilsen, E. B. (2025). A Picky Predator and Its Prey: How Snow Conditions and Ptarmigan Abundance Impact Gyrfalcon Feeding Behaviour and Breeding Success. *Ecology and Evolution*, *15*(4), e71228. https://doi.org/10.1002/ece3.71228

Smith, T., & Bookhagen, B. (2020). Assessing Multi-Temporal Snow-Volume Trends in High Mountain Asia From 1987 to 2016 Using High-Resolution Passive Microwave Data. *Frontiers in Earth Science*, *8*, 559175. https://doi.org/10.3389/feart.2020.559175

Stein, A. B., Bourquin, S. L., & McNutt, J. W. (2015). Avoiding Intraguild Competition: Leopard Feeding Ecology and Prey Caching in Northern Botswana. *African Journal of Wildlife Research*, *45*(2), 247. https://doi.org/10.3957/056.045.0247

St-Georges, M., Nadeau, S., Lambert, D., & Décarie, R. (1995). Winter habitat use by ptarmigan, snowshoe hares, red foxes, and river otters in the boreal forest – tundra transition zone of western Quebec. *Canadian Journal of Zoology*, *73*(4), 755–764. https://doi.org/10.1139/z95-089

Strong, C., Kochanski, A. K., & Crosman, E. T. (2014). A slab model of the Great Salt Lake for regional climate simulation. *Journal of Advances in Modeling Earth Systems*, *6*(3), 602–615. https://doi.org/10.1002/2014MS000305

Sturm, M., & Liston, G. E. (2021). Revisiting the Global Seasonal Snow Classification: An Updated Dataset for Earth System Applications. *Journal of Hydrometeorology*. https://doi.org/10.1175/JHM-D-21-0070.1

Sullender, B. K., Cunningham, C. X., Lundquist, J. D., & Prugh, L. R. (2023). Defining the danger zone: Critical snow properties for predator–prey interactions. *Oikos*, *2023*(10), e09925. https://doi.org/10.1111/oik.09925

Sullender, B. K., Ganz, T. R., Mower, R., Lundquist, J. D., Kertson, B. N., Newsome, T. M., Wirsing, A. J., & Prugh, L. R. (2025). Apex predators exploit advantageous snow conditions across hunting modes. *Journal of Animal Ecology*, 1365-2656.70170. https://doi.org/10.1111/1365-2656.70170

Swanson, A., Arnold, T., Kosmala, M., Forester, J., & Packer, C. (2016). In the absence of a "landscape of fear": How lions, hyenas, and cheetahs coexist. *Ecology and Evolution*, *6*(23), 8534–8545. https://doi.org/10.1002/ece3.2569

Taylor, G. P., Loikith, P. C., Aragon, C. M., Lee, H., & Waliser, D. E. (2023). CMIP6 model fidelity at simulating large-scale atmospheric circulation patterns and associated temperature and precipitation over the Pacific Northwest. *Climate Dynamics*, *60*(7–8), 2199–2218. https://doi.org/10.1007/s00382-022-06410-1

Telfer, E. S. (1970). Winter Habitat Selection by Moose and White-Tailed Deer. *The Journal of Wildlife Management*, *34*(3), 553. https://doi.org/10.2307/3798862

Telfer, E. S., & Kelsall, J. P. (1984). Adaptation of Some Large North American Mammals for Survival In Snow. *Ecology*, *65*(6), 1828–1834. https://doi.org/10.2307/1937779

Tittensor, D. P., Novaglio, C., Harrison, C. S., Heneghan, R. F., Barrier, N., Bianchi, D., Bopp, L., Bryndum-Buchholz, A., Britten, G. L., Büchner, M., Cheung, W. W. L., Christensen, V., Coll, M., Dunne, J. P., Eddy, T. D., Everett, J. D., Fernandes-Salvador, J. A., Fulton, E. A., Galbraith, E. D., … Blanchard, J. L. (2021). Next-generation ensemble projections reveal higher climate risks for marine ecosystems. *Nature Climate Change*, *11*(11), 973–981. https://doi.org/10.1038/s41558-021-01173-9

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*(12), 1351–1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Pe'er, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., … Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, *353*(6304), aad8466. https://doi.org/10.1126/science.aad8466

van de Kerk, M., Verbyla, D., Nolin, A. W., Sivy, K. J., & Prugh, L. R. (2018). Range-wide variation in the effect of spring snow phenology on Dall sheep population dynamics. *Environmental Research Letters*, *13*(7), 075008. https://doi.org/10.1088/1748-9326/aace64

Verstege, J. S., Johnson-Bice, S. M., & Roth, J. D. (2023). Arctic and red fox population responses to climate and cryosphere changes at the Arctic's edge. *Oecologia*, *202*(3), 589–599. https://doi.org/10.1007/s00442-023-05418-6

Volterra, V. (1927). Fluctuations in the abundance of a species considered mathematically. *Nature*, *119*(2983), 12–13.

West, L., Rafiq, K., Converse, S. J., Wilson, A. M., Jordan, N. R., Golabek, K. A., McNutt, J. W., & Abrahms, B. (2024). Droughts reshape apex predator space use and intraguild overlap. *Journal of Animal Ecology*, *93*(11), 1785–1798. https://doi.org/10.1111/1365-2656.14192

White, K. S., Pendleton, G. W., & Hood, E. (2009). Effects of Snow on Sitka Black-Tailed Deer Browse Availability and Nutritional Carrying Capacity in Southeastern Alaska. *The Journal of Wildlife Management*, *73*(4), 481–487. https://doi.org/10.2193/2007-499

Wilson, A. C., Nolin, A. W., & Bladon, K. D. (2021). Assessing the Role of Snow Cover for Post-Wildfire Revegetation Across the Pacific Northwest. *Journal of Geophysical Research: Biogeosciences*, *126*(11). https://doi.org/10.1029/2021JG006465

Wilson, R. R., & Durner, G. M. (2020). Seismic Survey Design and Effects on Maternal Polar Bear Dens. *The Journal of Wildlife Management*, *84*(2), 201–212. https://doi.org/10.1002/jwmg.21800

CHAPTER 6: CONCLUSIONS

My dissertation is built from a foundation of multiple lines of evidence. As part of intensive winter field campaigns, my field crew and I excavated a total of 982 snow pits over the course of four years (2021-2024). These observations included snow-tracking large mammals, repeated surveys in the same location to track how conditions change over time, and comparisons of upper layers to the full depth of the snowpack, all with the goal of establishing a mechanistic link between physical snow properties and wildlife movement. These snow pit measurements spanned three major ecosystems: Okanogan study area (n = 546), Northeast Washington (n = 39), and Denali National Park & Preserve, Alaska (n = 397). Besides use in three publications thus far (Breen et al., 2024; Prugh et al., 2024; Sullender et al., 2023), a cleaned and filtered version of these snow pit data are available publicly at the Oak Ridge National Laboratory Distributed Active Archive Center: https://doi.org/10.3334/ORNLDAAC/2188.

To complement our field observations, I was fortunate to have access to large mammal location data from two major wildlife research efforts. First, the Washington Predator Prey Project deployed 670 GPS collars on mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus canadensis*), bobcats (*Lynx rufus*), cougars (*Puma concolor*), coyotes (*Canis latrans*), and wolves (*Canis lupus*) from 2016-2022 (Bassing, 2022; Ganz, 2022; Ganz et al., 2024; Prugh et al., 2023). I use these data in Chapters 3 and 5. Secondly, I benefitted from association with the NASA's Arctic Boreal Vulnerability Experiment (ABoVE), which contributed to aggregating moose (*Alces alces*) GPS collar data across a wide swath of North America (Boelman et al., 2019; Cunningham et al., 2022). These data form the core of Chapter 4.

Finally, my work leveraged cutting edge models that represent physical snow processes at unprecedented temporal and spatial scales (Liston & Elder, 2006; Mower et al., 2024). With snow experts building and running these models, I used my field measurements and existing networks of snow observation stations (Natural Resources Conservation Service, 2025) to validate model output. I found that snow model output accurately represented the key processes and key metrics of snowpack, allowing me to directly use dynamic snow conditions as landscape features in my spatial analyses (Chapters 3 and 4), as well as quantify specific changes projected in climate models (Chapter 5). Using these three distinct lines of evidence – field observations, GPS collar data, and physically based snow modeling – I assessed how winter conditions affect wildlife species and community interactions, thereby influencing ecosystem function.

By combining simultaneous observations of snow and wildlife, my dissertation provides a useful framework to connect the otherwise disparate fields of snow science and wildlife ecology (Reinking et al., 2022). In Chapter 2, I found that snow density provides the strongest direct link to wildlife movement. This key variable – among hundreds of other measurable snow properties (C. Fierz et al., 2009) – interacts with snow depth to define where ungulates have reduced mobility compared with canids and felids, thereby providing an edge to the predators and a “danger zone” for prey. The utility of this density-and-depth framework was further underscored by strong GPS collar evidence (Chapter 3). Namely, certain snow conditions that maximize movement advantages for predators can be more influential than other components of habitat such as the dense forest and rugged terrain that cougars use as cover while stalking prey or the open, flat landscapes preferred by wolves for longer-distance chases. These findings enabled a quantitative assessment of the projected impact of climate change on predator-prey interactions across the Pacific Northwest (Chapter 5), as well as provide future researchers an entry point to link the cryosphere with the biosphere.

Snow-adapted species respond to the winter environment in myriad ways that influence broader scale metrics like population growth (Post et al., 1999), range limits (Johnston et al., 2012), genetic connectivity (Stenseth et al., 2004), and even potential persistence (Peers et al., 2020). Wildlife biologists have long noted that some large mammal species benefit from generally snowier conditions while others suffer (Mech & Boitani, 2003; Murie, 1944). Applying the more specific delineation of wildlife-relevant snow properties from Chapters 2 and 3, I found that, regardless of functional traits such as hunting mode, apex predators appear to exploit snow densities and depths that provide a movement advantage over ungulate prey (Chapter 3). This finding holds relevance for a wide range of predators with similar morphology (Murray & Larivière, 2002; Penczykowski et al., 2017; Telfer & Kelsall, 1984), indicating that predators better able to exploit given snow conditions may gain a competitive edge over sympatric carnivores (Atwood et al., 2009; Kolbe et al., 2007; Peers et al., 2020). On the other hand, winters serve as a nutritional bottleneck for ungulates (Kautz et al., 2020; Mahoney et al., 2018; Parker et al., 2009), with increased energy expenditure (Dailey & Hobbs, 1989; Parker et al., 1984) and reduced forage availability (Schwab & Pitt, 1991; Stien et al., 2010). We show that the demands of thermoregulation – specifically in moose, an exceptionally cold-adapted species – compound these negative impacts as habitat selection and behavioral shifts further reduce nutritional inputs (Chapter 4). We implicate winter conditions as a likely contributor to range contraction along the southern margin of moose distribution, describing a potential factor behind population-scale observations (Hoy et al., 2018; Ruprecht et al., 2016).

As wildlife navigate a rapidly warming planet, understanding how geophysical changes to snowpacks will translate to ecosystem-level impacts is critical. Unequivocal analyses indicate that snow will decline across many metrics: snow mass (Pulliainen et al., 2020), snowfall converting to rainfall (Nolin et al., 2021; Nolin & Daly, 2006), and snow cover extent and duration (Bormann et al., 2018; Brown & Mote, 2009). These projections are primarily interpreted in the context of hydrology (Brown & Mote, 2009; Immerzeel et al., 2020), geophysical processes (Musselman et al., 2018; Scaff et al., 2024), or single-species models focused on habitat suitability (Johnston et al., 2012; Rivrud et al., 2019). Although species interactions have a major role in structuring ecosystem function (Blois et al., 2013; Gilman et al., 2010; Post, 2013), significant challenges remain in representing dynamic and complex snow conditions at a wildlife-relevant scale (Reinking et al., 2022) and in resolving the computational demands of how these conditions are projected to change in the future (Norris et al., 2025). Our analysis in Chapter 5 – applying two climate change scenarios and modeling consequent changes in snow depth and density at a daily, 30m scale – addresses this gap and reveals that apex predators in the Pacific Northwest are likely to suffer disproportionately to the scale of geophysical changes. As hydrologists, wildlife biologists, natural resource managers, decision-makers, and winter enthusiasts alike grapple with our changing snowpacks, my dissertation outlines several key advances in our understanding of how snow shapes our world.

Finally, my dissertation raises key questions that merit deeper investigation. Most importantly, I do not explicitly link demographic parameters or population dynamics to my findings. Effective population modeling requires years of consistent monitoring to effectively account for the wide range of variables that influence large mammal populations. Future work to gather baseline data and continually track wildlife populations is of paramount importance to being able to step beyond changes to individual movement, behavior, and habitat selection towards forecasting expected population trends. Additionally, the extensive fieldwork and multi-taxa data collection efforts from the Washington Predator-Prey Project offer an opportunity to unpack wildlife dynamics in unprecedented detail, and future studies following the same data streams could serve as valuable barometers of how populations are responding to the changes identified in my dissertation and elsewhere (Bassing, 2022; Ganz, 2022). A longer time-series helps make sure that our findings are not an artifact of an unusual window of time but instead represent broader patterns. Although quantitative analysis relies on previously gathered data and therefore must be retrospective, ecology is a dynamic process. Ecologists must be prepared to match the pace of wildlife as we together navigate an uncertain and rapidly changing planet.

6.1 References

Atwood, T. C., Gese, E. M., & Kunkel, K. E. (2009). Spatial Partitioning of Predation Risk in a Multiple Predator–Multiple Prey System. *Journal of Wildlife Management*, *73*(6), 876–884. https://doi.org/10.2193/2008-325

Bassing, S. B. (2022). *Spatial and temporal patterns of predator-prey interactions in a large mammal community in eastern Washington* [PhD Thesis]. University of Washington.

Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., & Finnegan, S. (2013). Climate Change and the Past, Present, and Future of Biotic Interactions. *Science*, *341*(6145), 499–504. https://doi.org/10.1126/science.1237184

Boelman, N. T., Liston, G. E., Gurarie, E., Meddens, A. J. H., Mahoney, P. J., Kirchner, P. B., Bohrer, G., Brinkman, T. J., Cosgrove, C. L., Eitel, J. U. H., Hebblewhite, M., Kimball, J. S., LaPoint, S., Nolin, A. W., Pedersen, S. H., Prugh, L. R., Reinking, A. K., & Vierling, L. A. (2019). Integrating snow science and wildlife ecology in Arctic-boreal North America. *Environmental Research Letters*, *14*(1), 010401. https://doi.org/10.1088/1748-9326/aaeec1

Bormann, K. J., Brown, R. D., Derksen, C., & Painter, T. H. (2018). Estimating snow-cover trends from space. *Nature Climate Change*, *8*(11), 924–928. https://doi.org/10.1038/s41558-018-0318-3

Breen, C. M., Currier, W. R., Vuyovich, C., Miao, Z., & Prugh, L. R. (2024). Snow Depth Extraction From Time-Lapse Imagery Using a Keypoint Deep Learning Model. *Water Resources Research*, *60*(7), e2023WR036682. https://doi.org/10.1029/2023WR036682

Brown, R. D., & Mote, P. W. (2009). The Response of Northern Hemisphere Snow Cover to a Changing Climate*. *Journal of Climate*, *22*(8), 2124–2145. https://doi.org/10.1175/2008JCLI2665.1

C. Fierz, R. L. Armstrong, Y. Durand, P. Etchevers, E. Greene, D.M. McClung, K. Nishimura, P.K. Satyawali, & S.A. Sokratov. (2009). *The International Classification for Seasonal Snow on the Ground. IHP-VII Technical Documents in Hydrology N°83, IACS Contribution N°1, UNESCO-IHP, Paris.*

Cunningham, C. X., Liston, G. E., Reinking, A. K., Boelman, N. T., Brinkman, T. J., Joly, K., Hebblewhite, M., Boutin, S., Czetwertynski, S., Sielecki, L. E., & Prugh, L. R. (2022). Human and animal movements combine with snow to increase moose-vehicle collisions in winter. *Environmental Research Letters*, *17*(12), 125007. https://doi.org/10.1088/1748-9326/aca8bf

Dailey, T. V., & Hobbs, N. T. (1989). Travel in alpine terrain: Energy expenditures for locomotion by mountain goats and bighorn sheep. *Canadian Journal of Zoology*, *67*(10), 2368–2375. https://doi.org/10.1139/z89-335

Ganz, T. R. (2022). *Ungulate Responses to Predators in Complex Landscapes of Northern Washington* [PhD Thesis]. University of Washington.

Ganz, T. R., DeVivo, M. T., Wirsing, A. J., Bassing, S. B., Kertson, B. N., Walker, S. L., & Prugh, L. R. (2024). Cougars, wolves, and humans drive a dynamic landscape of fear for elk. *Ecology*, *105*(4), e4255. https://doi.org/10.1002/ecy.4255

Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution*, *25*(6), 325–331. https://doi.org/10.1016/j.tree.2010.03.002

Hoy, S. R., Peterson, R. O., & Vucetich, J. A. (2018). Climate warming is associated with smaller body size and shorter lifespans in moose near their southern range limit. *Global Change Biology*, *24*(6), 2488–2497. https://doi.org/10.1111/gcb.14015

Immerzeel, W. W., Lutz, A. F., Andrade, M., Bahl, A., Biemans, H., Bolch, T., Hyde, S., Brumby, S., Davies, B. J., Elmore, A. C., Emmer, A., Feng, M., Fernández, A., Haritashya, U., Kargel, J. S., Koppes, M., Kraaijenbrink, P. D. A., Kulkarni, A. V., Mayewski, P. A., … Baillie, J. E. M. (2020). Importance and vulnerability of the world's water towers. *Nature*, *577*(7790), 364–369. https://doi.org/10.1038/s41586-019-1822-y

Johnston, K. M., Freund, K. A., & Schmitz, O. J. (2012). Projected range shifting by montane mammals under climate change: Implications for Cascadia's National Parks. *Ecosphere*, *3*(11), 1–51. https://doi.org/10.1890/ES12-00077.1

Kautz, T. M., Belant, J. L., Beyer, D. E., Strickland, B. K., & Duquette, J. F. (2020). Influence of body mass and environmental conditions on winter mortality risk of a northern ungulate: Evidence for a late-winter survival bottleneck. *Ecology and Evolution*, *10*(3), 1666–1677. https://doi.org/10.1002/ece3.6026

Kolbe, J. A., Squires, J. R., Pletscher, D. H., & Ruggiero, L. F. (2007). The Effect of Snowmobile Trails on Coyote Movements Within Lynx Home Ranges. *Journal of Wildlife Management*, *71*(5), 1409–1418. https://doi.org/10.2193/2005-682

Liston, G. E., & Elder, K. (2006). A Distributed Snow-Evolution Modeling System (SnowModel). *Journal of Hydrometeorology*, *7*(6), 1259–1276. https://doi.org/10.1175/JHM548.1

Mahoney, P. J., Liston, G. E., LaPoint, S., Gurarie, E., Mangipane, B., Wells, A. G., Brinkman, T. J., Eitel, J. U. H., Hebblewhite, M., Nolin, A. W., Boelman, N., & Prugh, L. R. (2018). Navigating snowscapes: Scale-dependent responses of mountain sheep to snowpack properties. *Ecological Applications*, *28*(7), 1715–1729. https://doi.org/10.1002/eap.1773

Mech, L. D., & Boitani, L. (2003). Wolf Social Ecology. In *Wolves: Behavior, Ecology, and Conservation*. University of Chicago Press.

Mower, R., Gutmann, E. D., Liston, G. E., Lundquist, J., & Rasmussen, S. (2024). Parallel SnowModel (v1.0): A parallel implementation of a distributed snow-evolution modeling system (SnowModel). *Geoscientific Model Development*, *17*(10), 4135–4154. https://doi.org/10.5194/gmd-17-4135-2024

Murie, A. (1944). *The wolves of mount McKinley* (Issue 5). US Government Printing Office.

Murray, D. L., & Larivière, S. (2002). The relationship between foot size of wild canids and regional snow conditions: Evidence for selection against a high footload? *Journal of Zoology*, *256*(3), 289–299. https://doi.org/10.1017/S095283690200033X

Musselman, K. N., Lehner, F., Ikeda, K., Clark, M. P., Prein, A. F., Liu, C., Barlage, M., & Rasmussen, R. (2018). Projected increases and shifts in rain-on-snow flood risk over western North America. *Nature Climate Change*, *8*(9), 808–812. https://doi.org/10.1038/s41558-018-0236-4

Natural Resources Conservation Service. (2025). *Air & Water Database Reports* [Dataset]. National Water & Climate Center. https://nwcc-apps.sc.egov.usda.gov/awdb/site-plots/POR/WTEQ/WA/Muckamuck.html

Nolin, A. W., & Daly, C. (2006). Mapping "At Risk" Snow in the Pacific Northwest. *Journal of Hydrometeorology*, *7*(5), 1164–1171. https://doi.org/10.1175/JHM543.1

Nolin, A. W., Sproles, E. A., Rupp, D. E., Crumley, R. L., Webb, M. J., Palomaki, R. T., & Mar, E. (2021). New snow metrics for a warming world. *Hydrological Processes*, *35*(6). https://doi.org/10.1002/hyp.14262

Norris, J., Rahimi, S., Huang, L., Bass, B., Thackeray, C. W., & Hall, A. (2025). Uncertainty of 21st Century western U.S. snowfall loss derived from regional climate model large ensemble. *Npj Climate and Atmospheric Science*, *8*(1), 134. https://doi.org/10.1038/s41612-025-01002-2

Parker, K. L., Barboza, P. S., & Gillingham, M. P. (2009). Nutrition integrates environmental responses of ungulates. *Functional Ecology*, *23*(1), 57–69. https://doi.org/10.1111/j.1365-2435.2009.01528.x

Parker, K. L., Robbins, C. T., & Hanley, T. A. (1984). Energy Expenditures for Locomotion by Mule Deer and Elk. *The Journal of Wildlife Management*, *48*(2), 474. https://doi.org/10.2307/3801180

Peers, M. J. L., Majchrzak, Y. N., Menzies, A. K., Studd, E. K., Bastille-Rousseau, G., Boonstra, R., Humphries, M., Jung, T. S., Kenney, A. J., Krebs, C. J., Murray, D. L., & Boutin, S. (2020). Climate change increases predation risk for a keystone species of the boreal forest. *Nature Climate Change*, *10*(12), 1149–1153. https://doi.org/10.1038/s41558-020-00908-4

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

Post, E. (2013). *Ecology of climate change: The importance of biotic interactions*. Princeton University Press.

Post, E., Peterson, R. O., Stenseth, N. Chr., & McLaren, B. E. (1999). Ecosystem consequences of wolf behavioural response to climate. *Nature*, *401*(6756), 905–907. https://doi.org/10.1038/44814

Prugh, L. R., Cunningham, C. X., Windell, R. M., Kertson, B. N., Ganz, T. R., Walker, S. L., & Wirsing, A. J. (2023). Fear of large carnivores amplifies human-caused mortality for mesopredators. *Science*, *380*(6646), 754–758. https://doi.org/10.1126/science.adf2472

Prugh, L. R., Lundquist, J. D., Sullender, B. K., Cunningham, C. X., Dechow, J., Borg, B. L., Sousanes, P. J., Stehn, S., & Durand, M. T. (2024). Landscape heterogeneity buffers the impact of an extreme weather event on wildlife. *Communications Biology*, *7*(1), 1515. https://doi.org/10.1038/s42003-024-07195-1

Pulliainen, J., Luojus, K., Derksen, C., Mudryk, L., Lemmetyinen, J., Salminen, M., Ikonen, J., Takala, M., Cohen, J., Smolander, T., & Norberg, J. (2020). Patterns and trends of Northern Hemisphere snow mass from 1980 to 2018. *Nature*, *581*(7808), 294–298. https://doi.org/10.1038/s41586-020-2258-0

Reinking, A. K., Højlund Pedersen, S., Elder, K., Boelman, N. T., Glass, T. W., Oates, B. A., Bergen, S., Roberts, S., Prugh, L. R., Brinkman, T. J., Coughenour, M. B., Feltner, J. A., Barker, K. J., Bentzen, T. W., Pedersen, Å. Ø., Schmidt, N. M., & Liston, G. E. (2022). Collaborative wildlife–snow science: Integrating wildlife and snow expertise to improve research and management. *Ecosphere*, *13*(6). https://doi.org/10.1002/ecs2.4094

Rivrud, I. M., Meisingset, E. L., Loe, L. E., & Mysterud, A. (2019). Future suitability of habitat in a migratory ungulate under climate change. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1899), 20190442. https://doi.org/10.1098/rspb.2019.0442

Ruprecht, J. S., Hersey, K. R., Hafen, K., Monteith, K. L., DeCesare, N. J., Kauffman, M. J., & MacNulty, D. R. (2016). Reproduction in moose at their southern range limit. *Journal of Mammalogy*, *97*(5), 1355–1365. https://doi.org/10.1093/jmammal/gyw099

Scaff, L., Krogh, S. A., Musselman, K., Harpold, A., Li, Y., Lillo-Saavedra, M., Oyarzún, R., & Rasmussen, R. (2024). The Impacts of Changing Winter Warm Spells on Snow Ablation Over Western North America. *Water Resources Research*, *60*(5), e2023WR034492. https://doi.org/10.1029/2023WR034492

Schwab, F. E., & Pitt, M. D. (1991). Moose selection of canopy cover types related to operative temperature, forage, and snow depth. *Canadian Journal of Zoology*, *69*(12), 3071–3077. https://doi.org/10.1139/z91-431

Stenseth, N. Chr., Shabbar, A., Chan, K.-S., Boutin, S., Rueness, E. K., Ehrich, D., Hurrell, J. W., Lingjærde, O. Chr., & Jakobsen, K. S. (2004). Snow conditions may create an invisible barrier for lynx. *Proceedings of the National Academy of Sciences*, *101*(29), 10632–10634. https://doi.org/10.1073/pnas.0308674101

Stien, A., Loe, L. E., Mysterud, A., Severinsen, T., Kohler, J., & Langvatn, R. (2010). Icing events trigger range displacement in a high-arctic ungulate. *Ecology*, *91*(3), 915–920. https://doi.org/10.1890/09-0056.1

Sullender, B. K., Cunningham, C. X., Lundquist, J. D., & Prugh, L. R. (2023). Defining the danger zone: Critical snow properties for predator–prey interactions. *Oikos*, *2023*(10), e09925. https://doi.org/10.1111/oik.09925

Telfer, E. S., & Kelsall, J. P. (1984). Adaptation of Some Large North American Mammals for Survival In Snow. *Ecology*, *65*(6), 1828–1834. https://doi.org/10.2307/1937779

APPENDIX A: SUPPORTING INFORMATION FOR CHAPTER 2

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

Table A1. Effectiveness of deeper snow density as a predictor of moose sink depth and correlation with near-surface (<30 cm) snow density. We sampled snow density in 10 cm increments to the full depth of the snow pit, which was as deep as 80 cm from the surface, for a subset of moose tracks (n = 15; average track sink depth = 46.0 cm). We then used linear regression to determine how much the additional measurements would improve the density-sink depth relationship. *AvgDens0-80* represents bulk density (i.e., density averaged across the full depth of the snowpack).

Density Depth Class	R^2	Correlation with *AvgDens0-10*	Correlation with *AvgDens0-20*	Correlation with *AvgDens0-30*
AvgDens0-10	0.259	1.00		
AvgDens0-20	0.353	0.98	1.00	
AvgDens0-30	0.534	0.90	0.95	1.00
AvgDens0-40	0.525	0.79	0.87	0.97
AvgDens0-50	0.539	0.78	0.86	0.96
AvgDens0-60	0.500	0.78	0.86	0.95
AvgDens0-70	0.459	0.76	0.83	0.92
AvgDens0-80	0.394	0.74	0.80	0.88

Table A2. Regional comparison results. For each species occurring in both Alaska and Washington, we added region as an interaction term to the best overall single-variable (*AvgDens0-20*) generalized additive model. We compared fitted models using Akaike information criterion corrected for small sample sizes (AIC$_c$), which accounts for goodness of fit while penalizing models to minimize overfitting (Anderson & Burnham 2002). The relationship between sink depth and density varied by region for moose and wolves but not for coyotes. *K* represents number of parameters.

Species	Model Description	*K*	Log likelihood	AIC$_c$	ΔAIC$_c$
Coyote	*AvgDens0-20*	3	-572.806	1152.6	0
Coyote	*AvgDens0-20*Region*	5	-574.711	1160.8	8.17
Moose	*AvgDens0-20*Region*	9	-572.241	1163.9	0
Moose	*AvgDens0-20*	6	-579.736	1173.3	9.35
Wolf	*AvgDens0-20*	3	-398.454	803.6	0
Wolf	*AvgDens0-20*Region*	6	-395.359	804.8	1.17

Table A3. Pairwise predictor variable correlations. Because snow properties are non-independent, some properties cannot be included as predictor variables in the same model. We omitted all predictor variables with correlation >|0.7| (in bold below). *AvgDens* = snow surface density as measured by a 10x10cm 1000cc density cutter; *IceTop* = presence of ice layers; *HH* = thickness-weighted hand-hardness average using the 5-point stratigraphy scale; *AvgTuna* = sink depth of cylindrical penetrometer (ie tuna can); *TotalIce* = cumulative ice thickness. 0-10 = 0-10cm depth (ie top 10cm); 0-20 = 0-20cm; 0-30 = 0-30cm; 0-40 = 0-40cm; 0-50 = 0-50cm.

	AvgTuna	*AvgDens0-10*	*AvgDens0-20*	*AvgDens0-30*	*HH0-10*	*HH0-20*	*HH0-30*	*HH0-40*	*HH0-50*
AvgTuna	**1.00**	**-0.78**	**-0.75**	**-0.72**	-0.70	-0.64	-0.59	-0.52	-0.46
AvgDens0-10	**-0.78**	**1.00**	**0.95**	**0.91**	**0.75**	**0.74**	0.69	0.63	0.57
AvgDens0-20	**-0.75**	**0.95**	**1.00**	**0.98**	0.67	**0.74**	**0.71**	0.67	0.63
AvgDens0-30	**-0.72**	**0.91**	**0.98**	**1.00**	0.63	**0.72**	**0.71**	0.69	0.66
HH0-10	-0.70	**0.75**	0.67	0.63	**1.00**	**0.87**	**0.77**	0.67	0.60
HH0-20	-0.64	**0.74**	**0.74**	**0.72**	**0.87**	**1.00**	**0.94**	**0.86**	**0.80**
HH0-30	-0.59	0.69	**0.71**	**0.71**	**0.77**	**0.94**	**1.00**	**0.95**	**0.89**
HH0-40	-0.52	0.63	0.67	0.69	0.67	**0.86**	**0.95**	**1.00**	**0.97**
HH0-50	-0.46	0.57	0.63	0.66	0.60	**0.80**	**0.89**	**0.97**	**1.00**
IceTop10	-0.25	0.30	0.29	0.28	0.41	0.42	0.40	0.38	0.35
IceTop20	-0.22	0.29	0.30	0.30	0.35	0.41	0.41	0.40	0.38
IceTop30	-0.20	0.25	0.30	0.30	0.27	0.37	0.40	0.42	0.41
IceTop40	-0.13	0.17	0.23	0.26	0.17	0.28	0.32	0.39	0.40
IceTop50	-0.06	0.12	0.18	0.21	0.14	0.24	0.28	0.35	0.38
TotalIce10	-0.25	0.37	0.34	0.33	0.51	0.48	0.47	0.42	0.40
TotalIce20	-0.23	0.36	0.37	0.36	0.45	0.53	0.51	0.48	0.45
TotalIce30	-0.23	0.35	0.38	0.37	0.43	0.51	0.54	0.52	0.51
TotalIce40	-0.21	0.32	0.36	0.37	0.37	0.47	0.51	0.55	0.55
TotalIce50	-0.17	0.25	0.31	0.33	0.29	0.40	0.44	0.50	0.53

Table A3. continued.

	IceTop10	*IceTop20*	*IceTop30*	*IceTop40*	*IceTop50*	*TotalIce10*	*TotalIce20*	*TotalIce30*	*TotalIce40*	*TotalIce50*
AvgTuna	-0.25	-0.22	-0.20	-0.13	-0.06	-0.25	-0.23	-0.23	-0.21	-0.17
AvgDens0-10	0.30	0.29	0.25	0.17	0.12	0.37	0.36	0.35	0.32	0.25
AvgDens0-20	0.29	0.30	0.30	0.23	0.18	0.34	0.37	0.38	0.36	0.31
AvgDens0-30	0.28	0.30	0.30	0.26	0.21	0.33	0.36	0.37	0.37	0.33
HH0-10	0.41	0.35	0.27	0.17	0.14	0.51	0.45	0.43	0.37	0.29
HH0-20	0.42	0.41	0.37	0.28	0.24	0.48	0.53	0.51	0.47	0.40
HH0-30	0.40	0.41	0.40	0.32	0.28	0.47	0.51	0.54	0.51	0.44
HH0-40	0.38	0.40	0.42	0.39	0.35	0.42	0.48	0.52	0.55	0.50
HH0-50	0.35	0.38	0.41	0.40	0.38	0.40	0.45	0.51	0.55	0.53
IceTop10	**1.00**	**0.81**	0.66	0.55	0.52	**0.79**	0.75	0.67	0.59	0.51
IceTop20	**0.81**	**1.00**	**0.81**	0.68	0.64	0.64	**0.72**	**0.70**	0.62	0.54
IceTop30	0.66	**0.81**	**1.00**	**0.84**	**0.79**	0.52	0.58	0.65	0.66	0.62
IceTop40	0.55	0.68	**0.84**	**1.00**	**0.94**	0.44	0.49	0.55	0.66	0.67
IceTop50	0.52	0.64	**0.79**	**0.94**	**1.00**	0.41	0.46	0.52	0.62	0.67
TotalIce10	**0.79**	0.64	0.52	0.44	0.41	**1.00**	**0.87**	**0.80**	0.69	0.60
TotalIce20	**0.75**	**0.72**	0.58	0.49	0.46	**0.87**	**1.00**	**0.92**	**0.82**	**0.72**
TotalIce30	0.67	**0.70**	0.65	0.55	0.52	**0.80**	**0.92**	**1.00**	**0.92**	**0.83**
TotalIce40	0.59	0.62	0.66	0.66	0.62	0.69	**0.82**	**0.92**	**1.00**	**0.95**
TotalIce50	0.51	0.54	0.62	0.67	0.67	0.60	**0.72**	**0.83**	**0.95**	**1.00**

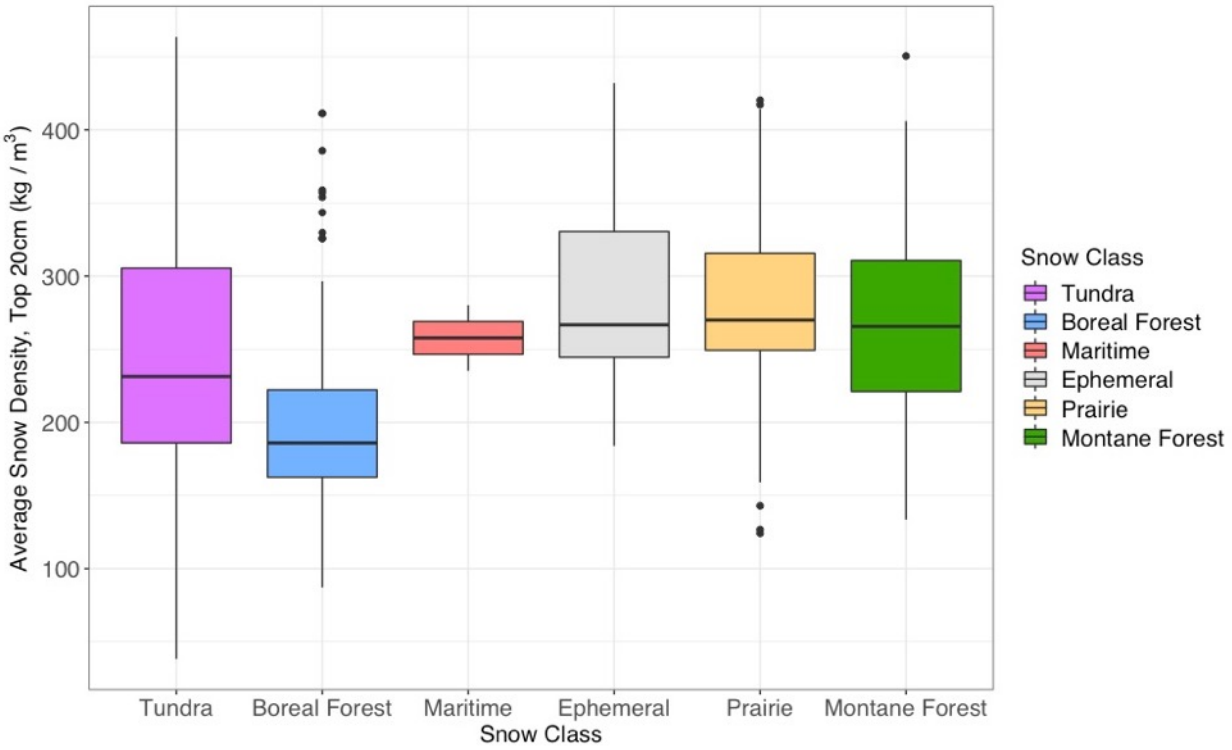

Figure A1. Near-surface (0-20cm) snow density by snow class. Snow classes as defined by Sturm et al. (1995) and Sturm & Liston (2021). An analysis of variance (ANOVA) yielded significant variation in snow density between classes ($F_{5,468} = 14.39$, $P < 0.001$). A post-hoc Tukey's Honestly Significant Difference test showed that snow observations conducted in the boreal forest snow class had the lowest density ($n = 107$, $\bar{x} = 197$ kg/m^3), followed by tundra ($n = 174$, $\bar{x} = 246$ kg/m^3). No significant differences were found between snow surface density for sites in maritime ($n = 2$, $\bar{x} = 258$ kg/m^3), ephemeral ($n = 37$, $\bar{x} = 290$ kg/m^3), prairie ($n = 36$, $\bar{x} = 279$ kg/m^3), or montane forest ($n = 118$, $\bar{x} = 265$ kg/m^3). An ANOVA and Tukey's HSD test indicated that tundra had more ice (*TotalIce50*) than boreal forest (1.26 cm more ice in top 50 cm; $P < 0.01$) and montane forest (2.0 cm more ice in top 50 cm; $P < 0.001$). There were no other significant differences in amount of ice across snow classes (*TotalIce50*; $F_{5,468} = 4.15$, $P < 0.01$).

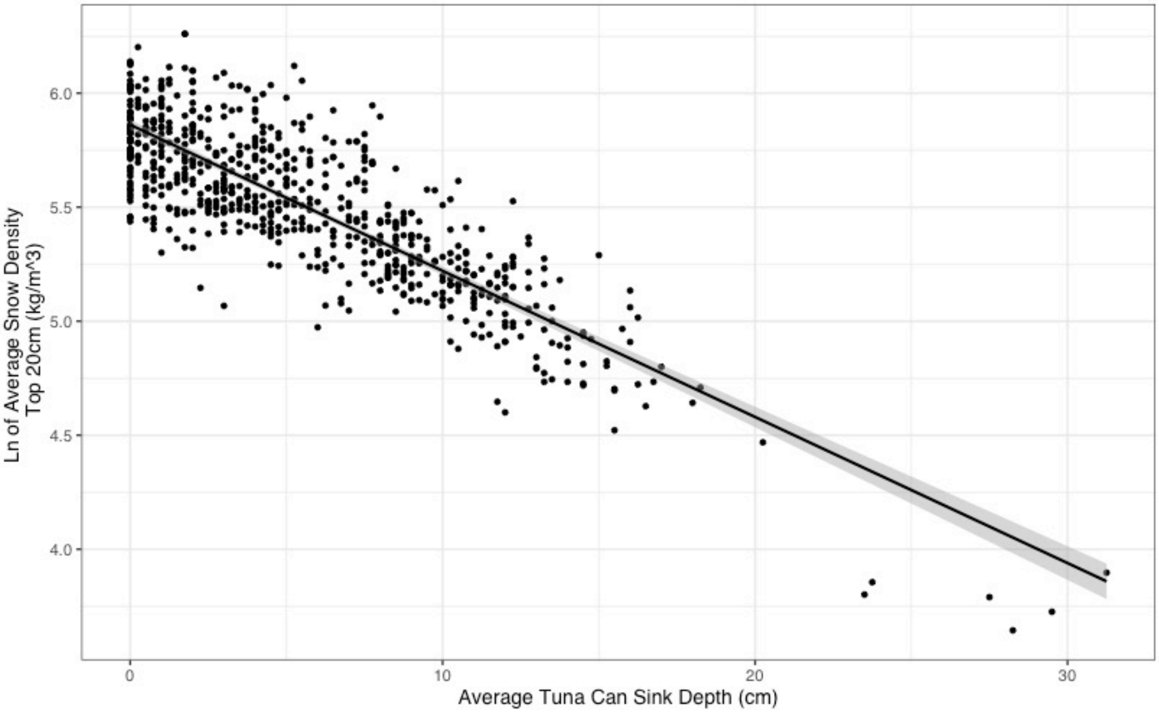

Figure A2. Relationship between tuna can sink depth and near-surface (0-20 cm) snow density. Tuna can sink depth is the average of two drops of our 200 g cylindrical penetrometer (7 oz tuna can, Chicken of the Sea Chunk Light; 8.2 cm diameter x 4.2 cm height) from a height of 50 cm above the snowpack. The average absolute difference in tuna can sink depth replicate measurements was 10% (0.6 cm / 5.8 cm), indicating relatively consistent performance. Tuna can sink depth is a good predictor of near-surface snow density (adjusted $R^2 = 0.72$), which can be modeled using linear regression as ln(*AvgDens0-20*) = 5.861 – 0.0641 * [*AvgTuna*]. Tuna can sink depth is also a good predictor of 0-10 cm snow density (adjusted $R^2 = 0.77$; ln[*AvgDens0-10*] = 5.865 - 0.0866 * [*AvgTuna*]).

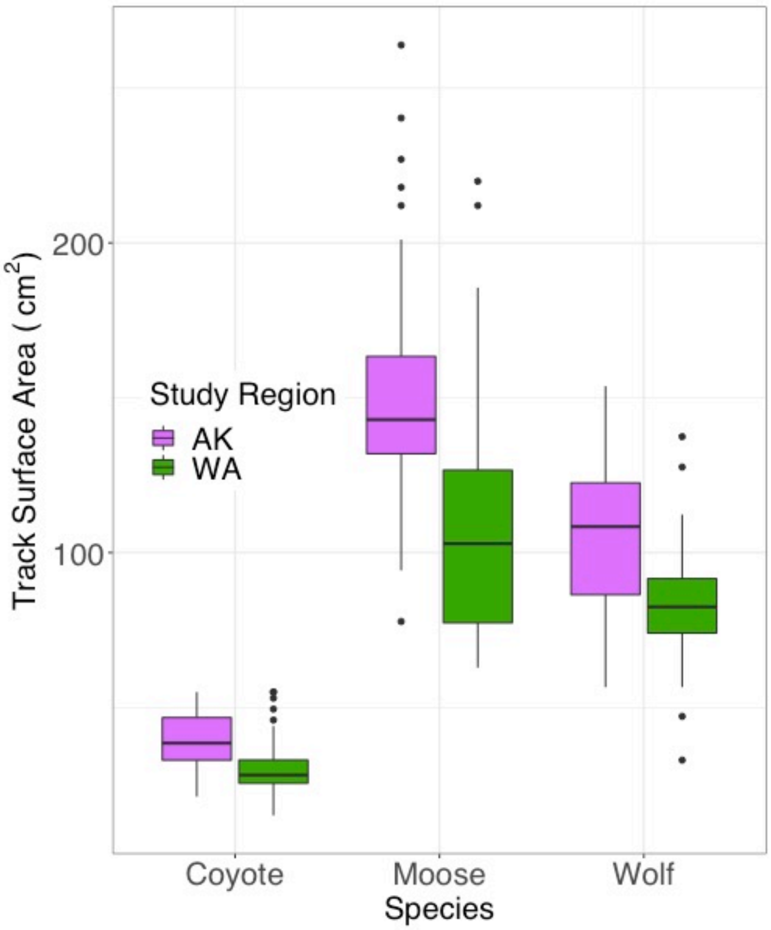

Figure A3. Regional differences in wildlife snow track surface area for coyotes, moose, and wolves. Track surface area is approximate given the challenges of determining track dimensions in soft snow and calculated using the area of an oval [pi * (*Track width*/2] * [*Track length*/2]). An analysis of variance (ANOVA) and post-hoc Tukey's Honestly Significant Difference test indicated that tracks in Alaska were significantly larger than those in Washington for all species: coyotes ($F_{1,177} = 60.8$, $P < 0.0001$, 10 cm^2 larger in AK), moose ($F_{1,137} = 37.3$, $P < 0.0001$, 41 cm^2 larger in AK), and wolves ($F_{1,123} = 37.3$, $P < 0.0001$, 22 cm^2 larger in AK).

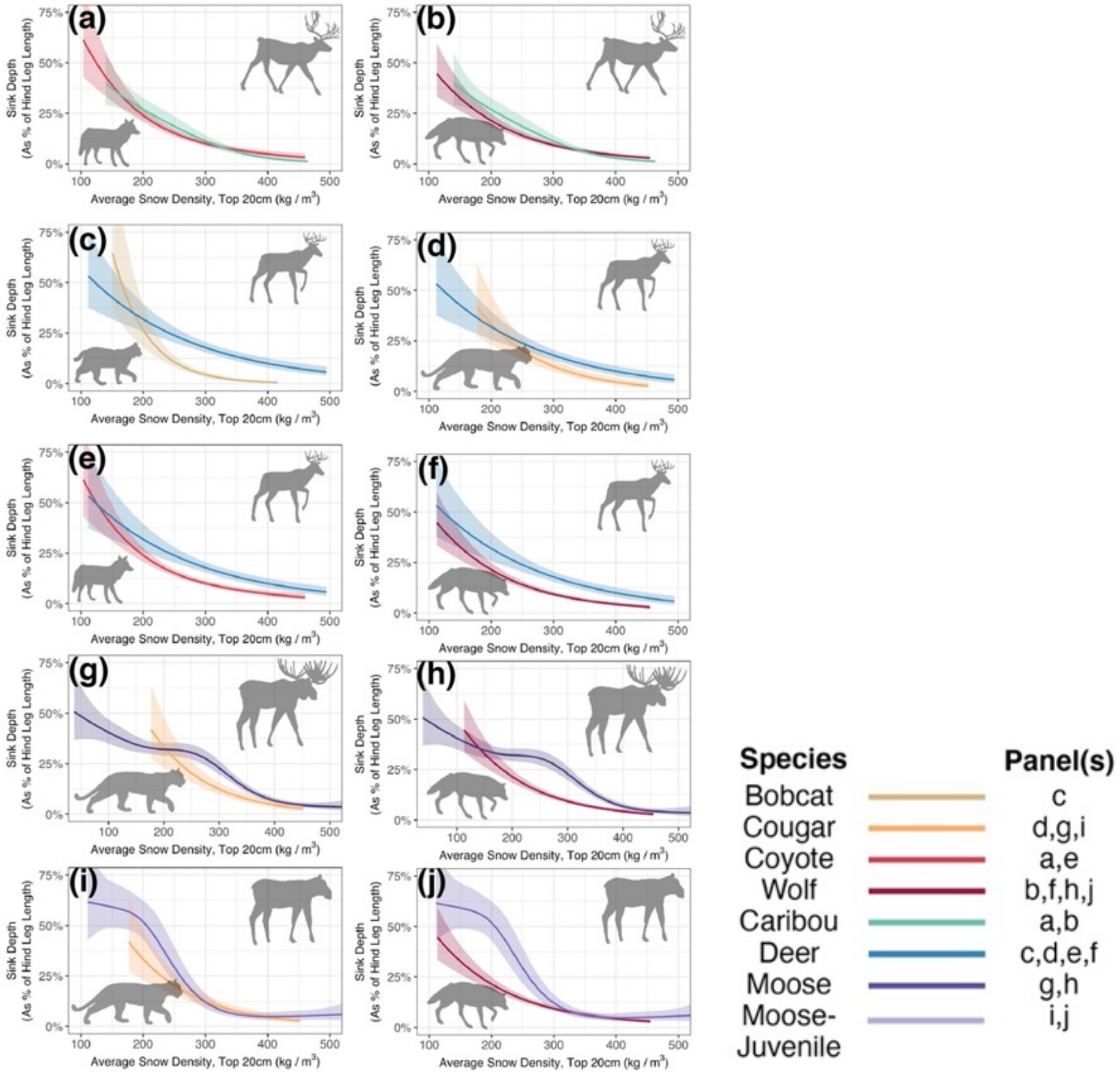

Figure A4. Modeled relative sink depths and 95% confidence intervals for predator-prey pairs. Each species’ sink depth was scaled to a percentage of hind leg length, creating a comparable metric of ease of movement. We calculated danger zones by subtracting the predator sink depth curve from the prey sink depth curve. If this difference in relative sink depth is positive, the prey is at a movement disadvantage, which we define as a danger zone. If this difference is negative, then there is no danger zone at that snow density.

APPENDIX B: SUPPORTING INFORMATION FOR CHAPTER 3

Apex predators exploit advantageous snow conditions across hunting modes

B.1: Additional Methods for Generating Deer Index

To generate annual predictions of mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) distribution, we used GPS collar data from 2016-2021. First, we omitted the three weeks of data immediately after capture for all individuals (Northrup et al. 2014, Van de Kerk et al. 2020). In order to avoid migratory movements, we defined winter as December 1 – March 1 (Bassing et al. 2023) and used net squared displacement to identify likely migration periods (Bunnefeld et al. 2011), excluding all observations of migrating individuals (1032 fixes for mule deer; 11 fixes for white-tailed deer). We excluded individuals with 50 or fewer observations per winter (12 animal-years for mule deer; 2 individuals across 17 animal-years for white-tailed deer). This left 142 unique mule deer (361 animal-years) and 90 unique white-tailed deer (143 animal-years). Because our goal was to create a range-wide index of likely winter deer distribution, we buffered each individual's 100% minimum convex polygon by its diameter and, for each observed location, we used the R package amt (Signer et al. 2019) to randomly generate 10 available locations within that individual's buffered winter range (Bassing et al. 2023).

Because we were interested in deer responses to dynamic covariates, we used annually updated land cover data from TerrAdapt:Cascadia (30m resolution; TerrAdapt 2022). These datasets use remote sensing to identify changes in landcover. We used human footprint, canopy cover, and combined detailed vegetation classes into three broad categories: open (snow/ice, barren, emergent wetland, mesic grass forb, and xeric grass forb), shrub (mesic shrub and xeric shrub), and forest (woody wetlands, deciduous, and conifer). For each of these three combined classes, we represented landcover as percent cover within a 250m-radius moving window at 30m resolution for deer (Ganz et al. 2022, Bassing et al. 2023). We split deer telemetry data by year and extracted each year's habitat covariates – TRI, slope, landcover, human footprint, and elevation – using *terra* (Hijmans 2024).

We used all extracted values in one model for mule deer and one model for white-tailed deer. First, we checked for collinearity among habitat covariates, using Akaike information criterion (AIC; Anderson and Burnham 2002) to select the most important of collinear ($|r| > 0.7$) variables for each species (slope and TRI; percent forest, percent open, and canopy cover). Next, we used these non-collinear variables in a binomial generalized additive model (GAM) fitted as four independent thin-plate spline smooths, fitted with restricted maximum likelihood using the *mgcv* package in R (Wood, S. N. 2017). The most parsimonious combination of variables for mule deer was TRI, percent forest, percent shrub, human footprint, and elevation, whereas for white-tailed deer the best combination was slope, percent forest, percent shrub, human footprint, and elevation (Tables S1 and S2). We used *k*-fold cross-validation to validate our deer models (Boyce et al. 2002, Morris et al. 2016), splitting our data into 5 bins with an equal number of animal-years (72 or 73 animal-years per bin for mule deer and 28 or 29 per bin for white-tailed deer). The Spearman rank correlation coefficient for mule deer was 0.989 and for white-tailed deer was 0.931, indicating excellent model performance.

Table B1. Most parsimonious correlated terrain covariates for ungulates (in bold). Terrain ruggedness index performed best for mule deer, whereas slope performed best for white-tailed deer.

Covariate	**Mule Deer AIC**	**Mule Deer ΔAIC**	**White-tailed Deer AIC**	**White-tailed Deer ΔAIC**
Terrain ruggedness index	**834393.8**	**0**	311064.9	1118.1
Slope	835723.2	1329.4	**309946.8**	**0**

Table B2. Most parsimonious correlated landcover covariates for ungulates (in bold). Percent forest performed best for both species of deer.

Covariate	**Mule Deer AIC**	**Mule Deer ΔAIC**	**White-tailed Deer AIC**	**White-tailed Deer ΔAIC**
Percent forest	**830101.2**	**0**	**310047.4**	**0**
Canopy cover	841317.4	11216.2	310387.1	339.7
Percent open	843615	13513.8	314400	4352.6

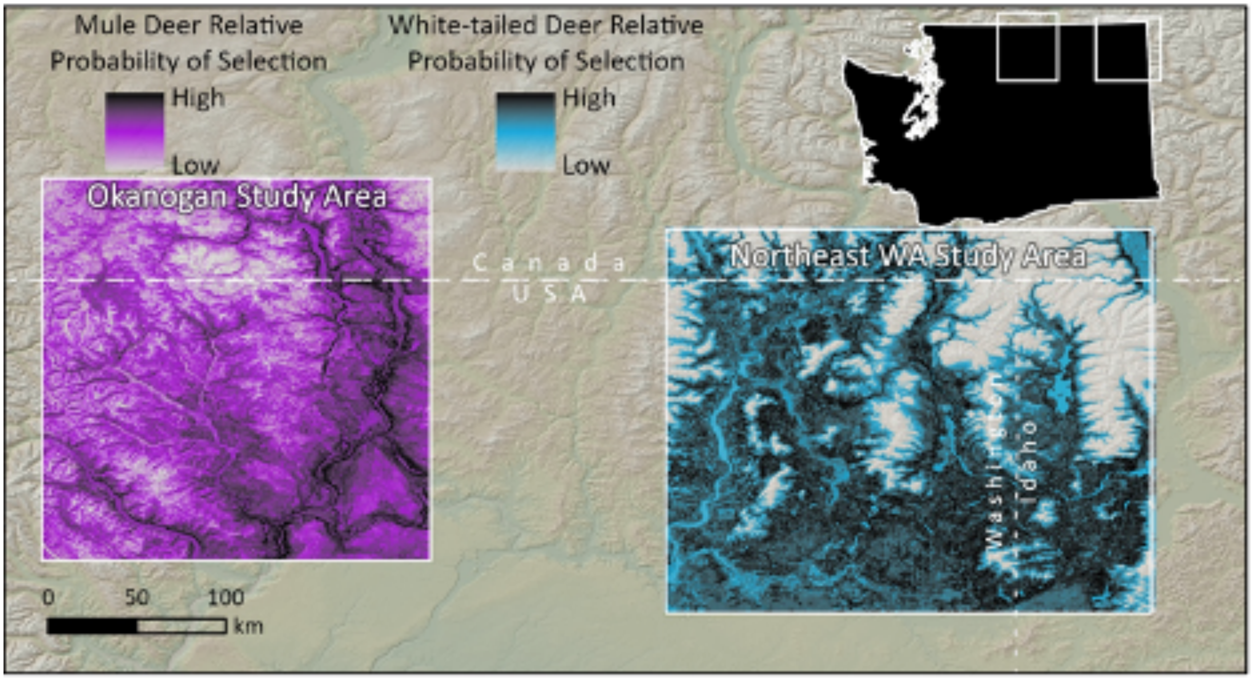

Figure B1. Results of deer resource selection functions for mule deer (Okanogan study area; purple) and white-tailed deer (NE WA study area; blue).

B.2: Additional Methods for SnowModel

We ran SnowModel simulations for the winters of 2017-2022 (defined as September through May) for the Okanogan and Northeast study areas using a water percolation scheme (Pflug et al. 2019) that provides realistic model representations of rain-on-snow and midseason melt, common in maritime snowpacks. We used the USGS National Elevation Dataset (NED) for topography on a 30m grid (Gesch et al. 2018), the North American Land Change Monitoring System (NALCMS) Land Cover 2015 map for vegetation on a 30m grid (Latifovic et al. 2016), and forcing variables from a Weather Research Forecast (WRF) model from the National Center for Atmospheric Research (NCAR) on approximately a 4-kilometer grid (Rasmussen et al. 2023).

Summary statistics from these comparisons (Table S3 and Figure S2) demonstrate good agreement between observations from 2017-2021 and modeled snow depth and density. We used the *pandas* and *xarray* libraries in Python (Hoyer and Hamman 2017, The pandas development team 2024) to extract bulk snow density (kg/m^3) and snow depth (m) at a daily resolution for each used and available carnivore GPS location, allowing us to assess the role of these snow properties in predator movement.

Table B3. SnowModel validation reporting root mean squared error (RMSE) and R2 values for snow density (reported as snow water equivalent [SWE], which is how SNOTEL sites measure bulk density) and snow depth. We collected observations Jan-Mar 2021 and 2022 and only measured the top 30cm of snow density. SWE values for observations are extrapolations and likely biased low. Locations of SNOTEL sites and field observations shown in Fig. B2.

Study Area	**SNOTEL Name / Observation**	**SWE R^2**	**SWE RMSE (m)**	**Snow Depth R^2**	**Snow Depth RMSE (m)**
Northeast	Bunchgrass Meadow	0.81	0.20	0.87	0.72
Northeast	Quartz Peak	0.72	0.19	0.80	0.59
Northeast	Sentinel Butte	0.86	0.09	0.87	0.29
Northeast	Field observations ($n = 22$)	0.16	0.13	0.50	0.50
Okanogan	Field observations ($n = 359$)	0.21	0.85	0.11	0.30
Okanogan	Hart's Pass	0.96	0.10	0.93	0.29
Okanogan	Muckamuck	0.85	0.08	0.87	0.14
Okanogan	Pope Ridge	0.87	0.09	0.84	0.19
Okanogan	Rainy Pass	0.93	0.15	0.95	0.55
Okanogan	Salmon Meadows	0.71	0.07	0.79	0.28
Okanogan	Swamp Creek	0.90	0.06	0.92	0.23
Okanogan	Trinity	0.65	0.32	0.78	0.88

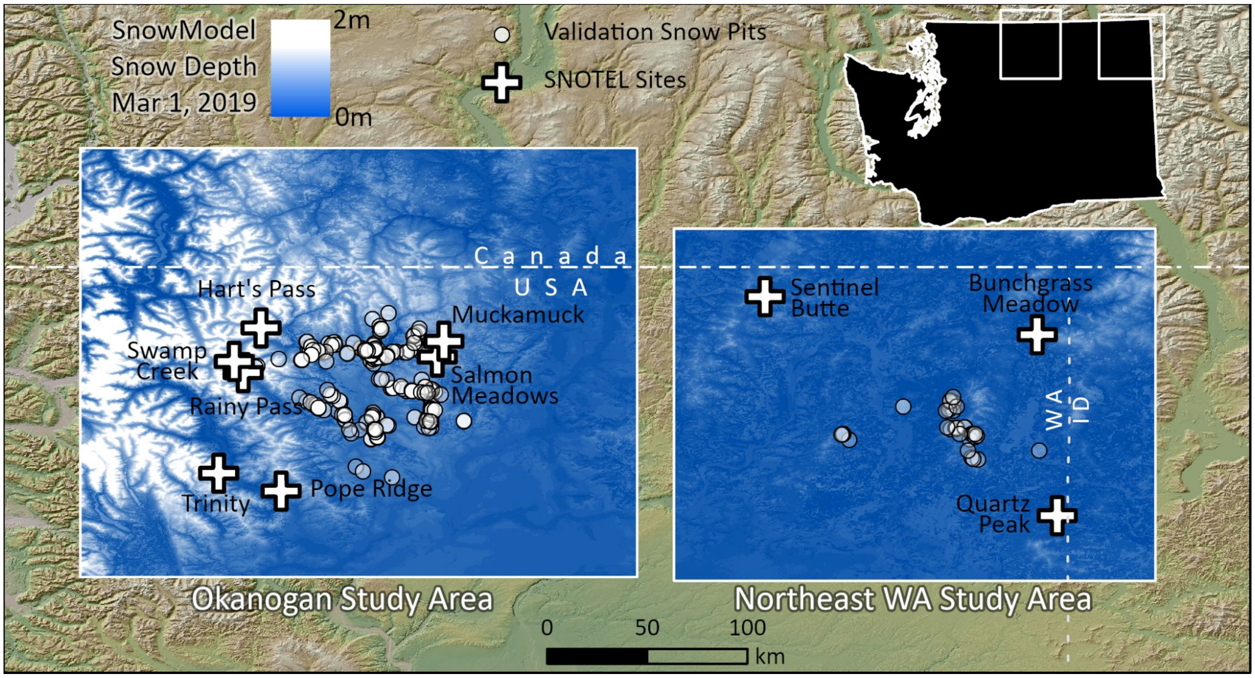

Figure B2. Sample SnowModel output (snow depth as of March 1, 2019) and sites used for model validation. Daily snow metrics analyzed for 2017-2022 for SNOTEL sites (white crosses; *n* = 10). We conducted field observations from Jan-Mar 2021 and Jan-Mar 2022 (white dots; *n* = 381).

B.3: Additional Methods for Kill Site Validation

We identified probable and known mortality locations between 1 November – 15 March of each year. We incorporated three data streams related to known and probably cougar kills: telemetry data, field investigations, and mortalities of collared ungulates. First, we used the cluster algorithm developed by Knopff et al. (2009) to identify clusters of telemetry locations from GPS-collared cougars. Specifically, the cluster algorithm identified locations within 200 m of each other within a 6-day period Knopff et al. (2009). Such clusters are commonly, but not exclusively associated with kill sites of ungulate prey (Knopff et al. 2009, Ruprecht et al. 2020). We conducted field investigations at a subset of cluster sites to determine if there was a carcass present and developed equations to predict the likelihood a cluster was a kill site based on characteristics of the cluster (Clark et al. 2014, Knopff et al. 2009). Our system was similar in vegetation, climate and terrain to the area studied by Clark et al. (2014), so we used the same model framework but estimated coefficients independently for our system to improve predictive capabilities. Specifically, we used logistic regression, with a cluster coded 1 if a kill was found and 0 if a carcass was not found. We included the following as covariates in our model, following Clark et al. (2014): (1) corrected points = the number of points at the cluster / fix success rate, (2) fidelity = the number of points at the cluster – the number of points away from the cluster, (3) average distance = the average distance between the points comprising the cluster to the centroid of the cluster (m), (4) binday = a binary indicator of if the cougar visited the site for more than one 24-hour period (coded 1) or only visited for one 24-hour period (coded 0), and (5) an interaction between corrected points and average distance.

From the logistic regression, we calculated the percent of true positives and true negative kill sites at different threshold values to distinguish sites likely to be a kill sites to clusters not likely to be a carcass. We tested threshold values in 0.1% increments from 0.1% to 100%. Then we used an ROC curve to examine tradeoffs between true positive and true negatives across the range of thresholds (Nahm 2022). We calculated the accuracy at each threshold level following Nahm (2022) and chose the threshold with the highest accuracy as our probability cutoff for sites likely to be kill sites or not. We then predicted the probability each cluster was a kill site, and classified these as likely kills when equal to or above the threshold and not likely to be a kill when below the threshold. Finally, we corrected this dataset for sites where we had conducted field investigations. That is, we removed clusters from the predicted kill site data set if we had visited the site and no cluster was found. Likewise, we retained clusters if we visited the site and a carcass was found but the predicted probably of being a kill site was below the threshold for optimal accuracy.

Concurrent with our study and in the same study areas, Ganz et al. (2022) collared mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) and investigated mortalities to determine cause of death. We included deer confirmed to have died by cougar predation in our dataset of cougar kills. Additionally, we also included deer where a cougar was possibly the cause of death, but this was unconfirmed. In these cases, hemorrhaged bite wounds could not be located but there was evidence (tracks, sign, patterns of consumption, and salivary DNA) a cougar was at the site soon after death.

We generated 5,503 telemetry clusters from 60 cougars from 1 November – 15 March for winter 2016-2017 through winter 2020-2021. We visited 187 clusters locations from 34 cougars. We found carcasses at 51% of sites (n = 95) and did not identify carcasses at the remaining 92 sites. Logistic regression to predict the likelihood a site was a cougar kill (model output table S4) performed well, and 74.7 % of predicted kills were true positives and 90.2% of sites predicted to not have a kill were correctly identified, using a probability threshold 53% to distinguish likely kills. Clusters were strongly and significantly (= 0.233, $P < 0.001$) driven by the number of points at the cluster (corrected for missing fixes). Clusters were also more likely to be a kill for sites where cougars displayed higher fidelity, and visited for more than one 24-hour period (Table S4). However, these covariates were non-significant at the 0.05 level. The interaction between average distance and corrected points indicated that a cluster was more likely to be a kill with a shorter average distance between telemetry points and the cluster centroid, especially as the number of corrected points at the cluster increased.

Table B4: Model output for the logistic regression predicting the probability a cluster is a kill site. We classified sites with >50% probability of being a kill site as probable cougar kills.

Covariate	**Coefficient**	**Standard Error**	***P*-value**
intercept	-2.502	0.574	0.00001
fidelity	0.029	0.017	0.08
binday	0.131	0.526	0.80
average distance	0.011	0.013	0.373
corrected points	0.233	0.064	0. 0003
Average distance x corrected points	-0.002	0.001	0.175

From the clusters generated by the algorithm, we identified 524 probable kills. We corrected this data to account for sites classified as likely kills but where a kill was not found at a cluster (i.e., false positives, n = 5). Likewise, we added cougar kills that we classified as likely non-kill clusters but where field investigation identified a cluster (i.e., false negatives, n = 13). In addition, we included cougar kills located during associated field investigations that were not identified by our algorithm (n = 16; L. Satterfield, *unpublished data*). Finally, we included the mortalities of 15 white-tailed deer and 5 mule deer where a cougar was either confirmed to be or possibly responsible for the mortality. None of these ungulate mortalities matched a cougar cluster that was predicted to be a kill site. In total, we identified 568 known and probable cougar kills across the three winters and two study areas. However, because we needed to condition used (actual) kill sites against available (randomly generated) locations from known individual cougar winter ranges, we restricted our analysis to a total of 389 kill sites, all from collared individuals.

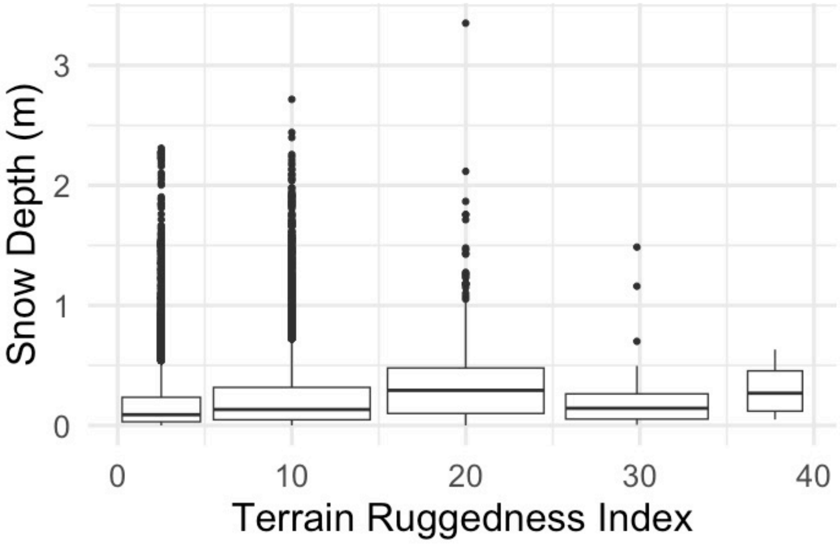

Figure B3. Boxplot showing relationship between terrain ruggedness index and snow depth for all available locations across our study areas. Boxplots are used rather than scatterplots due to volume of data (*n* = 276,008). Terrain ruggedness and snow depth are not correlated (Pearson's *r* = 0.20).

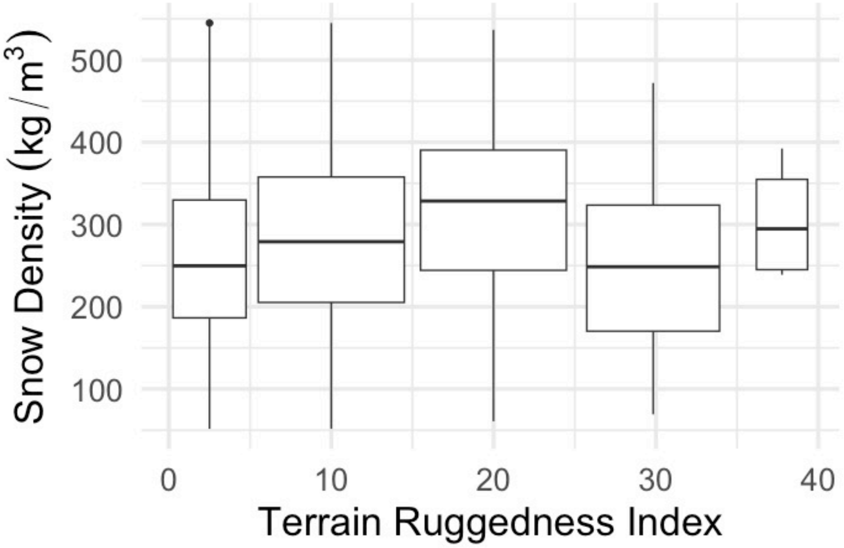

Figure B4. Boxplot showing relationship between terrain ruggedness index and snow density for all available locations across our study areas. Boxplots are used rather than scatterplots due to volume of data (*n* = 276,008). Terrain ruggedness and snow density are not correlated (Pearson's *r* = 0.14).

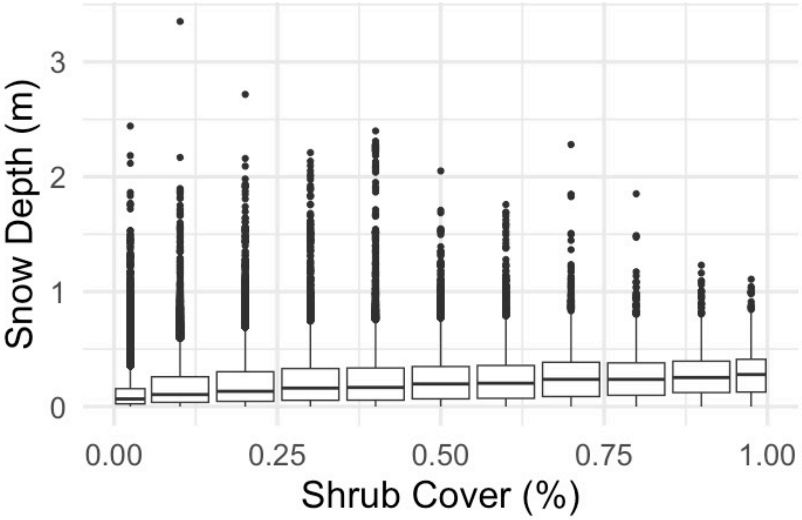

Figure B5. Boxplot showing relationship between shrub cover and snow depth for all available locations across our study areas. Boxplots are used rather than scatterplots due to volume of data (*n* = 276,008). Shrub cover and snow depth are not correlated (Pearson's *r* = 0.26).

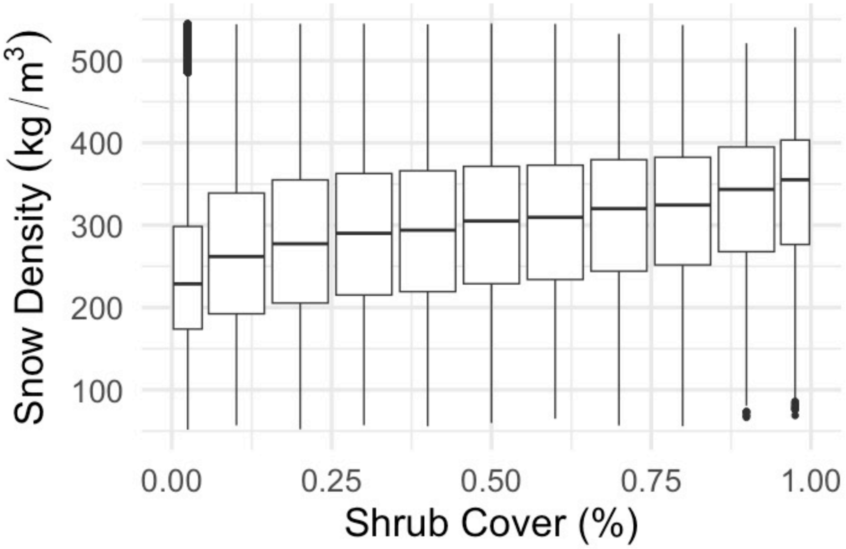

Figure B6. Boxplot showing relationship between shrub cover and snow density for all available locations across our study areas. Boxplots are used rather than scatterplots due to volume of data (*n* = 276,008). Although areas with higher shrub cover tend to have higher snow densities, this trend is statistically insignificant. Shrub cover and snow density are not correlated (Pearson's *r* = 0.27).

Table B5. Most parsimonious correlated terrain covariates for predators (in bold). Terrain ruggedness index performed better than all other combinations (ΔAIC > 2).

Covariate	Predator AIC	Predator ΔAIC
Terrain ruggedness index	**125701**	**0**
Slope	125712	11

Table B6. Most parsimonious correlated landcover covariates for predators (in bold). Percent shrub and canopy cover performed better than all other combinations (ΔAIC>2).

Covariate	Predator AIC	Predator ΔAIC
Percent shrub + canopy cover	**125359**	**0**
Canopy cover	125543	184
Percent shrub + percent forest	125681	322
Percent shrub + percent open	125844	485
Percent open	125966	607
Percent forest	126124	765
Percent shrub	126574	1215

Table B7. Most parsimonious combination of snow-related covariate for cougars. Depth:Density indicates an interaction term only (tensor product interaction), whereas Depth + Density + Depth:Density includes main effects of depth and density as well as an interaction term (collectively known as a full tensor product). The best performing model was a full tensor product with both depth and density.

Snow Variable	AIC	ΔAIC
Depth + Density + Depth:Density	87044.98	0
Depth + Densty	87097.09	52.11
Density	87144.55	99.57
Depth:Density	87145.65	100.67
Depth	87163.24	118.26

Table B8. Most parsimonious combination of snow-related covariate for wolves. Depth:Density indicates an interaction term only (tensor product interaction), whereas Depth + Density + Depth:Density includes main effects of depth and density as well as an interaction term (collectively known as a full tensor product). The best performing model was a full tensor product with both depth and density.

Snow Variable	**AIC**	**ΔAIC**
Depth + Density + Depth:Density	37140.27	0
Depth	37145.87	5.6
Depth + Densty	37146.08	5.81
Depth:Density	37151.33	11.06
Density	37151.86	11.59

Table S9. Most parsimonious combination of snow-related covariate for cougar kill sites. Depth:Density indicates an interaction term only (tensor product interaction), whereas Depth + Density + Depth:Density includes main effects of depth and density as well as an interaction term (collectively known as a full tensor product). The best performing model included an interaction-only term for depth and density.

Snow Variable	**AIC**	**ΔAIC**
Depth:Density	2080.5	0
Depth + Density + Depth:Density	2086.6	6.1
Depth + Densty	2087.4	6.9
Density	2089.3	8.8
Depth	2238.9	158.4

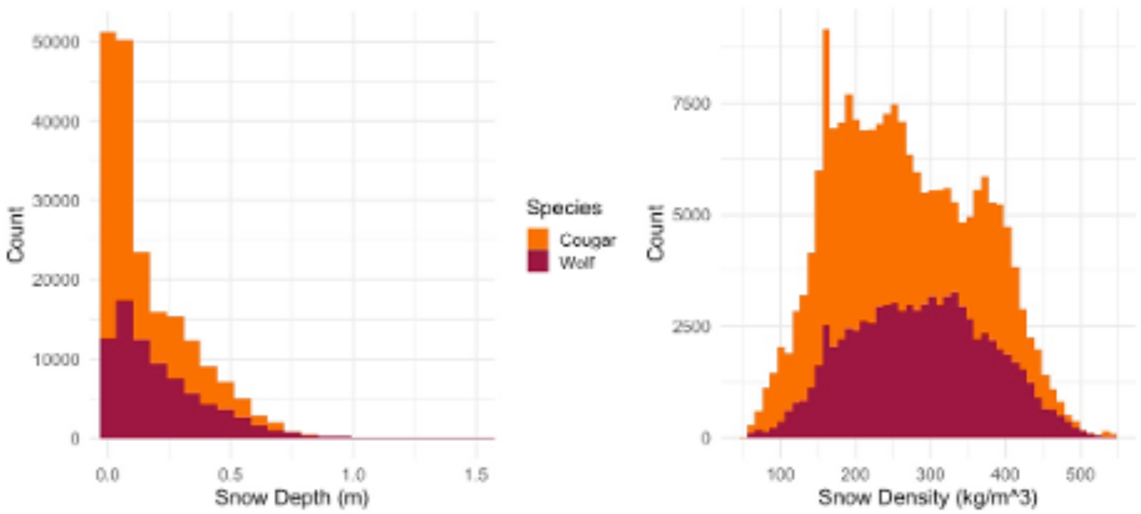

Figure B7. Comparison of available snow properties for cougars and wolves. Wilcoxon rank-sum tests indicated that wolves experienced deeper (n_{cougar}=196,102, n_{wolf} =79,906, W=6515864206, P<0.0001) and more dense (n_{cougar}=196,102, n_{wolf} =79,906, W=6923818000, P<0.0001) snow than cougars.

B.4 References

Anderson, D. R., and K. P. Burnham. 2002. Avoiding Pitfalls When Using Information-Theoretic Methods. The Journal of Wildlife Management 66:912.

Bassing, S. B., M. DeVivo, T. R. Ganz, B. N. Kertson, L. R. Prugh, T. Roussin, L. Satterfield, R. M. Windell, A. J. Wirsing, and B. Gardner. 2023. Are we telling the same story? Comparing inferences made from camera trap and telemetry data for wildlife monitoring. Ecological Applications 33:e2745.

Bunnefeld, N., L. Börger, B. Van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences: Quantifying migration patterns. Journal of Animal Ecology 80:466–476.

Clark, D. A., G. A. Davidson, B. K. Johnson, and R. G. Anthony. 2014. Cougar kill rates and prey selection in a multiple-prey system in northeast Oregon: Cougar Kill Rates and Prey Selection. The Journal of Wildlife Management 78:1161–1176.

Ganz, T. R., M. T. DeVivo, B. N. Kertson, T. Roussin, L. Satterfield, A. J. Wirsing, and L. R. Prugh. 2022a. Interactive effects of wildfires, season and predator activity shape mule deer movements. Journal of Animal Ecology 91:2273–2288.

Ganz, T. R., M. T. DeVivo, E. M. Reese, and L. R. Prugh. 2022b. Wildlife whodunnit: forensic identification of predators to inform wildlife management and conservation. Wildlife Society Bulletin.

Gesch DB, Evans GA, Oimoen MJ, Arundel S. 2018. The National Elevation Dataset. Pages 83–110. American Society for Photogrammetry and Remote Sensing. Available from https://pubs.usgs.gov/publication/70201572.

Hijmans, R. J. 2024. terra: Spatial Data Analysis.

Hoyer S, Hamman J. 2017. xarray: N-D labeled Arrays and Datasets in Python. Journal of Open Research Software **5**:10.

Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating Global Positioning System Telemetry Techniques for Estimating Cougar Predation Parameters. Journal of Wildlife Management 73:586–597.

Latifovic R, Homer C, Ressl R, Pouliot D, Hossain SN, Colditz RR, Olthof I, Giri CP, Victoria A. 2016. 20 North American land-change monitoring system. Remote sensing of land use and land cover: principles and applications:303. CRC Press.

Nahm, F. S. 2022. Receiver operating characteristic curve: overview and practical use for clinicians. Korean Journal of Anesthesiology 75:25–36.

Northrup, J. M., C. R. Anderson, and G. Wittemyer. 2014. Effects of helicopter capture and handling on movement behavior of mule deer. The Journal of Wildlife Management 78:731–738.

The pandas development team. 2024, September 20. pandas-dev/pandas: Pandas. Zenodo. Available from https://zenodo.org/doi/10.5281/zenodo.3509134 (accessed October 1, 2024).

Pflug JM, Liston GE, Nijssen B, Lundquist JD. 2019. Testing model representations of snowpack liquid water percolation across multiple climates. Water Resources Research 55:4820–4838. Wiley Online Library.

Rasmussen R, Liu C, Ikeda K, Chen F, Kim J-H, Schneider T, Gochis D, Dugger A, Viger R. 2023. Four-kilometer long-term regional hydroclimate reanalysis over the conterminous United States (CONUS). UCAR/NCAR-Research Data Archive.

Ruprecht, J., C. Eriksson, T. D. Forrester, D. A. Clark, M. Wisdom, M. M. Rowland, B. K. Johnson, and T. Levi. 2020. Integrating spatial capture-recapture models with variable individual identifiability. preprint, Ecology.

Signer, J., J. Fieberg, and T. Avgar. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and Evolution 9:880–890.

TerrAdapt. 2022. TerrAdapt:Cascadia.

Van de Kerk, M., S. Arthur, M. Bertram, B. Borg, J. Herriges, J. Lawler, B. Mangipane, C. Lambert Koizumi, B. Wendling, and L. Prugh. 2020. Environmental Influences on Dall’s Sheep Survival. The Journal of Wildlife Management 84:1127–1138.

Wood, S. N. 2017. Generalized additive models: an introduction with R. 2nd edition. Chapman and Hall/CRC.

APPENDIX C: SUPPORTING INFORMATION FOR CHAPTER 4

Warm winters, hot moose: temperature drives activity and habitat trade-offs across a cold-adapted species' range

C.1 GPS Collar Temperature Bias Correction

Ambient air temperature strongly influences ungulate movements and behavior (Street *et al* 2015, Jennewein *et al* 2020, Felton *et al* 2024), and extreme winter conditions can cause unusual mammal movements (Prugh *et al* 2024). Although single-location temperature observations such as those from weather station networks have been used in some animal behavior analyses, instrumented weather stations may be far away from actual animal locations in large and remote study areas (Street *et al* 2015, Ericsson *et al* 2015) and therefore may poorly represent local conditions experienced by individuals (Burkholder *et al* 2022, Reinking *et al* 2022).

Since many models of satellite GPS wildlife collars include on-board thermometers, collar data may provide spatially distributed temperature data that is temporally linked to the position and movements of the animal in question (Wilmers *et al* 2015). However, the observed temperature is dependent on animal body temperature, collar position on the body, and microsite habitat features – for example, exposure to solar radiation may cause fluctuations in temperature if the collar is exposed to sun, shaded by the animal's body, or shaded by local vegetation (Street *et al* 2015, Studd *et al* 2019). Nonetheless, some research has used collars' raw temperature data because it provides a useful foundation for inference even if the absolute numbers are biased (Van Beest *et al* 2012). Numerous solutions exist to resolve collar-ambient temperature discrepancies, including simply subtracting a month- and latitude-based temperature offset from collar-recorded temperature (Ericsson *et al* 2015, Montgomery *et al* 2019), more intensive generalized linear mixed modeling (Messeri *et al* 2019), or even including individual animal physiology to improve model fit (Postlewaite 2023).

Because we needed accurate and consistent collar temperatures to compare moose responses across study areas, we developed a series of generalized linear mixed models (GLMMs; Brooks *et al* 2017, Muff *et al* 2020) for each study area to bias-correct observed moose collar temperatures. First, we aggregated observations from four networks of meteorological stations to correct moose-related temperature bias: the GHCN – Hourly (GHCNh; Menne *et al* 2012), the NRCS SNOTEL stations (Natural Resources Conservation Service 2025), the Global Terrestrial Network for Permafrost (Urban and Clow 2018), and Environment and Climate Change Canada Historical Station Data (Environment and Climate Change Canada 2025). Next, we extracted the nearest weather station observation for each moose location in each study area.

We constructed a series of GLMMs of weather station temperature using the *glmmTMB* package in R (Brooks *et al* 2017). We used month as a categorical fixed effect (to account for seasonal changes in solar radiation; Ericsson *et al* 2015) and both collar temperature and the square of collar temperature as fixed effects to represent non-linear effects at temperature extremes (Montgomery *et al* 2019). Because individual physiology influences body heat and therefore temperature offsets (Thompson *et al* 2020, Postlewaite 2023), we included individual-year as a random effect intended to capture individual variation in, for example, body mass, collar model, collar position, baseline internal temperature, and parturition status. Our full GLMMs modeled weather station temperature as a function of month as a fixed effect, random intercepts based on individual-water year, and collar temperature and square of collar temperature with random slopes based on individual-water year. We used these models to predict the actual temperature at each moose location (hereafter, bias-corrected collar temperature).

The most parsimonious model for collar bias correction included the full GLMM, with terms for month, collar temperature, the quadratic form of collar temperature, random individual-year intercept, and random slopes for both collar temperature and the quadratic of collar temperature based on individual-year. After bias correction, the correlation between observed temperature and collar temperature improved from 0.69 to 0.80 (Pearson's *r*; Table C6).

C.2 SnowModel Validation

Although our bias-corrected collar temperatures offered the best representation of weather conditions at each moose location, this approach did not resolve temperatures at other locations potentially available to that animal, a fundamental requirement of habitat selection methods (Johnson *et al* 2006, Thurfjell *et al* 2014, Chatterjee *et al* 2024). Thus, we used SnowModel, a physics-based modeling system, to derive temperature (Liston and Elder 2006b) and snow depth (Liston and Elder 2006a). SnowModel combines spatially and temporally distributed meteorological variables with topography and land cover type, numerically resolving physical processes such as lapse rate, snow accumulation, and blowing-snow redistribution. Because our study design required modeling distributed temperatures in complex topography during the coldest months of the year, accurate representation of cold-air pooling (i.e., inversions) was especially important (Lundquist *et al* 2008). We developed a new submodule within SnowModel, following Lundquist et al. (2008), to derive a time-evolving temperature inversion index that accounted for cold-air pooling, in addition to SnowModel's standard topographic air temperature adjustments (Liston and Elder 2006b). Furthermore, we implemented a temperature profile submodule to represent ambient air temperature at moose collar height using standard vertical temperature gradient relationships (e.g., Arya 2001).

Overall, we found strong agreement between daily SnowModel temperatures and both hourly (Pearson's $r = 0.919$; root mean square error [RMSE] = 5.8°C) and average daily (Pearson's $r = 0.973$; RMSE = 3.7°C) temperatures at a network of weather stations across our study areas (Old Crow $n = 2$, Alberta-North $n = 1$, Alberta-British Columbia $n = 1$, Meeteetse $n = 3$, Snowy Range $n = 1$). We also found agreement between modeled and observed snow depth across all study areas (overall Pearson's $r = 0.911$; RMSE = 0.16 m). We used a total of 16 SNOTEL sites (Meeteetse n = 6; Snowy Range n = 10; Natural Resources Conservation Service 2025) and 159 grid cells from the Canadian Meteorological Centre snow depth analysis data (Old Crow n = 102; Alberta-North n = 9; Alberta-British Columbia n = 48; Brown and Brasnett 2010).

C.3 Behavioral Delineation

We used hidden Markov models to delineate moose behavioral state into two general categories. While we cannot directly infer specific behaviors of an encamped moose (i.e., eating vs. sleeping), prior behavioral studies have found support for classifying behavior into encamped and traveling states for northern ungulates and, in particular, moose (Ditmer *et al* 2018, Beumer *et al* 2023, Calhoun *et al* 2024, Bassing *et al* 2024). The maximum fix rate in our study (four hours) is identical to that of other studies classifying activity patterns as broadly "active" or "less active" (Picardi *et al* 2022, Bassing *et al* 2024).

Because optimization in HMMs is sensitive to initial parameter values (i.e., priors), we first fitted different sets of initial values to a simple model with only step length and turning angle, keeping the solution with the lowest negative log-likelihood (McClintock *et al* 2020, Calhoun *et al* 2024). We then used these best initial values to fit the more complex model (Klappstein *et al* 2023), which calculated the most likely transition probabilities as a function of time (in hours; as a 24-hour cycle via the cosinor method per Cornelissen 2014), bias-corrected temperature (in °C, as recorded by GPS collar), and snow depth (in m, as modeled by SnowModel).

We used the *suncalc* package in R (Thieurmel and Elmarhraoui 2022) to classify activity data into dawn, day, dusk, or night based on astronomical twilight, when the center of the sun is between 0 and 18 degrees below the horizon. We defined dawn as from the start of astronomical twilight until sunrise, day as sunrise to sunset, dusk as sunset to the end of astronomical twilight, and night as the period between twilights (Nouvellet *et al* 2012). For Old Crow moose, all observations during polar night (5 December – 6 January) were defined as night. We used the *mgcv* package (Wood 2017) in R for all GAMMs, with restricted maximum likelihood and four basis functions (i.e., $k = 5$) as a compromise between precision and computational efficiency.

C.4 References

Arya S P 2001 *Introduction to Micrometeorology* vol 79 (San Diego, CA: Academic Press)

Bassing S B, Satterfield L, Ganz T R, DeVivo M, Kertson B N, Roussin T, Wirsing A J and Gardner B 2024 Predator–prey space use and landscape features influence movement behaviors in a large-mammal community *Ecology* **105** e4448

Beumer L T, Schmidt N M, Pohle J, Signer J, Chimienti M, Desforges J, Hansen L H, Højlund Pedersen S, Rudd D A, Stelvig M and Van Beest F M 2023 Accounting for behaviour in fine-scale habitat selection: A case study highlighting methodological intricacies *Journal of Animal Ecology* **92** 1937–53

Brooks M E, Kristensen K, Benthem K J ,van, Magnusson A, Berg C W, Nielsen A, Skaug H J, Mächler M and Bolker B M 2017 glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling *The R Journal* **9** 378

Brown R and Brasnett B 2010 Canadian Meteorological Centre (CMC) daily snow depth analysis data, version 1 *NASA National Snow and Ice Data Center Distributed Active Archive Center (DAAC) data set* W9FOYWH0EQZ3

Burkholder B O, Harris R B, DeCesare N J, Boccadori S J and Garrott R A 2022 Winter habitat selection by female moose in southwestern Montana and effects of snow and temperature *Wildlife Biology* **2022** e01040

Calhoun K L, Connor T, Gaynor K M, Van Scoyoc A, McInturff A, Kreling S E S and Brashares J S 2024 Movement behavior in a dominant ungulate underlies successful adjustment to a rapidly changing landscape following megafire *Mov Ecol* **12** 53

Chatterjee N, Wolfson D, Kim D, Velez J, Freeman S, Bacheler N M, Shertzer K, Taylor J C and Fieberg J 2024 Modelling individual variability in habitat selection and movement using integrated step-selection analysis *Methods Ecol Evol* **15** 1034–47

Cornelissen G 2014 Cosinor-based rhythmometry *Theor Biol Med Model* **11** 16

Ditmer M A, Moen R A, Windels S K, Forester J D, Ness T E and Harris T R 2018 Moose at their bioclimatic edge alter their behavior based on weather, landscape, and predators *Current Zoology* **64** 419–32

Environment and Climate Change Canada 2025 Historical Station Data Online: https://climate.weather.gc.ca/index_e.html

Ericsson G, Dettki H, Neumann W, Arnemo J M and Singh N J 2015 Offset between GPS collar-recorded temperature in moose and ambient weather station data *Eur J Wildl Res* **61** 919–22

Felton A M, Wam H K, Borowski Z, Granhus A, Juvany L, Matala J, Melin M, Wallgren M and Mårell A 2024 Climate change and deer in boreal and temperate regions: From physiology to population dynamics and species distributions *Global Change Biology* **30** e17505

Jennewein J S, Hebblewhite M, Mahoney P, Gilbert S, Meddens A J H, Boelman N T, Joly K, Jones K, Kellie K A, Brainerd S, Vierling L A and Eitel J U H 2020 Behavioral modifications by a large-northern herbivore to mitigate warming conditions *Mov Ecol* **8** 39

Johnson C J, Nielsen S E, Merrill E H, Mcdonald T L and Boyce M S 2006 Resource Selection Functions Based on Use–Availability Data: Theoretical Motivation and Evaluation Methods *Journal of Wildlife Management* **70** 347–57

Klappstein N J, Thomas L and Michelot T 2023 Flexible hidden Markov models for behaviour-dependent habitat selection *Mov Ecol* **11** 30

Liston G E and Elder K 2006a A Distributed Snow-Evolution Modeling System (SnowModel) *Journal of Hydrometeorology* **7** 1259–76

Liston G E and Elder K 2006b A Meteorological Distribution System for High-Resolution Terrestrial Modeling (MicroMet) *Journal of Hydrometeorology* **7** 217–34

Lundquist J D, Pepin N and Rochford C 2008 Automated algorithm for mapping regions of cold-air pooling in complex terrain *J. Geophys. Res.* **113** 2008JD009879

McClintock B T, Langrock R, Gimenez O, Cam E, Borchers D L, Glennie R and Patterson T A 2020 Uncovering ecological state dynamics with hidden Markov models ed T Coulson *Ecology Letters* **23** 1878–903

Menne M J, Durre I, Vose R S, Gleason B E and Houston T G 2012 An Overview of the Global Historical Climatology Network-Daily Database *Journal of Atmospheric and Oceanic Technology* **29** 897–910

Messeri A, Becciolini V, Messeri G, Morabito M, Crisci A, Orlandini S and Ponzetta M P 2019 Wild ungulates and environmental temperature: analysis on the possible utilization of data from sensor placed on GPS collars *Int J Biometeorol* **63** 293–300

Montgomery R A, Redilla K M, Moll R J, Van Moorter B, Rolandsen C M, Millspaugh J J and Solberg E J 2019 Movement modeling reveals the complex nature of the response of moose to ambient temperatures during summer *Journal of Mammalogy* **100** 169–77

Muff S, Signer J and Fieberg J 2020 Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation ed E V Wal *Journal of Animal Ecology* **89** 80–92

Natural Resources Conservation Service 2025 Air & Water Database Reports Online: https://nwcc-apps.sc.egov.usda.gov/awdb/site-plots/POR/WTEQ/WA/Muckamuck.html

Nouvellet P, Rasmussen G S A, Macdonald D W and Courchamp F 2012 Noisy clocks and silent sunrises: measurement methods of daily activity pattern ed A Braae *Journal of Zoology* **286** 179–84

Picardi S, Coates P, Kolar J, O'Neil S, Mathews S and Dahlgren D 2022 Behavioural state-dependent habitat selection and implications for animal translocations *Journal of Applied Ecology* **59** 624–35

Postlewaite S 2023 *no.inn_inspera_175270327_99190289.pdf* Master in Applied Ecology & Natural Resource Management (Zurich University of Applied Sciences and Inland Norway University)

Prugh L R, Lundquist J D, Sullender B K, Cunningham C X, Dechow J, Borg B L, Sousanes P J, Stehn S and Durand M T 2024 Landscape heterogeneity buffers the impact of an extreme weather event on wildlife *Commun Biol* **7** 1515

Reinking A K, Højlund Pedersen S, Elder K, Boelman N T, Glass T W, Oates B A, Bergen S, Roberts S, Prugh L R, Brinkman T J, Coughenour M B, Feltner J A, Barker K J, Bentzen T W, Pedersen Å Ø, Schmidt N M and Liston G E 2022 Collaborative wildlife–snow science: Integrating wildlife and snow expertise to improve research and management *Ecosphere* **13** Online: https://onlinelibrary.wiley.com/doi/10.1002/ecs2.4094

Street G M, Rodgers A R and Fryxell J M 2015 Mid-day temperature variation influences seasonal habitat selection by moose: Temperature Dependent Moose Habitat Selection *Jour. Wild. Mgmt.* **79** 505–12

Studd E K, Landry-Cuerrier M, Menzies A K, Boutin S, McAdam A G, Lane J E and Humphries M M 2019 Behavioral classification of low-frequency acceleration and temperature data from a free-ranging small mammal *Ecology and Evolution* **9** 619–30

Thieurmel B and Elmarhraoui A 2022 suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase Online: https://CRAN.R-project.org/package=suncalc

Thompson D P, Crouse J A, Jaques S and Barboza P S 2020 Redefining physiological responses of moose (Alces alces) to warm environmental conditions *Journal of Thermal Biology* **90** 102581

Thurfjell H, Ciuti S and Boyce M S 2014 Applications of step-selection functions in ecology and conservation *Mov Ecol* **2** 4

Urban F E and Clow G D 2018 DOI/GTN-P climate and active-layer data acquired in the National Petroleum Reserve–Alaska and the Arctic National Wildlife Refuge, 1998–2019

Van Beest F M, Van Moorter B and Milner J M 2012 Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate *Animal Behaviour* **84** 723–35

Wilmers C C, Nickel B, Bryce C M, Smith J A, Wheat R E and Yovovich V 2015 The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology *Ecology* **96** 1741–53

Wood S N 2017 *Generalized additive models: an introduction with R* (Chapman and Hall/CRC)

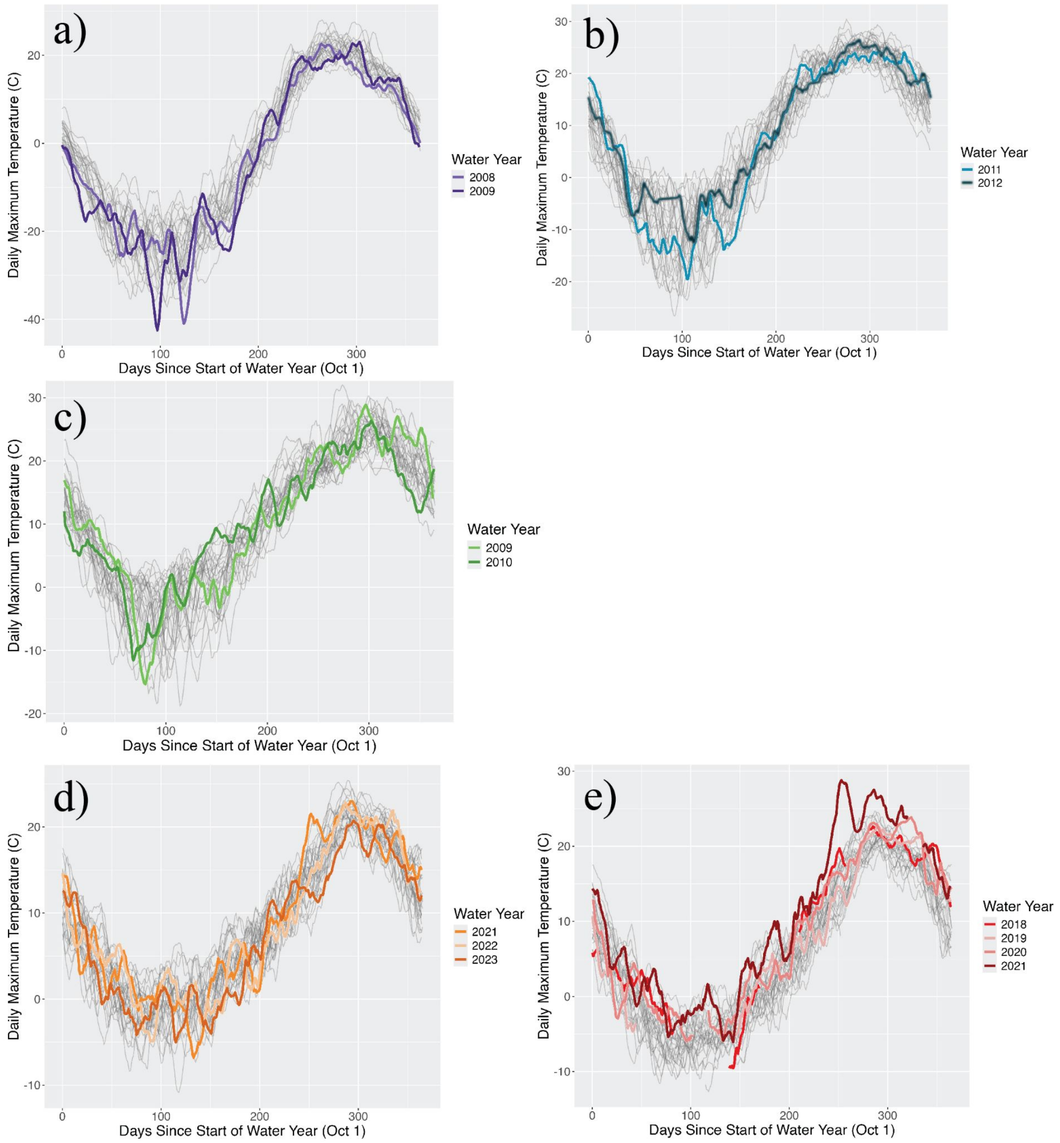

Figure C1. Maximum daily temperatures during years of this study compared with most recent 30-year (1995-2025) climate normals for (a) Old Crow, (b) Alberta-North, (c) Alberta-British Columbia, (d) Meeteetse, and (e) Snowy Range study areas. All temperatures are 15-day moving averages. Our study took place during winter months only (December-February; water year days 61-150), during which Old Crow included the lowest daily temperatures in the 30-year record (a) and Alberta-North included the highest sustained average winter temperatures (b). All other winters were fairly average with long-term normals. Data from GHCN-Daily and SNOTEL.

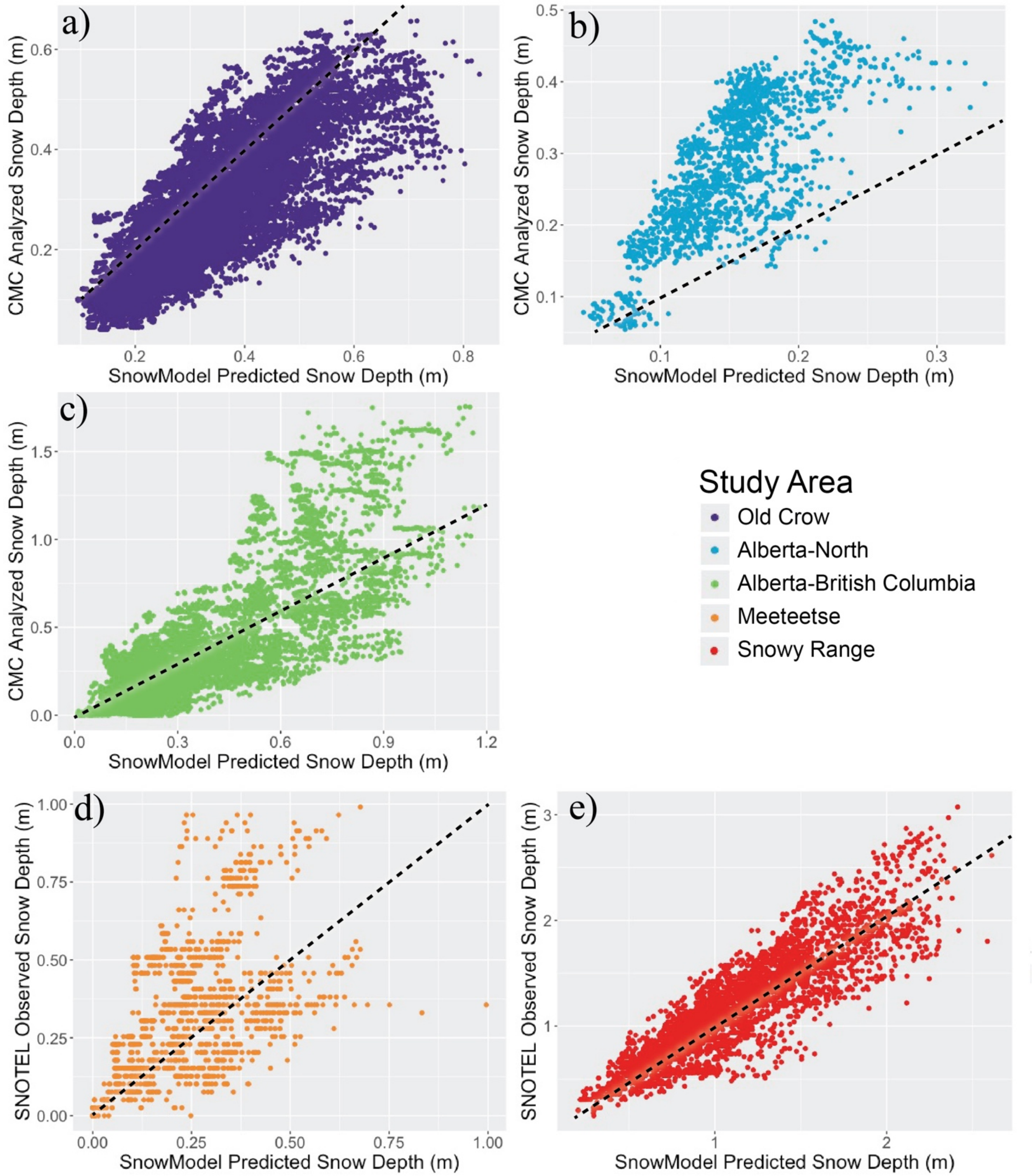

Figure C2. SnowModel validation. Predicted snow depth for (a) Old Crow, (b) Alberta-North, (c) Alberta-British Columbia, (d) Meeteetse, and (e) Snowy Range study areas compared against observed snow depth. In all panels, the dotted line shows a 1:1 correspondence between predicted and observed snow depth. In (a-c), Canadian Meteorological Centre (CMC) Daily

Snow Depth Analysis Data (Version 1) was used, a gridded product combining in-situ measurements, reanalysis, and interpolation (*n* daily grid cells = 102 for Old Crow, *n* = 9 for Alberta-North, and *n* = 48 for Alberta-British Columbia). In (d) and (e), SNOTEL stations were used (*n* = 6 for Meeteetse; *n* = 10 for Snowy Range). When all data were pooled, the overall Pearson's *r* was 0.911 with a root mean squared error of 0.16. Correlation varied by study area: OC Pearson's *r* = 0.815, ABN *r* = 0.733, ABC *r* = 0.789, ME *r* = 0.523, and SR *r* = 0.886.

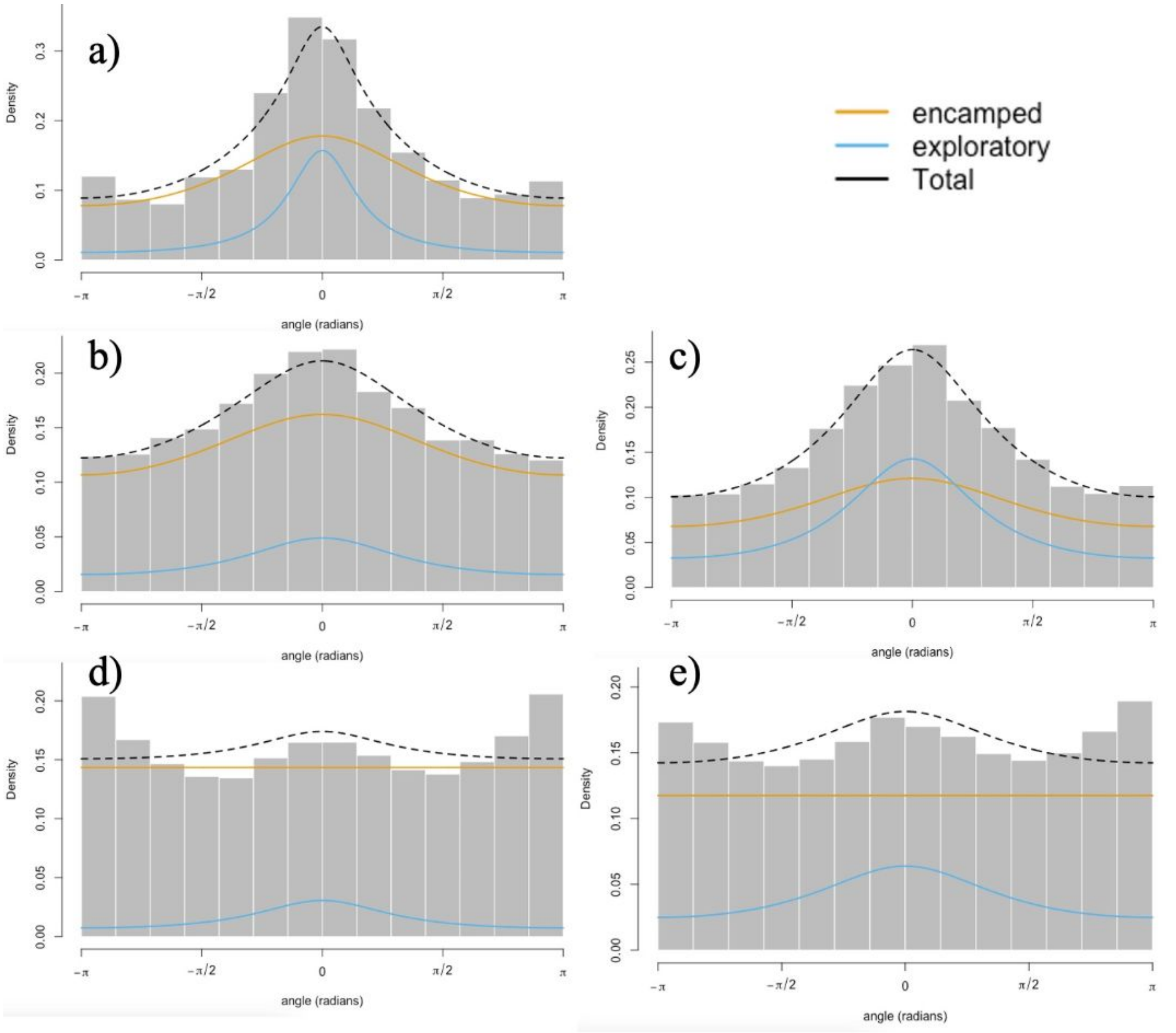

Figure C3. Turn angle distribution for hidden Markov Models for (A) Old Crow, (B) Alberta-North, (C) Alberta-British Columbia, (D) Meeteetse, and (E) Snowy Range moose populations. Orange lines represent the modeled distribution of turn angles for animals in an encamped state, blue lines represent the modeled distribution of turn angles for animals in an exploratory state, and dotted black line and histogram bars represent the observed distribution of all animal steps.

Table C1. Old Crow moose collar bias correction model results. Models sorted by AIC, with the most parsimonious model ranked highest. There was equivalent support (ΔAIC < 2) for a full model with all terms included and a model with only month (as a factor) and temperature.

Model	**ΔAIC**	**Degrees of Freedom**
Month + Temp	0	8
Full model	1.89	9
Temp + Temp^2	83.18	7
Temp	83.76	6
Month	87.56	7
Month + Temp^2	89.55	8
Random effects only	169.92	5

Table C2. Alberta-North moose collar bias correction model results. Models sorted by AIC, with the most parsimonious model ranked highest.

Model	**ΔAIC**	**Degrees of Freedom**
Full model	0	9
Month + Temp	11.1	8
Month + Temp^2	125.8	8
Month	131.4	7
Temp + Temp^2	377.1	7
Temp	383.8	6
Random effects only	506.6	5

Table C3. Alberta-British Columbia moose collar bias correction model results. Models sorted by AIC, with the most parsimonious model ranked highest.

Model	**ΔAIC**	**Degrees of Freedom**
Full model	0	9
Month + Temp	2.49	8
Month + Temp^2	40.39	8
Month	42.33	7
Temp + Temp^2	1100.03	7
Temp	1104.35	6
Random effects only	1148.15	5

Table C4. Meeteetse moose collar bias correction model results. Models sorted by AIC, with the most parsimonious model ranked highest.

Model	**ΔAIC**	**Degrees of Freedom**
Full model	0	9
Month + Temp	133.9	8
Month + Temp^2	208.5	8
Month	339.5	7
Temp + Temp^2	2975.3	7
Temp	3111.4	6
Random effects only	3320.9	5

Table C5. Snowy Range moose collar bias correction model results. Models sorted by AIC, with the most parsimonious model ranked highest.

Model	**ΔAIC**	**Degrees of Freedom**
Full model	0	9
Temp + Temp^2	141.6	8
Temp	178.9	8
Month + Temp	318.7	7
Month + Temp^2	691	7
Month	832.4	6
Random effects only	1010	5

Table C6. Moose collar temperature bias correction using weather station data. Correlations are given as Pearson's *r*.

Population	**Number of Weather Stations**	**Mean distance from weather station (km)**	**SD distance from weather station (km)**	**Correlation, before bias correction**	**Correlation, after bias correction**
OC	4	73.486	23.844	0.828	0.865
ABN	2	18.97	11.09	0.766	0.828
ABC	4	51.778	28.969	0.623	0.712
ME	5	13.192	5.744	0.662	0.773
SR	9	13.45	6.853	0.556	0.805
Total/Average	**24**	**34.1752**	**15.3**	**0.687**	**0.7966**

APPENDIX D: SUPPORTING INFORMATION FOR CHAPTER 5

Climate change diminishes snow-mediated movement advantage for apex predators

D.1 Additional Methods

Given the inherent uncertainty in climate projections, natural variability, and variance in GCM performance across different regions, timescales, and output parameters (Deser et al., 2012; Lybarger et al., 2024; Taylor et al., 2023), projections drawn from multiple GCMs are widely acknowledged to be more robust than single-model inference (Ahmed et al., 2019; Duan et al., 2019; Knutti, Furrer, et al., 2010; Pavan & Doblas-Reyes, 2000). Specifically, a simple multi-model ensemble mean reduces bias and increases skill, especially when a sufficient number of GCMs are used (i.e., ~10 models; Clark et al., 2021; Knutti, Abramowitz, et al., 2010; Pierce et al., 2009; Sanderson et al., 2017). Thus, we calculated the multi-model mean from the following 15 global climate models from the CMIP6 family: ACCESS-CM2, ACCESS-ESM1-5, BCC-CSM2-MR, CAMS-CSM1-0, CanESM5, CESM2-WACCM, CMCC-CM2-SR5, FGOALS-g3, FIO-ESM-2-0, IITM-ESM, MIROC6, MRI-ESM2-0, NESM3, NorESM2-MM, and TaiESM1. We used the University of Washington Climate Impacts Group's Pacific Northwest Climate Projection Tool (Rogers & Mauger, 2021) to extract each model's output across the Pacific Northwest region (41.5-49.5°N, 125-111°W) for mid-century (2040-2069) projections relative to a baseline of 1950-1999.

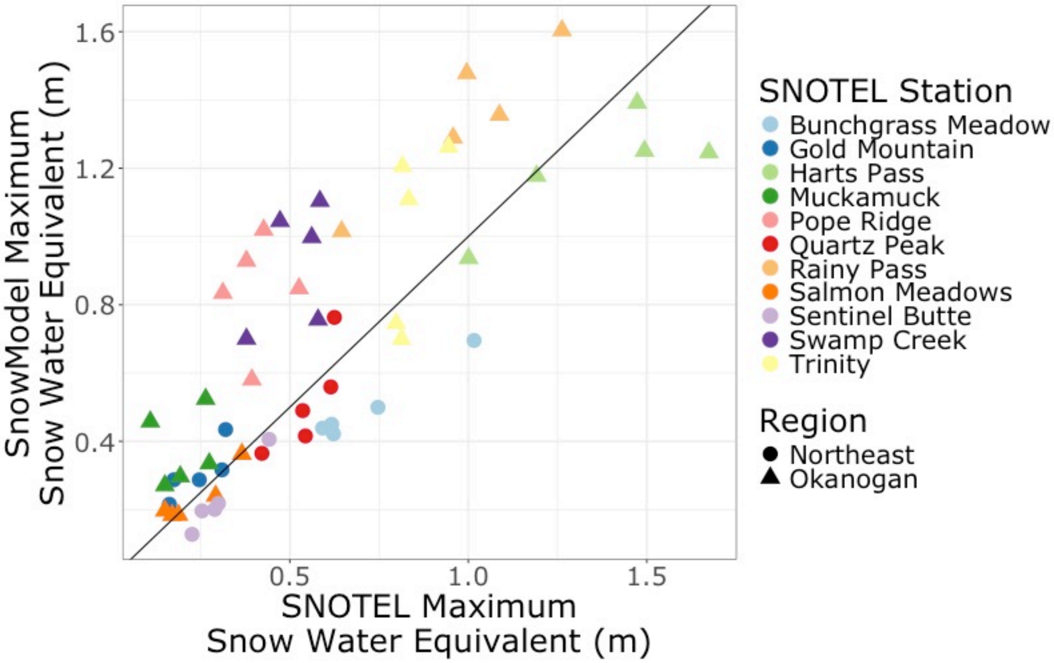

Figure D1. SnowModel validation, using maximum annual snow water equivalent (SWE) for each of 11 SNOTEL stations across the baseline period of 2018-2022. Black line shows a 1:1 line for reference. Strong correlation (Pearson’s R = 0.81) indicates good model performance, as well as a lack of regional bias.

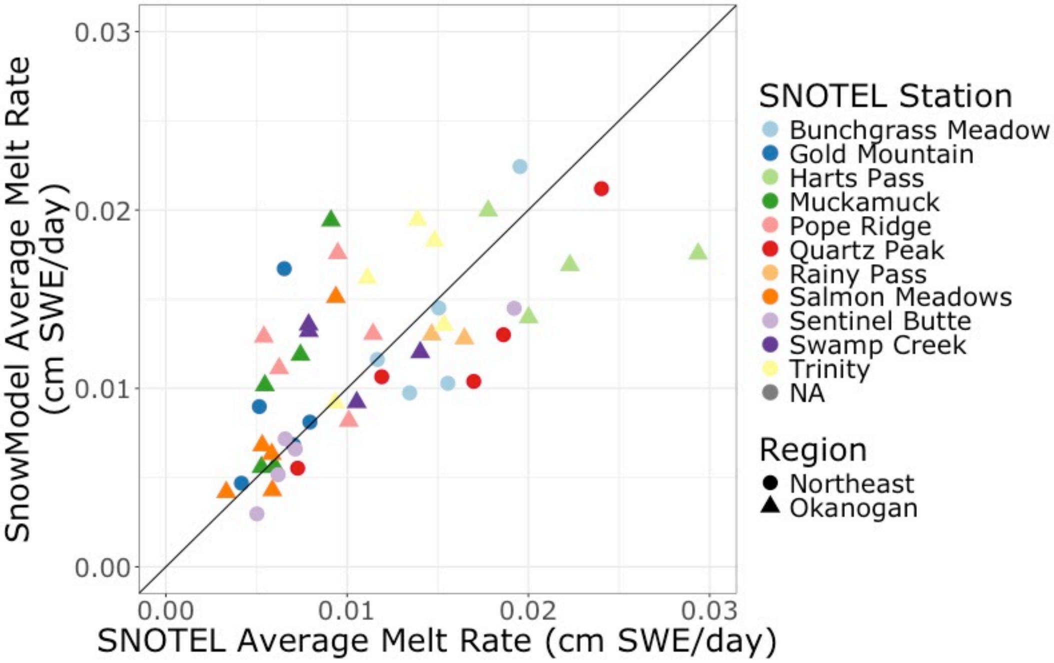

Figure D2. SnowModel validation, using average melt rate from peak annual snow water equivalent (SWE) until snow loss, for each of 11 SNOTEL stations across the baseline period of 2018-2022. Black line shows a 1:1 line for reference. Good correlation (Pearson’s R = 0.67) indicates acceptable model performance and a lack of regional bias.

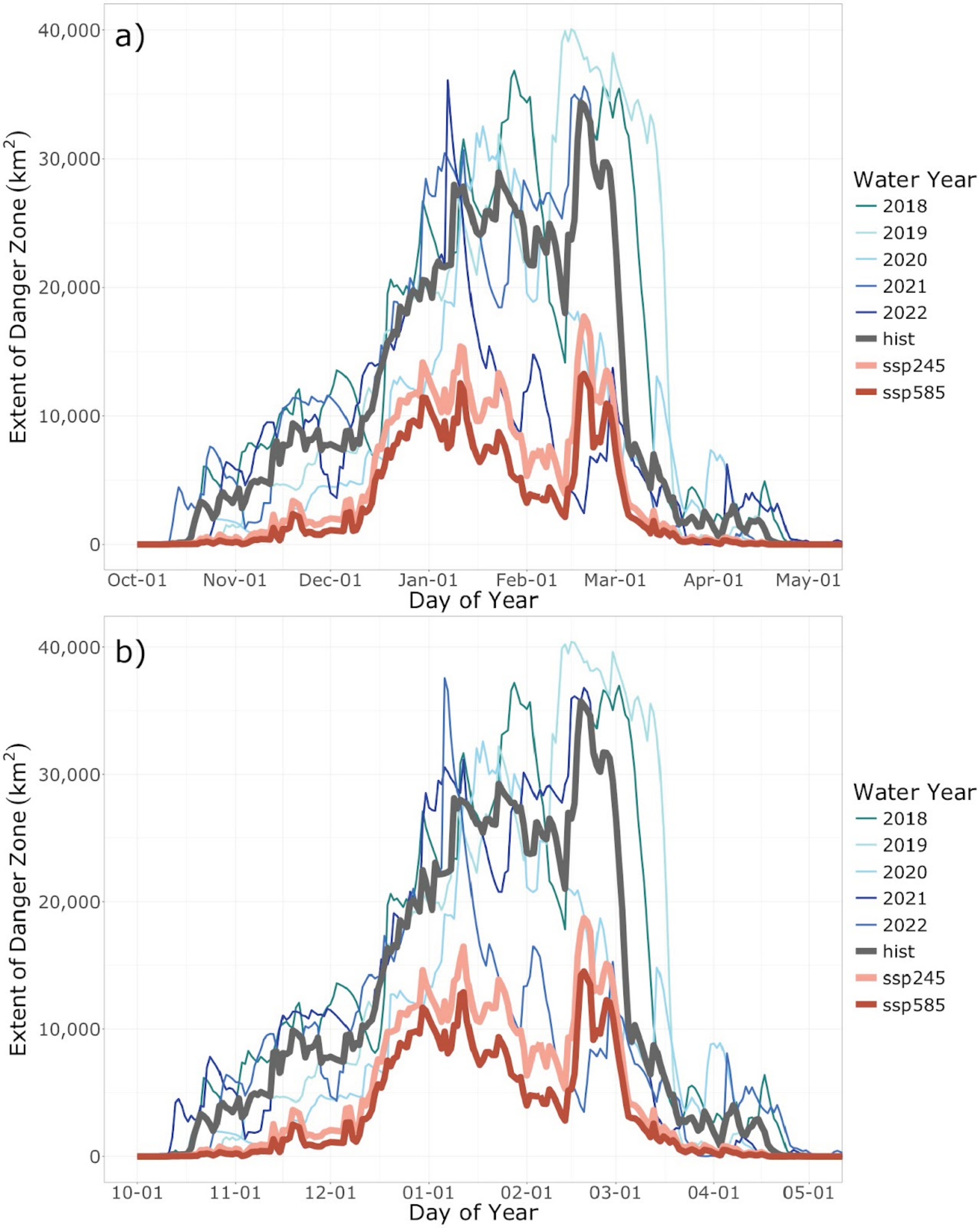

Figure D3. Comparison of total areal extent of snow conditions that provide an advantage to (a) cougars or (b) wolves over deer ("danger zone"). Both panels show annual time series of total danger zone extent, Oct 1 - May 1, across both study areas for individual years used in baseline (blue), as well as baseline median (gray), SSP2-4.5 median (moderate climate change scenario; pink), and SSP5-8.5 median (severe climate change scenario; brown). Due to similarities in foot loading, snow density-track sink depth relationship, and thresholds of support (Sullender et al. 2023), cougars and wolves gain a movement advantage over ungulate prey at nearly identical conditions. Thus, (a) and (b) show nearly identical results, although throughout the year, wolves (b) have a slightly greater areal extent than cougars (a) over which they gain an advantage over prey.

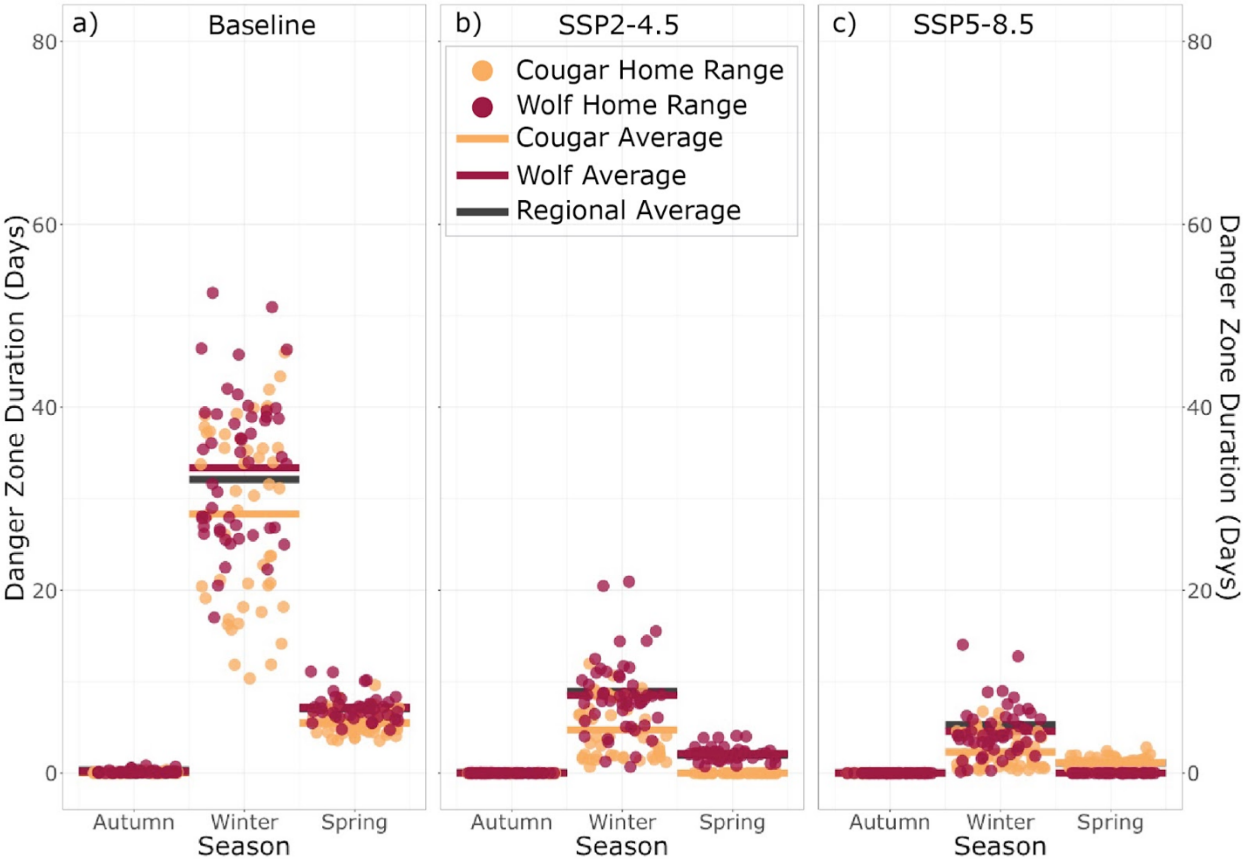

Figure D4. Seasonal comparison of average duration of predator-advantaged snow conditions (danger zones) within each individual predator's home range within the Northeast study area. Durations calculated for (a) baseline snow conditions (2018-2022), (b) moderate climate change scenario (SSP2-4.5), and (c) severe climate change scenario (SSP5-8.5). Predator home ranges defined as the isopleth bounding the 95% kernel density estimate for GPS-collared animals, computed for each year, each season, and each individual. Seasons defined as autumn including Sep-Nov, winter Dec-Feb, and spring Mar-May.

VITA

Benjamin Knight Sullender is a graduate researcher in the Prugh Lab at the University of Washington School of Environmental and Forest Sciences. His research combines spatial analysis, movement ecology, and climate modeling with a deep love of mountains, the creatures that inhabit them, and the snow that blankets them. He holds a Bachelor of Arts in Environmental Studies from Carleton College and a Master of Science in Conservation Biology and Sustainable Development from the University of Wisconsin-Madison.