Population ecology of mountain goats in relation to climate, weather and snow avalanches

by

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B.Sc., Humboldt State University, 1995
M.Sc., University of Nevada Reno, 1999

A Dissertation Submitted in Partial Fulfillment of the
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We acknowledge and respect the Lək̓ʷəŋən (Songhees and Esquimalt) Peoples on whose territory the university stands, and the Lək̓ʷəŋən and WSÁNEĆ Peoples whose historical relationships with the land continue to this day. We also acknowledge the Tlingit People on whose traditional territory this research was conducted.

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Abstract

Weather and climate exert profound influences on wildlife populations. In mountain environments climate is changing rapidly, compared with surrounding lowland areas, highlighting the importance of understanding the population ecology of species inhabiting these sensitive and biodiverse systems. My dissertation research focused on how weather and climate, and related phenomena (i.e. snow avalanches), influence the population ecology of mountain goats – a sentinel species on mountain environments. I used long-term field data collected from individually marked animals (421 individuals over 17 years across 4 study areas in coastal Alaska) combined with remote-sensing environmental data to assess a suite of research questions. First, however, I synthesized existing information about how mountain goats are influenced by weather and climate in order to comprehensively understand the state of our knowledge and identify knowledge gaps (Chapter 2). Next, I examined how climate and life-history trade-offs shape mountain goat reproductive demography (Chapter 3). These analyses revealed age-specific patterns in reproductive performance were negatively influenced by previous parturition success, late-winter snow depth and summer temperature. Highlighting the importance of intrinsic and extrinsic factors on reproduction, these results also filled an important data gap by enabling parameterization and implementation of mountain goat population modeling simulations used to evaluate relative strength of winter vs summer effects and later analyses (described below). The remainder of my research focused on examining the extent that snow avalanches represent a climate-linked driver of mountain goat populations. In Chapter 4, principal findings revealed that avalanches comprise a major source of mortality (36% of all mortalities, on average) and can remove up to 22% of a population annually. Given the low realized population growth rate previously reported for mountain goats (i.e. 1-4%), such impacts may exert significant demographic consequences. To quantify such impacts, I next developed and implemented a population modeling approach to explicitly examine and quantify how avalanches, across a range of scenarios, influence population growth and dynamics, including recovery times (Chapter 5). Ultimately, I determined that mountain goats can sustain modest population growth (1.5%) during average avalanche conditions, but during severe years (i.e. when 23% of a population dies from avalanches) populations can experience significant declines (15%) that require extended periods (11 years, or 1.5 mountain goat generations) for recovery to baseline levels. Overall, my research contributes several dimensions of new knowledge about how weather and climate-linked factors influence mountain goats populations, and offer important insights about the functionality of mountain ecosystems in the face of changing climate conditions.

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Acknowledgements

To steal a line from my extraordinary academic advisor, Dr. Chris Darimont, “Science is better together”. Indeed my work is the outgrowth of many outstanding collaborations and relationships – spanning a diverse array of mentors, colleagues, friends and family. First, I’d like to acknowledge my excellent graduate studies committee in including Drs. Chris Darimont, Eran Hood (my off-campus supervisor), Chris Bone and Taal Levi. I’ve much appreciated and benefitted from my opportunities to learn from and develop relationships with this top-notch group of scientists. Their generosity with time, guidance, kindness and good humor was, in no small measure, key to the success of this project and my academic experience overall.

A key personal motivation for this project involved integrating wildlife ecology with climate and snow science. In this regard, I’d like to thank my snow and avalanche science collaborators Gabe Wolken, Erich Pietzsch, Yves Bühler and Kathreen Wikstrom-Jones for their support, insights and contributions. The extended network of scientists with Alaska Climate Adaptation Science Center offered a unique and much valued opportunity to engage more broadly in diverse aspects of climate science. The synthetic work comprising Chapter 2 involved a remarkable collaboration with a diverse team of North American mountain goat ecologists and environmental scientists – much thanks to Becky Cadsand, Steeve Côté, Tabitha Graves, Sandra Hamel, Rich Harris, Forest Hayes, Eran Hood, Kevin Hurley, Tyler Jessen, Bill Jex, Erich Peitzsch, Wesley Sarmento, Helen Schwantje, and Joel Berger. More broadly, several scientists have offered insightful and concise technical review (both formally and informally) of earlier versions of this research, I wish to thanks: Kurt Jenkins, Steve Gordon, Justin Gude, Anne Hubbs, Darryl Lutz, Kim McConkey, and Steve Wilson (Chapter 2); Anthony Crupi, Calum

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Deep into writing goats

Tele skis waxed and ready

Powder snow awaits

Co-Authorship Statement

Chapters 2 through 5 of this dissertation were co-authored. The following outlines my contributions, and that of each of the authors. I use the CRediT (Contributor Roles Taxonomy) framework and definitions to describe author contributions. I also provide the publication status of each chapter.

Chapter 2

K. S. White, B. Cadsand, S. D. Côté, T. Graves, S. Hamel, R. B. Harris, F. P. Hayes, E. Hood, K. Hurley, T. Jessen, B. Jex, E. Peitzsch, W. Sarmento, H. Schwantje, and J. Berger. 2025. Mountain sentinels in a changing world: review and conservation implications of weather and climate effects on mountain goats (*Oreamnos americanus*). *Global Ecology and Conservation*, e03364.

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Chapter 3

White, K. S., T. Levi, E. Hood, and C. T. Darimont. *In review.* Life-history trade-offs and environmental variability shape reproductive demography in a mountain sentinel. *Journal of Animal Ecology.*

Author contributions: Conceptualization: KSW; Methodology: KSW, TL; Investigation: KSW, TL; Visualization: KSW; Funding acquisition: KSW, EH; Project administration: KSW, EH, CTD; Supervision: EH, CTD; Writing – original draft: KSW; Writing – review & editing: All Authors

Chapter 4

White, K. S., E. Hood, G. J. Wolken, E. H. Peitzsch, Y. Bühler, K. Wikstrom Jones, and C. T. Darimont. 2024. Snow avalanches are a primary climate-linked driver of mountain ungulate populations. *Communications Biology*, 7: 423.

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Chapter 5

White, K. S., T. Levi, E. Hood, and C. T. Darimont. *In review.* Snow avalanches and the impact of climate-linked extreme events on mountain wildlife population dynamics and resilience. *Global Change Biology*.

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Chapter 1. Introduction

Environmental change plays an important role in driving population dynamics and patterns of biodiversity (Ozgul et al. 2010, Bellard et al. 2012, Mills 2013, Gilbert et al. 2020). Increasingly, such dynamics are influenced by variation in weather conditions and linked to longer-term processes of climate change (Bellard et al. 2012, Harris et al. 2018). High-elevation alpine and mountain environments are among the ecosystems most sensitive, and rapidly changing, due to climate change (Pepin et al. 2022, Schmeller et al. 2022). These systems are strongly driven by abiotic controls with factors such as snowfall, rain and wind being especially amplified, relative to surrounding lowlands areas, due to orographic effects (Roe 2005). By extension, species living in these extreme environments possess specialized adaptations for coping with such conditions. Ultimately, understanding interrelationships between mountain climate, weather and alpine-adapted species is an important precondition for evaluating and forecasting future climate-linked changes in alpine ecosystems and beyond.

Snow is an ubiquitous and influential feature of mountain environments. Blanketing the ground for nine months of the year, snow exerts important effects on ecological processes and alpine organisms (Williams et al. 2015, Penczykowski et al. 2017). The water contained within snow, for instance, provides important ecosystem services, nourishing plant and animal (including human) communities with local as well as wide-reaching downstream benefits (Immerzeel et al. 2010). Snow can also impose challenges. Heavy accumulations of snow can constrain life-supporting processes, sometimes leading to extraordinary biological responses designed to avoid such challenges, including hibernation (Humphries et al. 2003, Pigeon et al. 2016) and long-distance migration (Alerstam et al. 2003). Most organisms, however, actively endure snowy winter conditions and persist via a variety of behavioral, morphological and physiological adaptations and tactics.

Adaptations to snow, however, have limits. Evolutionary and biological responses are often tuned to average conditions, shifting in effectiveness depending on variability in environmental conditions with implications for population performance (Smith 2011a, Harris et al. 2018, Walsh et al. 2020). Extreme snow events, for example, exert catastrophic impacts on population dynamics when they near, or exceed, the adaptive capability of an organism (Schmidt et al. 2019). Yet, even under less extreme circumstances, variability in the distribution, abundance and physical properties of snow represent an important factor, and routinely exert biologically meaningful, sometimes profound, impacts of population dynamics (Penczykowski et al. 2017, Boelman et al. 2019, Reinking et al. 2022).

Snow influences the population ecology of cold-adapted species through both direct and indirect pathways. Most previous study has focused on indirect, ecological pathways by which snow influences animal behavior and population ecology (Williams et al. 2015, Penczykowski et al. 2017, Reinking et al. 2022). For example, snow can comprise a barrier to movement and elevate energetic costs of locomotion (Dailey and Hobbs 1989), leading to depletion of endogenous nutritional reserves critical for survival during the long winter period (Parker et al. 2009). Snow also can bury forage resources, thereby restricting access and assimilation of nutritional resources (Visscher et al. 2006, White et al. 2009). In mammalian predator-prey systems, prey capture efficiency can be strongly influenced by snowpack properties (Horne et al. 2019, Peers et al. 2020, Sullender et al. 2023). In spring and summer, snow distribution and melt play an important role in plant phenology and the distribution of emergent, high quality food resources available for herbivores (Fox 1991, Pettorelli et al. 2007, John et al. 2024). Snow patches can also provide relief from harassing insects and serve as thermal refugia – especially important for cold-adapted species with limited tolerance for hot weather (Ion and Kershaw 1989, Sarmento et al. 2019, Hayes and Berger 2023). Taken together, these ecological mechanisms illustrate the diverse ways that snow can influence the population ecology of animals, offering important insights and a conceptual framework needed to understand and predict responses across an array of ecological contexts.

Direct physical mechanisms related to snow movement, while less studied, also hold potential to exert substantial impacts on population ecology and ecological dynamics. The process of avalanching snow, for instance, is a major source of disturbance in alpine (and downslope) environments (Bebi et al. 2009, 2022), and is widespread among mountain regions of the world (Glazovskaya 1998). Snow avalanches can occur through multiple mechanistic pathways that are principally influenced by variation in slope steepness, and the physical processes associated with accumulating snow (i.e. temperature, precipitation, and wind) and the structural properties of the resulting snowpack (McClung and Schaerer 2006). For example, avalanches can occur following a deep snow event – the heavy mass subject to strong gravitational forces and ultimately sliding on steep, poorly bonded surfaces. However, a heavy snow event is not a necessary precondition, and avalanches can also occur when weak layers form in the snowpack, creating instabilities that are prone to sliding even with minimal snow loading. Whereas multiple additional variations in conditions can occur, consequences in all cases can be similarly impactful and generate downslope movements of snow capable of destroying mature forests and more. Avalanches, and the disturbances created in their wake, are thus a major driver of habitat and plant community composition in mountain environments (Rixen et al. 2007, Bebi et al. 2009).

Such impacts can be beneficial and deleterious. By promoting habitat heterogeneity at both large- and micro-scales, avalanches can increase organismal diversity and abundance (Muller and Straub 2016, Requena et al. 2022, Alba et al. 2023). In addition, the removal and redistribution of snow in avalanche habitats may also have implications for vegetative phenology, providing earlier and more extended access of freshly emergent, high quality forages to the benefit of herbivores (Garcia-Gonzalez and Cuartas 1996, Serrouya et al. 2011).

Yet, utilization of avalanche terrain by wildlife can also be costly and increase vulnerability. Anecdotal reports, for example, have documented avalanche mortality among a variety of mountain wildlife species, including alpine chamois (*Rupicapra rupicapra*), bighorn sheep (*Ovis canadensis sierrae),* caribou (*Rangifer tarandus),* Dall's sheep (*Ovis dalli dalli),* elk (*Cervus canadensis),* grizzly bears *(Ursus arctos)* and mountain goats (*Oreamnos americanus*)(Burles and Hoefs 1984, Ernst 2002, Jonas et al. 2008a, White et al. 2011, Conner et al. 2018, Skladanowski et al. 2021). However, despite the potential for causing substantial demographic impacts, our understanding of the extent avalanches impact population dynamics is limited and remains an important knowledge gap. Overall, the study of how mass movements of snow influence ecological processes is an emerging discipline, and holds important potential to aid our understanding of how climate-linked environmental variability influences population and landscape ecology.

My PhD research builds upon this body of knowledge, utilizing the underlying conceptual frameworks to broadly examine how organisms are influenced by environmental variability. Specifically, I set out to understand how variation in climate, weather and, by extension, snow avalanches influence the behavioral and population biology of mountain wildlife. ‘A climbing bearded beast the color of winter’, mountain goats (Figure 1.1) are an iconic species of North American mountain landscapes and cultures (Chadwick 1983, Rofkar 2014, Jessen et al. 2022, Greening (La’goot) 2024) – and well suited for study of alpine ecosystems and processes. Despite their extraordinary adaptations for persisting in mountain environments (i.e. highly insulative coat, climbing morphology), their population dynamics can be strongly influenced by variation in climate, weather conditions and associated ecosystem processes (Pettorelli et al. 2007, Langman et al. 2015, Lewinson and Stefanyshyn 2016, White et al. 2018). As such, mountain goats are considered a sentinel species of mountain environments – one for which knowledge can offer insights about the functioning of mountain ecosystems as a whole

Figure 1.1. Mountain goat (*Oreamnos americanus)*, or Jánwu, in coastal Alaska.

(*sensu* Hazen et al. 2019). Thus, through study of mountain goats and climate-linked processes, my objective is to advance our mechanistic understanding about how alpine environments function and associated implications. Ultimately, this work aims to increase our capacity to understand how sensitive, and already rapidly changing, mountain ecosystems are likely to be impacted by projected shifts in future climate (Pepin et al. 2022, Schmeller et al. 2022). My research is interdisciplinary, collaborative and occurred at the cross-section of animal population ecology and climate – snow science (Figure 1.2). My initial objective (Chapter 2) involved broadly synthesizing existing literature about weather and climate effects on mountain goat population biology in order to identify the state of our knowledge, research gaps and conservation implications. This wide-reaching, collaborative effort involved leading a diverse

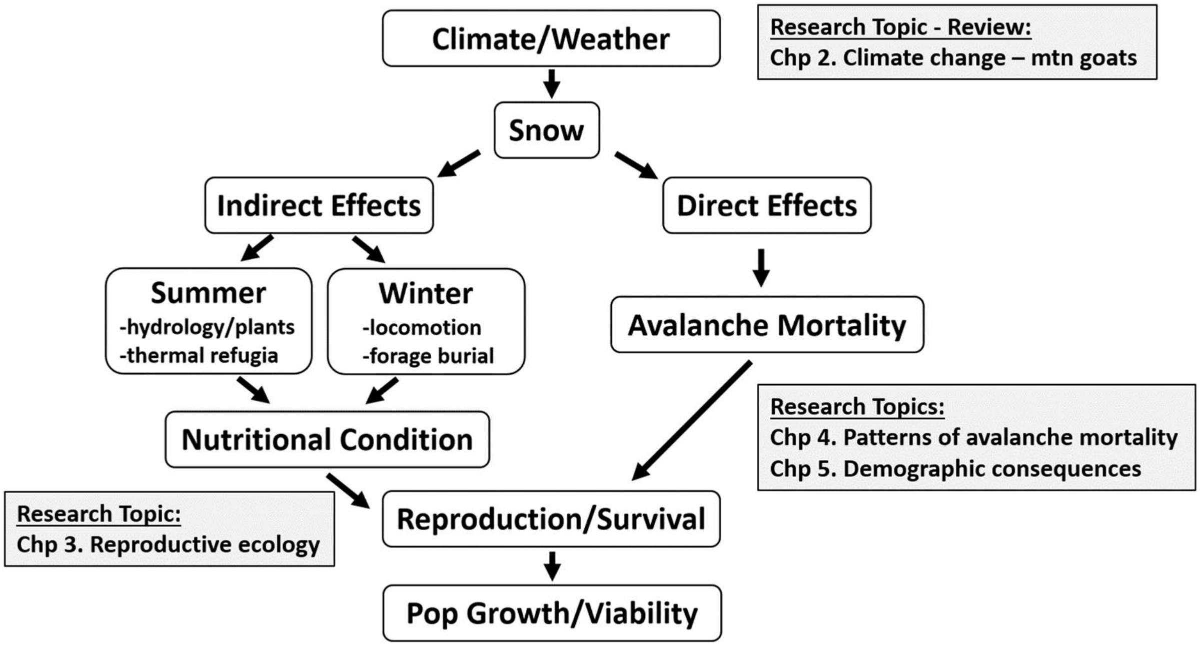

Figure 1.2. Theoretical framework for understanding climate and weather related effects, mediated through snow, on mountain goat population ecology. PhD dissertation chapters are annotated in reference to the subject areas and mechanisms they investigate.

team of mountain goat specialists and snow–climate scientists, and provided an excellent foundation for subsequent investigation of ecological and conservation relevant research topics.

Conducting ecological research using extensive, long-term data from individually-marked animals can offer valuable opportunities to attain key insights about population ecology (Clutton-Brock and Sheldon 2010, Festa-Bianchet et al. 2017a). Over the course of a 17-year period, I monitored a sample of radio-marked mountain goats (n = 421) in four separate study areas in coastal Alaska. These field data, along with remote-sensing data resources developed with collaborators (described below), provided the basis for my subsequent PhD research and offered the opportunity to address a suite of research questions.

Drawing upon population ecology theoretical frameworks, in Chapter 3, we investigated intrinsic and extrinsic drivers of mountain goat reproductive performance and life-history trade-offs (Gaillard et al. 2000, Hamel et al. 2010, Festa-Bianchet et al. 2019). Specifically, we examined how variation in summer and winter weather conditions influenced age-specific reproduction, including the extent that performance was affected by costs of previous reproduction. Finally, we developed and implemented a population modeling approach to further quantify how variation in observed summer and winter weather conditions influenced population growth rate – thus providing insight about the relative importance of summer vs winter weather on reproductive demography.

The final components of my PhD research focused on investigating how snow avalanches influence the behavioral and population ecology of mountain goats. Chapter 4 focused on describing spatiotemporal patterns in avalanche-caused mortality and examining whether individual incidence of mortality was related to avalanche vulnerability (i.e. use of avalanche terrain). This involved integration of mountain goat movement and survival monitoring data (421 instrumented individuals, <800,000 GPS locations, 4 study areas) with avalanche hazard indication maps derived using a Rapid Mass Movement Simulations (RAMMS; Christen et al. 2010, Bühler et al. 2022) modeling approach. These investigations enabled understanding of the relative importance of avalanche-caused mortality across study areas and years, what sex- and age-components were most impacted, and whether mortality was directly related to seasonal use patterns of avalanche terrain.

Building off of these results, in Chapter 5 we developed and implemented a population modeling approach designed to simulate, across a range of empirically derived scenarios, the effects of avalanches on mountain goat population growth and recovery time (in cases when impacts elicited population declines). This analyses involved an examination of whether, and under what conditions, avalanche-caused was mortality was additive vs compensatory. In addition, we calculated recurrence intervals of avalanche impacts to provide broader demographic relevance. Specifically, we not only identified statistical extremes but also biologically extreme events (i.e. those taking < 1 mountain goat generation for recovery), thereby further anchoring our results, and the concept of 'extreme events', in an explicit, demographic context (*sensu* Smith 2011b). In sum, these investigations of mountain goat – avalanche relationships are novel and hold potential to advance our understanding of how climate-linked extreme events impact sensitive mountain wildlife populations, and carry important conservation implications.

Chapter 2. Mountain sentinels in a changing world: review and conservation implications of weather and climate effects on mountain goats (*Oreamnos americanus*).

Adapted from: White, K. S., B. Cadsand, S. D. Côté, T. Graves, S. Hamel, R. B. Harris, F. P. Hayes, E. Hood, K. Hurley, T. Jessen, B. Jex, E. Peitzsch, W. Sarmento, H. Schwantje, and J. Berger. 2025. Mountain sentinels in a changing world: review and conservation implications of weather and climate effects on mountain goats (*Oreamnos americanus*). *Global Ecology and Conservation*, e03364. https://www.sciencedirect.com/science/article/pii/S2351989424005687

2.1 Chapter Summary

Climate change is occurring at an accelerated rate in high-elevation alpine and mountain ecosystems. Cold-adapted, mountain species are at risk due to forecasted change and knowledge is needed to respond to current and future conservation challenges. Mountain goats (*Oreamnos americanus*) are an iconic species of North American mountain cultures and landscapes, and due to specialized adaptations for life in cold, mountainous environments they are particularly sensitive to changes in weather and climate. As sentinels of change in alpine ecosystems, the study of mountain goats offers insight into the ecological effects and conservation challenges associated with climate change in these sensitive and biodiverse environments. Here, we synthesize existing knowledge about how climate change is expected to influence environmental conditions experienced by mountain goats and associated mechanistic changes to behavior, nutritional ecology, demography, health, and interspecific interactions. In many instances,

climate change effects are likely to be negative and additive to existing threats (such as human disturbance, hunting, disease, predation) though benefits are expected in some cases. Changes in climate and mountain environments will necessitate re-examination and modification of population monitoring, management, and conservation strategies. Specifically, spatiotemporal (and other) aspects of monitoring and management may need to be adjusted to accommodate emerging and novel conservation challenges. Yet, key data and knowledge gaps remain and should be addressed to advance conservation and decision-making capabilities. For mountain goats and similarly climate-sensitive alpine herbivores, effective conservation will ultimately benefit from collaborations among diverse networks guided by well-planned, strategic visions focused on common ground – namely the resiliency and persistence of culturally and ecologically significant mountain species and the alpine environment they inhabit.

2.2 Introduction

Mountains comprise 25% of the Earth's surface area and, due to an extraordinary diversity of terrain, environmental complexity and ecological niches, host 85% of the world's mammal, avian, and amphibian species (Rahbek et al. 2019). Indeed, mountain regions are considered cradles of global biodiversity, contribute major ecological services, and serve as refuges for imperiled species, yet are also particularly vulnerable to climate change (Immerzeel et al. 2010, Rahbek et al. 2019, Pepin et al. 2022). Similar to polar systems, climate in mountain environments is changing more rapidly than surrounding lowland areas (Pepin et al. 2022). The practical difficulties of study in rugged and remote landscapes, however, has limited our knowledge of mountain ecosystems and associated climate impacts, relative to more accessible ecoregions (Cady et al. 2023). In such context, studying sentinel species can offer an effective means for evaluating climate change impacts and developing conservation strategies. Sentinel species respond quickly and clearly to environmental changes, revealing shifts in climate, ecosystem structure, and function that might otherwise go unnoticed (Hazen et al. 2019), thereby providing insights for conserving complex or hard-to-study ecosystems such as mountain environments.

Cold-adapted montane species, subjected to extreme conditions, have evolved traits suited to narrow biophysical niches, rendering them highly sensitive to climate variation and making them valuable sentinel species for assessing climate impacts (Ray et al. 2013, White et al. 2018). Mountain ungulates, for instance, have evolved specialized morphological, behavioral, and life-history adaptations finely-tuned for living in extreme environments (Schaller 1977, Shackleton 1997, Festa-Bianchet and Côté 2008). Optimization for alpine life, however, entails costs. Specialization predisposes mountain ungulates to heightened sensitivity to environmental change, with climate change and associated stochastic events representing increasing concerns to species viability and persistence (White et al. 2018, Lovari et al. 2020). This is in contrast with generalist species that are typically better adapted to coping with rapidly changing environments (Thuiller et al. 2005, Moritz and Agudo 2013). Thereby, mountain ungulates are an ecologically significant group: in addition to being emblematic of global mountain cultures and landscapes, comprising 32 species distributed across 70 countries (Shackleton 1997), they warrant broad recognition as effective sentinel species.

Moreover, climate-linked prehistoric range constrictions and population extirpations offer a prominent example of sentinel species functionality and add to a broader portfolio of mechanistic responses that provide deeper and more detailed knowledge about environmental change. For example, following the Last Glacial Maximum (26 – 19 thousand years ago; Clark et al. 2009), several cold-adapted species of North American mountains have experienced dramatic recessions of range. Notable exemplars include least weasels (*Mustela nivalis*), pikas (*Ochotona princeps*), yellow-bellied marmots (*Marmota flaviventris*), and mountain goats (*Oreamnos americanus*), all of which experienced northward range constrictions of several hundred kilometers and shifts to higher elevation habitats (Grayson 2011, Hayes and Berger 2023). Mountain goats offer an outstanding example – the range of both the extant form and its extinct relative, Harrington's mountain goat (*O. harringtoni*), originally extended far beyond current distributions deep into Utah and western Texas (US), and farther south into northern Mexico (Mead et al. 1986, 1987, Hayes and Berger 2023).

Mountain goats are an archetypical, climate-sensitive alpine species, exemplified by their tight association with cold, mountain environments and periglacial zones (Figure 2.1)(Chadwick 1983, Hayes and Berger 2023). Distributed across northwestern North America among some of the largest and most geographically diverse mountain ranges worldwide, mountain goats often occur in relatively small, naturally fragmented and demographically vulnerable populations (Hamel et al. 2006, Stowell 2006, Shafer et al. 2012, White et al. 2021a). Indeed, the specialization required to persist in extreme mountain environments (Figure 2.2) characterized by cold temperatures, deep snow, powerful wind, and short growing seasons has led to a conservative reproductive strategy that prioritizes survival relative to reproduction and translates into low capacity for population growth. Such characteristics are common to many organisms that inhabit mountain ecosystems and lead to heightened sensitivity when change occurs outside of adaptive norms, thereby posing challenges in the face of projected environmental change (Antão et al. 2022).

As globally emblematic sentinels of mountain environments, increased knowledge of mountain goats and its climate-sensitive ecology offers key opportunities for understanding the status and fate of mountain ecosystems more broadly. Our aim is thus to synthesize knowledge about how variation in weather and climate affect mountain goats across their native North American distribution, supplementing species-specific information with documented patterns in other alpine ungulates and broader generalized relationships, where appropriate. We principally focus on mountain goat relationships in their native range because of the confounding influence of introduction to non-native range, regarding weather and climate effects. Based on field investigations and quantitative modeling approaches, we assess mechanistic weather and climate-related linkages to key aspects of mountain goat population ecology (Figure 2.3). We structure our understanding about projected climate change impacts in relation to existing conservation issues oriented towards health and environmental threats. In addition, we identify key data and knowledge gaps that should be addressed to advance conservation and decision-making capabilities. Ultimately, we offer guidance for ensuring persistence, resiliency, and sustainability of mountain goats that is broadly applicable to other mountain sentinels and alpine ecosystems.

2.3 Methods

2.3.1 Compilation and synthesis of published research

To assess the aforementioned themes, we compiled and synthesized peer-reviewed literature using the Web of Science publication reference database spanning a period during 1904-2023. Specifically, we conducted a query using the terms "mountain goat" and "*Oreamnos americanus*" (search date: 27 June 2023). All references were manually verified to ensure accuracy, and publication key word terms were standardized to maintain consistency. To identify dominant research themes, we used the network diagraming program VOSviewer (v. 1.16.19) to characterize the relative frequency and relationships among research topic areas (Van Eck and Waltman 2010, 2019). This method employs a modularity-based clustering algorithm based on co-occurrence, co-citation and co-author pairing to identify common themes and positionality among nodes (i.e. principal topics of research) (Waltman et al. 2010). The size and positionality of the nodes is related to the proportional strength of co-occurrence and co-citation (Van Eck and Waltman 2010, 2019). Specifically, we used the LonLin modularity algorithm method to construct the network, constraining minimum cluster size to 5 groups (Waltman et al. 2010, Van Eck and Waltman 2019).

2.3.2 Descriptive characteristics of published studies

We compiled records and metadata from 258 mountain goat studies published in 91 different peer-reviewed journals during 1904 – 2023. Of the 10 native North American ungulates (n = 29,320 studies), mountain goats (n = 258) have the fewest number of publications, with the exception of thinhorn sheep (*Ovis dalli*, n = 200 publication), a species with a much more limited geographic distribution (Appendix A). Among mountain goats, the three most common topics of study were population dynamics, reproduction, and survival (Figure 2.4a). Of the 14 states, provinces, and territories with mountain goats, the most commonly reported study locations were

Alaska, Alberta, and British Columbia, and generally reflected the relative abundance of species across their range (Festa-Bianchet and Côté 2008). Climate, inclusive of snow, summer temperature and climate change topics, had a relatively low representation in published studies (Figure 2.4b). The underrepresentation of climate is likely due to the relatively recent awareness and scientific focus on climate change (Haunschild et al. 2016) combined with the complexity of conducting empirical studies, underscoring the need for increasing our understanding of this subject area.

2.4 Synthetic review

2.4.1 Climate change in western North American mountain environments

Evidence from long-term climate data has led to clear scientific consensus that global climate is changing as a result of human activities (Hock et al. 2019, Lynas et al. 2021). Within this broader context, change is occurring more rapidly in high-elevation alpine and mountain ecosystems relative to the global mean (Diaz et al. 2003, Pepin et al. 2022). The process by which disproportionate effects occur at higher elevation (termed "alpine amplification") is mediated by positive-feedback dynamics driven by increased heat absorption when snow cover and thus albedo (i.e. reflection of solar radiation away from the Earth's surface) are reduced. In addition, changes in atmospheric circulation patterns drive heat-flux poleward; a secondary process that leads to an additive effect in mountain regions at high latitudes (Mountain Research Initiative EDW Working Group 2015, Pepin et al. 2022). As a result, such regions are experiencing a wide range of climate change-related effects that include increased temperatures, changes in the amount and timing of precipitation (both rain and snow), which in turn affect alpine ecosystem productivity (Broadbent et al. 2024), and increasingly frequent extreme weather events such as heat waves or intense rain and snowfall episodes (Shanley et al. 2015, Foord 2016, Musselman et al. 2018, Maxwell et al. 2019, Peeters et al. 2019). Because mountainous terrain has strong, independent effects on weather and climate (i.e. due to orographic lifting, rain-shadow effects, and others), local- and regional-scale variability is pronounced. Future changes in climate will likely vary accordingly, with differing effects at the northern margins of Canadian (Yukon and Northwest Territories) and Alaskan populations in contrast to those at the southern edges of native range in southwestern Montana, central Idaho and the northern Cascade Range (see Figure 2.5, Appendix A). Snow conditions in mountain regions, for example, vary substantially at small spatial scales based on local topographic characteristics that influence wind patterns, temperature, and likelihood of rain versus snow. Given the already high variability of weather patterns at small geographic scales in mountain ecosystems, climate change is likely to exacerbate environmental stochasticity at local scales.

In areas of western North America inhabited by mountain goats, climate change is generally expected to lead to warmer summers and less snowy winters (Figure 2.5), with an increase in extreme weather events such as summer heat waves and greater variability in winter snow conditions such as exceptional snowfall events, increased prevalence of rain-on-snow and freeze/thaw cycles, changing patterns of wind driven deposition, and snowpack structure and stability (Shanley et al. 2015, Foord 2016, Musselman et al. 2018, Peitzsch et al. 2021). In moisture-rich, coastal mountain areas, variability may be particularly pronounced because average winter temperatures are often near the freezing point, so small shifts in temperature can produce large, ecologically-significant changes in snowpack, depending upon whether precipitation falls as rain or snow (Figure 2.5, Appendix A)(Shanley et al. 2015). In colder, drier interior ranges (Fig, 1), changes in winter climate effects may be more incremental, at least in the near-term, because baseline temperatures are further from snow climate tipping points (Figure 2.5, Appendix A). However, sub-freezing winter warming may increase atmospheric water-holding capacity, leading to increased snowfall in such areas (Figure 2.5, Appendix A)(Quante et al. 2021).

2.4.2 Climate-mediated landscape and habitat changes

Mountain goats spend most of the year (October-May) in landscapes dominated by snow and wind; a physical environment that has given rise to specialized morphological and physiological adaptations, behavior, and life-history strategies. Although snow is typically deep (up to 4 m in coastal areas) and restricts mobility in winter, thin and melting snowpacks allow more widespread use of the landscape during the shoulder seasons. Seasonally-warming temperatures initiate melting cycles that continue into late summer at the highest elevations. As snow retreats upward, a dynamic mosaic of melting patches precedes a "green wave" of emergent, highly nutritious vegetation along the margins of the snow (Fox 1991, Bischof et al. 2012), facilitating diverse feeding options in space and time (Pettorelli et al. 2007, Hamel et al. 2009a, 2009b). Snow patches that persist into summer can also act as important resting habitats by allowing mountain goats, and other cold-adapted species, access to cooler habitats and relief from biting insects especially during the hottest periods (Sarmento et al. 2019, Hayes and Berger 2023).

Climate-mediated alterations of winter snowpack and increases in summer temperature influence the quality and availability of forage resources for alpine ungulates (Lenart et al. 2002), as well as the distribution and availability of snow-patch habitats. Warmer spring and summer temperatures accelerate green-up and reduce the time period and spatial variability during which nutritious, early phenological-stage forages are available (Pettorelli et al. 2007, Post et al. 2008); though in some instances earlier green-up can extend the plant growing season leading to beneficial effects (Brambilla et al. 2024). In drier, more marginal areas of the species' distribution, warmer temperatures and earlier-melting snow can instead promote drought-like conditions, shorten overall growing seasons, and/or reduce forage resource productivity, quality, and availability, ultimately leading to impacts on reproductive performance (Stevens 1983, Bailey 1991, Jenkins et al. 2012, Gamon et al. 2013). These conditions may also disrupt the previously predictable spatial pattern of green-up, which could make it more difficult to find nutritious vegetation when available [as documented in deer (*Odocoileus* spp.); Aikens et al. 2020]. For short-distance vertical migrants such as mountain ungulates, however, short-term spatial and altitudinal redistribution to account for unexpected, stochastic shifts in resource availability and environmental conditions is possible and may reduce negative impacts (John et al. 2024). Independent of plant phenology dynamics, temperature can also affect nutritional characteristics. For example, warmer temperatures, leading to faster plant growth and increased lignification of cell walls, result in reduced digestibility of plant tissue and lowered diet quality (Bø and Hjeljord 1991, Weladji et al. 2002). Thus, one effect of warmer summers is an overall decline of forage quality, which, even if small, can have marked effects on animal condition and productivity via multiplier effects (White 1983, McArt et al. 2009). Overall, relationships between climate change, rates of snowmelt, and forage resources are complex, and will likely exert the greatest influence on populations that are food limited or near carrying capacity. Such effects are expected to be most pronounced in marginal habitats, during extreme weather years, and when population densities are high.

Climate change has resulted in geographically extensive and relatively rapid changes in mountain goat habitat. Increasing temperature at high-elevation has facilitated upward advances of sub-alpine shrub and conifer plant communities, resulting in forest encroachment and subsequent shrinkage of forage-abundant alpine meadow habitats (Greenwood and Jump 2014, Dial et al. 2016); though, in some warmer, drier mountain systems, encroachment may also result from fire suppression (Kuramoto and Bliss 1970, Martin 2000). Corresponding upward advancement of alpine plant communities is expected to lag behind thermal suitability due to biogeochemical constraints and slow soil development at the highest elevations (Hagedorn et al. 2019), further exacerbating tree-line encroachment effects on alpine meadow habitats. Ultimately, due to the conical shape of most western North American mountains, the areal extent of alpine habitat and consequent carrying capacity of mountain goats in native ranges is expected to change and, in many places, decline over the long-term (Figure 2.6)(Elsen and Tingley 2015, White et al. 2018, Gude et al. 2022). Thus, currently unoccupied alpine range is unlikely to provide adequate suitable habitat for mountain goats under climate change. In addition, the loss of important alpine habitat may, in some places, restrict essential corridors for connectivity between habitat patches or mountain goat populations given the species reluctance to move across low elevation basins (i.e. Harris et al. 2022). This may cause further long-term detrimental effects on landscape, genetic, and demographic connectivity among mountain goat populations. Shafer et al. (2012), for example, found that local-scale genetic differentiation of mountain goats in coastal Alaska was best predicted by summer habitat connectivity, suggesting that reduction in alpine habitat from forest encroachment is likely to restrict large-scale movement and dispersal. Indeed, extant patterns of mountain goat population genetic structure are strongly influenced by geographical barriers to movement such as deglaciated fiords, icefields, unsuitable low elevation habitats (including forest and non-forest types), and human development (Shafer et al. 2011, Parks et al. 2015, White et al. 2021a, Young et al. 2022).

In drier, interior areas, warming summer temperatures increase the frequency, intensity, and geographic extent of wildfires. Such events can have direct and indirect effects on wildlife including mountain goats (Johnson 1983, Nietvelt et al. 2018, Sanderfoot et al. 2021). Smoke and air pollution, for example, is associated with wildfires and impacts respiratory health and physiology (Sanderfoot et al. 2021). In addition, wildfires can also destroy important forested winter range habitats and have detrimental effects on local and regional mountain goat populations. In southwestern British Columbia, for example, mountain goat winter ranges that were highly impacted by fire were 75% less likely to be occupied and contained 80% fewer mountain goats than comparable unburned winter ranges (Nietvelt et al. 2018). Although wildfire is rare and not a pronounced threat in wet, temperate mountain goat ranges, it can be a significant factor in drier, wildfire-prone parts of their range, especially when fires reduce snow intercepting forest canopy and lead to deeper winter snowpack (Johnson 1983, Nietvelt et al. 2018). However, less destructive, low-intensity wildfires or prescribed burns may, in some circumstances, have beneficial effects by promoting productive understory plant communities. These communities have been documented to be used frequently by goats (Brandborg 1955, Foster and Rahs 1985, Poole et al. 2010), and in some cases facilitated population expansions (Johnson 1983, Houston et al. 1994).

2.4.3 Responses to variation in summer weather

Understanding how climate change affects population ecology of mountain goats, or other high elevation sentinels, is challenging because it requires long-term studies (i.e. climate is generally defined as weather patterns over a >30 year period). Thus, much of our knowledge about how climate may affect mountain goats is derived from shorter-term studies focused on how variation in weather influences behavior and population ecology, including statistically relating individual- and population-level processes to seasonal weather conditions across relatively large geographies. Models derived from such relationships can ultimately be used to predict how changes may occur across longer time scales to infer future climate change effects on mountain goat populations across a range of plausible scenarios (*sensu* White et al. 2018).

Weather and climate are expected to affect mountain goats in a seasonally-integrated fashion (Parker et al. 2009). For example, during the relatively short plant growing season, mountain goats accumulate substantial body fat and protein reserves, with body mass estimated to increase up to 38% between early-June and late-September (Côté and Festa-Bianchet 2003, Festa-Bianchet and Côté 2008). Such resources are needed to nutritionally finance demands of the long winter season, a period when individuals are in a negative energy balance. Most mountain goat mortalities occur during late-winter or early-spring when animals are most nutritionally stressed, with individuals in better body condition expected to have a higher likelihood of survival (White et al. 2011, Harris et al. 2020). Consequently, even though malnutrition-related mortalities most commonly occur in late-winter, deaths can be directly related to the previous summer's thermal and foraging conditions (White et al. 2011, Harris et al. 2024).

The nutritional and physiological state of mountain goats are influenced by morphological adaptations tuned to long-term climate patterns but may be subject to detrimental impacts when rapid change or stochastic perturbations occur. For example, mountain goats are extraordinarily well-adapted to living in the cold environmental conditions that characterize the mountainous environments they inhabit. The principal morphological adaptation to cold temperatures is a long, highly insulative white coat that begins to molt during early-summer; an event that is typically well-timed for providing heat relief during warm summer days (Déry et al. 2019, Nowak et al. 2020). Molting phenology is sex- and age-specific, and some individuals (particularly parturient females) often retain winter coats into mid-summer. Although mountain goats can adjust molt timing in response to plant phenology (Déry et al. 2019), imperfectly-timed molting associated with extreme events or short-term weather variability may predispose them to thermal stress. For example, early-summer heat waves that occur when individuals still retain thick winter coats may heighten thermal stress. This dynamic will likely be exacerbated by climate change, especially if increasing weather variability leads to more incidences of temporal mismatch and attendant deleterious effects on mountain goat thermal dynamics.

Challenges associated with increasing temperature can be partially ameliorated by behavioral adjustments. In coastal Alaska, mountain goats reduce activity during the warmest parts of the day (Frederick 2015, Michaud et al. 2024) and are also less active during warm, clear days than cool, rainy days (Fox 1978). Mountain goats also alter habitat selection in response to summer temperature, preferentially using cooler habitats during warm periods. To escape heat, mountain goats may shift to cooler, higher-elevation sites (Fox 1978, Frederick 2015, Hayes 2023, Michaud et al. 2024). In some interior areas, however, they use lower-elevation subalpine forest, which provide shady habitats, to mitigate thermal stress (Michaud et al. 2024). Additionally, use of remnant summer snow patches or areas adjacent to glaciers offer thermal refugia and insect relief during the warmest days (Sarmento et al. 2019, Hayes and Berger 2023).

Behavioral strategies to mitigate thermal stressors, whether direct (i.e. heat) or indirect (i.e. insects), may incur nutritional costs or increased predation-risk. Shifting from nutritionally-productive alpine meadow habitats to more forage-depauperate high-elevation rocky sites may reduce nutritional intake rates, whereas shifting to subalpine forest sites may incur increased risk of predation from stalking predators that rely on concealment (Michaud et al. 2024), such as cougars (*Felis concolor*) whose range extensively overlaps that of mountain goats. Specifically, mountain goat reliance on escape terrain to reduce risk of predation (Sarmento and Berger 2020) may mandate suboptimal trade-offs when leaving the safety of cliffs to access cool microclimates that increase predation-risk (Hayes 2023). Although these trade-offs in selection are expected to be region- and even population-specific, they are likely to have negative consequences for mountain goat populations.

Temperature related effects on plant phenology during the spring green-up period have direct effects on availability of high-quality food which, in turn, affects animal performance, including reproductive success (Côté and Festa-Bianchet 2001, Pettorelli et al. 2007, Hamel et al. 2009a, 2009b). Because lactation is energetically costly, timing parturition to coincide with emergent, early phenological-stage forage resources impacts the provisioning and survival of offspring. If mountain goats are unable to adjust parturition timing to accommodate shifts toward more variable and, possibly, earlier and more abbreviated green-up, as expected with climate change, the temporal mismatch may negatively affect reproductive performance [as documented for caribou (*Rangifer tarandus groenlandicus*) in the arctic; Post and Forchhammer 2008]. Yet, limited information is available about temporal coupling of green-up and reproductive performance in mountain goats and further studies are needed to more clearly understand relationships (Table 2.1).

In sum, behavioral trade-offs and alteration of summer forage nutritional dynamics associated with increasing summer temperature are expected to have negative consequences for mountain goats from both nutritional and demographic perspectives. Indeed, long-term research conducted in multiple study areas across coastal Alaska indicated that increasing summer temperatures were correlated with reduced mountain goat annual survival (White et al. 2011) and is expected to translate into long-term reductions in population growth under a range of different climate change scenarios (White et al. 2018). Recent analyses of long-term mountain goat survival data in western Washington revealed similar negative relationships between spring/summer temperatures (and also precipitation) and adult survival, suggesting similar climate change implications at the population level (Harris et al. 2024). Nonetheless, further understanding of spatial variability in demographic responses is needed (Table 2.1), especially for interior populations, given recent studies suggesting behavioral responses to summer thermal stress differ between coastal and some interior areas (e.g. Hayes 2023, Hayes and Berger 2023, Michaud et al. 2024).

2.4.4 Responses to variation in winter weather

Winter snow depth exerts strong regulatory effects on the nutritional and energetic budget of mountain goats. Not only does snow reduce availability of winter forages through burial (Fox 1983, White et al. 2009), it increases energetic costs of locomotion and restricts movement (Dailey and Hobbs 1989, Poole et al. 2009, Richard et al. 2014, Shakeri et al. 2021). As a result, both adult and juvenile survival decline in years with high snowfall (Hamel et al. 2010, White et al. 2011, Théoret-Gosselin et al. 2015, Harris et al. 2024). During mild conditions, nutritional and locomotory constraints are relaxed leading to higher survival, and interactive effects on reproduction. Delayed or reduced accumulation of snow in high-elevation areas during autumn can be beneficial by extending the period when forage is readily accessible (as documented in deer; Hurley et al. 2014, Ortega et al. 2024), with comparable benefits also occurring in spring when low snow packs melt earlier and likewise extend the growing season (Brambilla et al. 2024). During the late-autumn breeding season, while traveling over wide areas in search of mates and engaging in rut related behavior, males rapidly diminish nutritional stores necessary for overwinter survival (Pelletier et al. 2009, Shakeri et al. 2021), and may especially benefit from a lengthened snow-free season. Such relationships, however, may be complicated by dynamic interactions between snow accumulation during winter and snow patch retention the following summer. Because snow patches can provide thermal refugia and ectoparasite avoidance services during summer, in some instances, winter snow may indirectly play a key role in ameliorating periods of summer heat stress (Sarmento et al. 2019, Hayes and Berger 2023).

Structural characteristics of the snowpack, in addition to total snow depth and cover, can exert strong effects on populations via direct physical pathways. Avalanches, for instance, constitute a major source of mountain goat deaths, comprising 23-65% of the mortalities in coastal Alaska (White et al. 2024b). Translated into direct demographic impacts, 8% of individuals in such populations die annually due to avalanches, on average, with up to 22% of a population being killed in a "worst case scenario" year (White et al. 2024b). The implications of avalanche mortalities for often small, isolated mountain goat populations can be significant, given the species low reproductive rates, slow life-history strategy and resultant heightened sensitivity to negative perturbations (Festa-Bianchet and Côté 2008, Festa-Bianchet et al. 2019). Documented growth rates among native populations, for instance, typically range between 1-4% (Hamel et al. 2006, Rice and Gay 2010, White et al. 2021a), suggesting high levels of avalanche mortality exert substantial negative impacts on population trajectories. Moreover, unlike other causes of death such as predation and malnutrition that may selectively remove immature and old animals from the population, animals killed by avalanches largely comprise a random subset of the entire population (White et al. 2024b). As a result, avalanche mortalities include a significant fraction of prime-aged mountain goats of high reproductive value and likely exacerbates impacts on populations (White et al. 2024b).

Projected declines in snowfall are expected to generally benefit mountain goat populations through nutritional and energetic pathways. However, positive effects of less severe winters may be offset by broader warming trends. For example, demographic simulations in coastal Alaska suggest reduced snowfall is likely to be outweighed by negative effects of increasing summer temperature (White et al. 2018). This occurs because the rate-of-change and negative effects of summer temperature will likely be greater than the corresponding positive effects of reduced winter snowfall – i.e. over time, snowfall effects on energetics and nutritional physiology diminish and eventually become negligible. Furthermore, reduced snowfall does not necessarily translate to lowered avalanche risk given the multiple pathways through which avalanches can occur (McClung and Schaerer 2006). Episodic winter warming, for instance, alters the structure and stability of the snowpack and can increase the likelihood of avalanches (Schweizer et al. 2003). While questions remain about how climate change will alter avalanche risk, existing evidence suggest changes in avalanche occurrence will vary geographically and track projected increases in weather variability, particularly extreme events (Ballesteros-Cánovas et al. 2018, Giacona et al. 2021, Peitzsch et al. 2021).

2.4.5 Health

Species-specific understanding of climate impacts on mountain goat health is limited and knowledge gaps are prevalent. Here, we summarize knowledge about mountain goat health concerns in relation to climate change, supplementing this information with documented patterns in other alpine ungulates and broader generalized relationships. Such synthesis offers insight about projected changes and guidance for future research and monitoring.

Host-parasite relationships and other components of health (*sensu* Stephen 2022) are directly and indirectly affected by weather, nutritional ecology, and distribution. Animals in robust nutritional condition are less apt to incur physiological stress and may have stronger immune responses to pathogens and parasites. As a species adapted to cooler climates, mountain goat populations distributed across remote, isolated areas will likely experience increased exposure to expanding infectious agents and parasites (particularly vector-borne pathogens and temperature-dependent nematode parasites) as temperatures warm (Kutz et al. 2005, 2013, Carlsson et al. 2012, Aleuy and Kutz 2020). Such impacts can reduce individual fitness (as noted among other cold-adapted species; Kutz et al. 2017, Aleuy et al. 2018, Cohen et al. 2020). In contrast to other mountain ungulates, current evidence suggests that mountain goats have relatively limited exposure to many infectious diseases present in other alpine ungulates, including wild sheep (*Ovis canadensis, O. dalli*), at least in the northwestern portion of the range (Lowrey et al. 2018). However, in an isolated Nevada mountain range, outbreaks of polymicrobial respiratory disease in mountain goats have been documented (Blanchong et al. 2018, Wolff et al. 2019) and highlight the potential of such emerging threats, especially in areas with sympatric bighorn sheep or domestic animals. Appropriately, the risk of respiratory disease outbreaks is already considered a central management concern in some areas (Gude et al. 2022). Yet, the extent to which mountain goat populations, with limited historic exposure to disease and parasites, are vulnerable to climate-mediated expansion of novel infectious organisms (and their vectors) is not fully understood and represents an important conservation and monitoring consideration.

Changes in the availability and quality of summer forage, alteration of foraging dynamics, as well as winter severity and snow conditions can negatively impact individual body fat and protein reserves (see above). Poor body condition may lead to individuals being predisposed to, and deleteriously affected by, secondary factors such as predators (including humans; Frid and Dill 2002), disturbance (i.e. endocrine stress response effects on reproduction; Dulude-de Broin et al. 2020), insect harassment, and, importantly, pathogen and parasite exposure. For example, *Parapoxvirus* (contagious ecthyma) occurs in mountain goats (Samuel et al. 1975, Tryland et al. 2018), and has been extensively investigated in closely related domestic goats and sheep (Nandi et al. 2011). Studies suggest that responses are most acute among naïve, stressed animals, such as young animals, which are more severely affected than older, healthier individuals (Samuel et al. 1975, Nandi et al. 2011). Reduced nutritional condition and subsequent physiological stress responses can also decrease neonatal quality and survival (Douhard et al. 2018), and reproductive rates through reduced conception, maintenance of pregnancies and maternal care of neonates (Barboza and Parker 2008, Monteith et al. 2013, Stephenson et al. 2020a). In addition, the innate and acquired immune system responses of animals can be affected, putting them at a higher risk of acquiring enzootic or novel infections (Acevedo-Whitehouse and Duffus 2009, Hing et al. 2016). Some infections can compromise or alter digestive system function directly or through modifications of the gut microbiome leading to further nutritional stress and, ultimately, negative impacts to reproduction and survival (Acevedo-Whitehouse and Duffus 2009). Sustained physiological stress caused by longer-term environmental stressors and poor body condition can also cause increased shedding of infectious agents and severity of clinical symptoms that can lead to higher rates of disease prevalence and morbidity (Hing et al. 2016). Such conditions can potentially shift formerly stable host-parasite equilibriums to become more pathogenic (Hing et al. 2016).

Predicting the impact of environmental stressors on immunity and infection rates is complex because effects can interact or be additive, accumulate over time and manifest at multiple levels (Acevedo-Whitehouse and Duffus 2009). Further, the timing and duration of the stressor, as well as physiological differences across individuals, can determine whether a stressor will result in enhancement or suppression of the immune system (Martin 2009). Recently developed methods such as the measurement of microbiomes and gene-based techniques (i.e. allowing for estimation of gene transmission rates) will clearly improve our understanding of disease susceptibility (Bowen et al. 2020, 2022). Including such advancements in baseline monitoring programs will enhance monitoring of population health and allow linkages to climate change (Bowen et al. 2020, 2022).

2.4.6 The potential for climate-induced interspecific interactions

Changes in weather and climate may influence complex multi-trophic interactions and can be especially acute in heavily managed ecosystems. For example, human modification of landscapes combined with climate variability has imposed profound impacts on interspecific relationships and community ecology of large mammals in western North America (Serrouya et al. 2021, DeMars et al. 2023). Large-scale logging in British Columbia increased moose (*Alces alces americanus*) abundance and subsequently wolves (*Canis lupus*) to the detriment of spatially-widespread but locally rare caribou. Such instances of apparent competition, where an abundant prey species numerically subsidize generalist predators and result in disproportionately negative impacts on relatively rare, secondary prey species, can also apply to mountain ungulates like Dall's sheep (*Ovis d. dalli*; Arthur and Prugh 2010) and Sierra Nevada bighorn sheep (*Ovis c. sierrae;* Johnson et al. 2013). Mountain goats are likely to be similarly vulnerable given their comparable ecological position, relatively small population sizes, and sensitivity to stochastic predation events (i.e. Dulude-de Broin et al. 2020). Such relationships may be accentuated when climate conditions exert strong effects on the population ecology of predators, such as wolves (Mahoney et al. 2020), or coincide with the colonization of novel predators such as cougars

(Knopff et al. 2014). Mountain goat health may also be indirectly affected by climate change through predator-prey apparent-competition pathways, if species such as moose, elk (*Cervus elaphus canadensis*), and deer increase in abundance or naturally expand their range into mountain goat habitat. Increased sympatry with felids may also increase exposure to the intracellular parasite *Toxoplasma gondii.* The life cycle of *T. gondii* involves a wild or domestic felid definitive host with infection of intermediate mammalian hosts, such as wild and domestic ungulates, being associated with abortion and neonatal mortality (as documented in bighorn sheep; Fisk et al. 2023).

2.5 Conclusions: mountain sentinels in a changing alpine world

2.5.1 Cold-adapted, mountain species as a conservation model

An ice age relic of modern-day Pleistocene landscapes, mountain goats are sentinels of change in alpine ecosystems and reflective of expected challenges faced by other cold-adapted, alpine species with sensitivities to shifts in weather and climate. Their adaptation to harsh mountain conditions has led to a conservative reproductive strategy that prioritizes survival relative to reproduction, resulting in low population growth. This specialization, common to organisms inhabiting mountain ecosystems, makes them highly sensitive to climate shifts occurring outside of adaptive norms (Figure 2.7), often leading to population declines and slow rates of recovery. The study of mountain goats therefore offers a window into the status and, perhaps, fate of increasingly imperiled alpine ecosystems. Importantly, the central ecological position of mountain goats fosters insights about climate-linked bottom-up (i.e. plant community ecology) and top-down (i.e. predator and scavenger dynamics) processes in alpine ecosystems. As a sentinel species, mountain goats are also deeply regarded among human cultures, which by extension facilitates conservation attention and investment that can broadly benefit alpine environments. Thus, the continued study and monitoring of mountain goats can play a key role in advancing understanding of an array of alpine species assemblages and ecosystem processes that are experiencing disproportionately rapid changes in climate.

2.5.2 Conservation challenges, mitigation, and adaptation strategies.

Our knowledge of the ecology and climate-linked relationships of mountain goats, and other cold-adapted alpine species, is growing and aids our ability to refine conservation strategies, yet unresolved questions and challenges remain. Projected changes in climate are likely to have short- and long-term effects on key biological events such as breeding, parturition, altitudinal migration and seasonal use of habitats. Changes in plant phenology, summer growing-season length, and winter severity and duration will affect population productivity and abundance. Collectively, such change may result in habitat selection and distributional shifts, patterns that may require revising delineation and protection of critical habitats from resource extraction and development activities. Likewise, reevaluation and adjustment of timing windows, during which key habitats must be protected from any disturbance, is also needed. For example, if parturition dates or winter-range residency periods shift in response to climate change, then timing windows currently used for conservation in management contexts may need to be adjusted accordingly. Increases in cumulative stressors may also increase the value of protecting certain populations from disturbance that could previously sustain some level of impact. Ultimately, distributional shifts may also involve crossing jurisdictional boundaries, resulting in changing management and conservation implications and responsibilities (John and Post 2022).

Mountain goats and other alpine ungulates have been utilized for human subsistence purposes for millennia (Rofkar 2014, Yravedra and Cobo-Sánchez 2015, Greening (La'goot) 2024), with hunting continuing today in traditional subsistence and modernized forms. In many remote areas, hunting represents the sole direct human impact on the species and thus the principal management lever for mitigating deleterious change. Consequently, in cases where mountain goat populations decline, or become more variable, in response to long-term trends or greater stochasticity in short-term weather patterns, harvest managers may need to increasingly anticipate changing hunting season timing and quotas accordingly. Due to multiple factors, mountain goat harvest is already not sustainable or has been curtailed in some parts of their range historically (Hamel et al. 2006, McDonough and Selinger 2008, Rice and Gay 2010, DeCesare and Smith 2018, White et al. 2021a), a situation likely to become more common given additive effects of climate change. Ultimately, climate change may result in enhanced sensitivity to existing anthropogenic impacts and reduced resilience, likely requiring more conservative management to assure population viability or, in cases where appropriate, sustainable harvest.

Mitigating climate change impacts is challenging but may occur at large and small scales. At global or national scales, policies focused on minimizing human contributions to climate change are likely to be beneficial to mountain goats by reducing change in the environmental conditions to which they are adapted. At local scales, strategic efforts to minimize demographic impacts to populations and habitats will help improve resilience and buffer negative effects of climate change. Protection of biologically critical habitats from industrial impacts (e.g. logging, mining, commercial activities) and excessive human disturbance will be increasingly beneficial (Northern Wild Sheep and Goat Council 2020). Efforts to reduce high intensity wildfires may aid in retaining integrity of certain winter range habitats in relatively dry, wildfire-prone areas, such as southwestern British Columbia (Nietvelt et al. 2018).

Strategies considered to buttress vulnerable or declining populations have included mountain goat introduction (into suitable habitats outside of their historical range), augmentation (where populations are small but extant and threats can be mitigated), and reintroduction (where native populations have become extirpated). Historically, introductions have been widely implemented (Hurley and Clark 2006, Paul 2009) but can yield unintended consequences including impacts to naïve, endemic vegetation (Houston et al. 1994, Happe et al. 2020), competition with native ungulates (Flesch et al. 2016), and increased potential for disease transport and transmission (Wolff et al. 2014, 2016). As a consequence, implementation of such strategies has been controversial given differing philosophies about assisted migration and ecological impacts (Hellmann et al. 2008, Harris et al. 2020, Hayes and Berger 2024). Augmentation and reintroduction, on the other hand, often benefit from widespread societal support given the prospect of ecological restoration. Although reintroductions of mountain ungulates can effectively contribute to and restore biodiversity (Rivieccio et al. 2022), they can also lead to unintended consequences on local ecological communities by increasing competition with other vulnerable populations (Lovari et al. 2014) or through transmission of emerging diseases or parasites (Kock et al. 2010). Moreover, mountain goat translocations involve risks of increased mortality (Myatt et al. 2010, Harris et al. 2024) and establishment success is variable (Harris et al. 2020). For example, less than 50% of past mountain goat reintroduction and augmentation programs into native habitats have been successful (Harris and Steele 2014), and, if not implemented appropriately, augmentation may lead to deleterious effects on extant mountain goat populations. Yet, in some instances, appropriately implemented translocations may offer a means for accomplishing management objectives (Gude et al. 2022, Hayes and Berger 2024). Regardless of the strategy used, individuals moved to new areas remain susceptible to the same climate-related stresses as residents (Harris et al. 2024).

2.5.3 Information needs and research gaps

Substantial progress has been made to advance our understanding of mountain goats across a broad array of climate-relevant ecological topics. Yet, due to the difficulty of conducting studies in mountain environments, the species remains among the least studied and monitored large mammals in North America (Figure A1). Increasing our understanding of how climate change and variability impact mountain goat populations across their full range is needed to effectively address emerging conservation challenges. To this end, identification of key information needs and research gaps (Table 2.1) represents an important step for advancing conservation capabilities.

To fully understand the dynamics of how mountain goats are influenced by weather and climate change, further knowledge is required at small-scales that utilize mechanistic frameworks, as well as at larger scales to document broader, species-wide patterns. Such work will enable more accurate projection of how populations may be affected at different management and conservation scales (e.g. local, state/provincial, federal). Long-term, intensive monitoring across a representative array of sites holds great potential for mechanistically relating climate conditions to demographic and other ecological responses (Festa-Bianchet et al. 2017b, Festa-Bianchet et al. 2019). Across broader domains, expansion of the spatial extent and temporal frequency of monitoring can provide an improved scientific basis for documenting change and developing appropriate conservation and management strategies. Within this context, explicitly integrating Indigenous and local knowledge, as well as contemporary monitoring, into long-term frameworks represents a key element of comprehensive assessments (Jessen et al. 2022). Such data may extend historical baselines, fill monitoring gaps, and stimulate novel hypotheses. Ultimately, more extensive, updated approaches are needed to utilize and expand existing knowledge and data resources to assess future ecological scenarios and support decision analyses to optimize monitoring strategies (i.e. Gude et al. 2022).

Improved characterization of the physical drivers of population dynamics and associated ecological covariates also represents important considerations regarding monitoring. Specifically, more emphasis is needed on characterizing weather and snow conditions at finer spatiotemporal scales, particularly in sparsely sampled high elevation areas (Reinking et al. 2022). Across broader spatiotemporal scales (typically > 4 km^2), remote sensing data are increasingly available and well suited for monitoring short- and long-term changes in weather and climate. In addition, standardized characterization of plant phenology, forage quality and availability, snow ablation patterns and winter snowpack characteristics (i.e. rain-on-snow events, persistent weak layers) are informative monitoring metrics (Berman et al. 2020, Reinking et al. 2022). Such data can enable accurate assessment of bottom-up influences of weather and nutrition on mountain goat population performance. Longer-time horizon monitoring such as changes in shrubline – tree-line ecotones, habitat composition and distribution likewise represent important monitoring considerations. Collection and analysis of data across broad, regional- and range-wide extents is particularly crucial for understanding population responses across the full continuum of species-wide conditions.

2.5.4 On sentinel species and conservation effectiveness

Mountain goats persist in extreme physical environments. They invoke strong cultural fascination and appreciation and have a deep-rooted history with Indigenous peoples throughout their range (Rofkar 2014, Jessen et al. 2022, Greening (La'goot) 2024). Ecologically, they illuminate the narrow margin by which alpine species contend for survival in environments experiencing rapid changes in climate. Indeed, mountain goats are sentinels of change in mountain ecosystems, and given the sensitivity with which small changes at the margin of existence can translate into large effects, uncertainty about the future viability of mountain goats and other sensitive alpine species is deserving of broader attention.

Successful conservation requires effective communication at multiple levels, including the general public, governmental and non-governmental entities, and the scientific community. Nested within this approach, and highlighted here, is meaningful communication with Indigenous communities that hold deep insights having maintained relationships with mountain goats and their environment for millennia (Rofkar 2014, Greening (La'goot) 2024) – relationships that may be jeopardized by climate change. For example, Jessen et al. (2022) showed that longstanding relationships between humans and mountain goats on the central coast of British Columbia are at risk due to climate change, based on historical observations coupled with scientific data. Multi-faceted communication strategies, and in some cases co-management authority among government bodies and agencies, is critical to facilitate sharing of reliable ecological knowledge and biocultural wisdom to all groups, so that appropriate strategies can be devised that improve conservation outcomes. Indeed, wide-reaching and major conservation issues such as climate change demand collaborations among diverse networks guided by well-planned, strategic visions focused on common ground – namely the resiliency and persistence of sentinel mountain species and the environments in which they inhabit.

Table 2.1 Key information needs and research gaps identified for advancing our understanding of climate change effects on mountain goats. Topics were identified by an expert panel comprised of mountain goat research and management specialists. Participation and contributions were coordinated by the Northern Wild Sheep and Goat Council – the professional society of North American mountain ungulate biologists.

Subject	Key information needs and research gaps
Weather and climate	• Acquisition of finer resolution weather and climate data at the individual mountain goat and population-level scales. • Improved capability to characterize the frequency and spatial extent of rain-on-snow events. • Improved capability for understanding, characterizing and predicting how weather events influence snow-pack stability and avalanche risk. • Improved understanding of extreme weather events, including spatiotemporal prevalence as well as impacts on mountain goats and their habitats.
Habitat ecology	• Improved understanding of how fire influences mountain goat habitat, including specific impacts of burn severity on forested winter range, relationships between the current and historic role of fire in subalpine zones and treeline encroachment, and efficacy of management tools such as prescribed burning and mechanical removal for maintaining or restoring habitat integrity. • Improved spatiotemporal understanding about how water availability, including persistent snow, influences alpine forage nutritional characteristics (including secondary plant compound concentration) and ultimately mountain goat movement, habitat selection, and site occupancy. • Expansion of knowledge about spatiotemporal variation in alpine plant phenology, and how it influences plant growth, biomass, and nutritional composition of key forage species. Fine-scale experimental studies combined with larger-scale (remote-sensing) long-term monitoring are well suited for addressing these needs.
Physiology and health	• Assess disease/parasite distribution, timing, prevalence, impacts on mountain goat health (including pathogens and impacts of increases of biting flies in the alpine) and associated projected changes in risk. • Improved understanding about how increased environmental stress, expected with climate change, may impact individual- and population-level health and immunity/resistance to disease and/or parasites • Detailed understanding of thermal stress physiology, thresholds, and behavioral responses.
Population ecology and behavior	• Improved mechanistic understanding of weather and climate effects on mountain goat behavior and population ecology including growth, reproduction, and adult and neonate survival - in both coastal and interior systems. • Improved understanding of spatiotemporal variability and importance of avalanches as a cause of climate-linked winter mortality and the implications on population dynamics, but also whether avalanche habitats can be beneficial and preferentially used during non-winter months. • Comprehensive understanding of how weather- and climate-linked effects vary spatially and determination of regions/populations that are "winners vs losers" from climate change.

	• Improved understanding of weather and climate interactions with predation risk from apparent competition and the effects of range expansions of novel predators (e.g., cougar), including impacts of exploitative and interference competition and also how mismatched white camouflage in landscapes lacking snow influences predation-risk. • Increased efforts to conduct comparative and standardized studies, especially long-term studies involving marked animals, across diverse geographies to improve understanding of spatial and ecotypic variability in demography and population performance. • Increased spatiotemporal understanding of how landscape, demographic, and genetic connectivity are important to persistence, sustainability, and resiliency of populations.
Management	• Assessing climate change influences on mountain goat distribution in relation to management boundaries. Mountain goats may, at times, be managed (i.e. harvest quotas) at small spatial scales (sub-population level) and distributional shifts may necessitate re-evaluation of management boundaries and area-specific sustainable harvest strategies. • Development of robustly parameterized population models, which account for weather- and climate-linked effects on vital rates, for examining outcomes of management scenarios. • Improved understanding of optimal management strategies that achieve species/ecosystem objectives, at different spatiotemporal scales in relation to projected changes in weather and climate. Re-evaluating the effectiveness of monitoring approaches may be necessary to ensure objectives can be appropriately evaluated, given projected change.

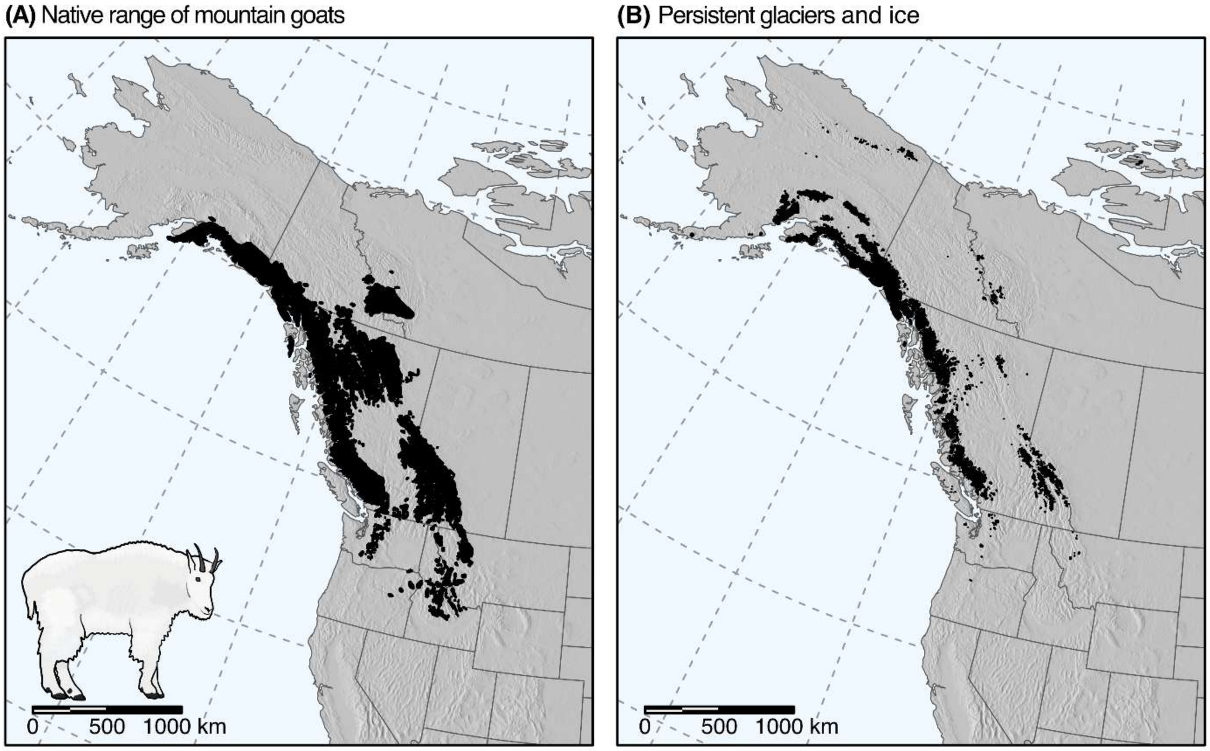

Figure 2.1. (A) The native distribution of mountain goats (*Oreamnos americanus*)(Mountain Goat Management Team 2010) and (B) persistent glaciers and ice in western North America (B) (adapted with permission from Hayes 2023).

Figure 2.2. Morphological, behavioral and ecological responses of mountain goats in relation to climate and related phenomena. (A) male mountain goat in thick, late-winter pelage, near Juneau Icefield, Alaska; (B) mountain goats sheltering in deep snow following an extreme snowfall event that deposited 2.4 m of snow over 6 days, near Porcupine Mountain, Alaska; (C) female mountain goat in early-autumn, Berners Bay, Alaska; (D) mountain goats seeking thermal relief by bedding on a snow patch in summer, Glacier NP, Montana; (E) mountain goat in relatively thin summer pelage bedded on a snow patch with few insects visible, Glacier NP, Montana; (F) mountain goat nursery group in early-summer with highly nutritious emergent vegetation (*Carex macrochaeta*) in the foreground, near Herbert Glacier, Alaska.

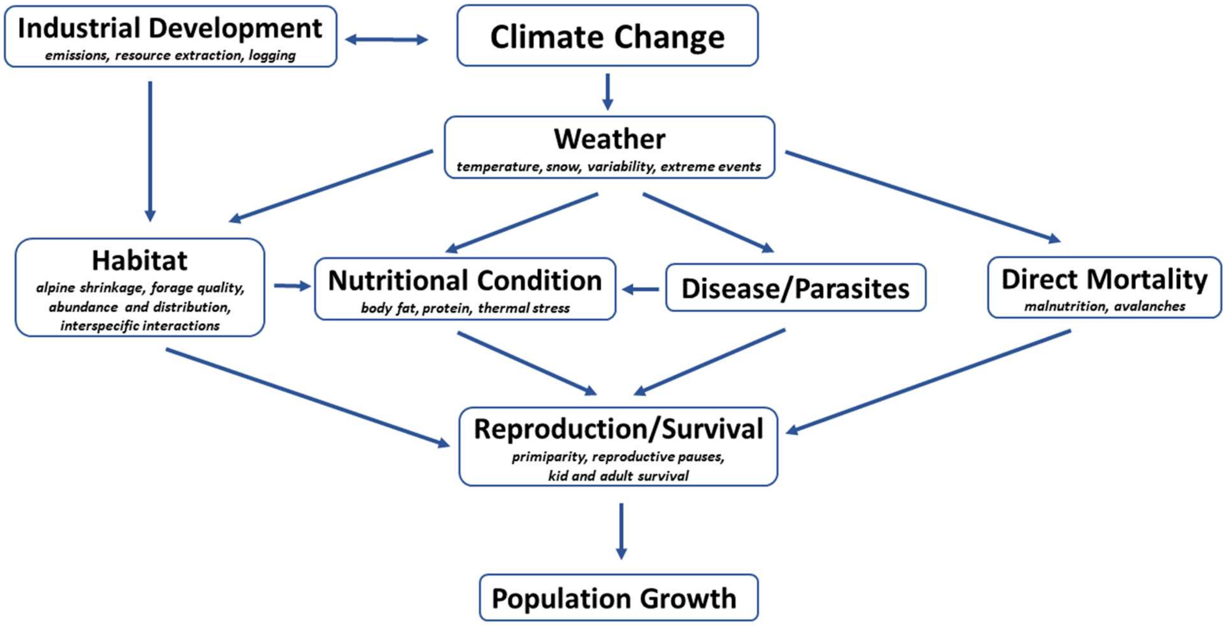

Figure 2.3. Schematic of relationships between climate change and other factors influencing mountain goat population ecology.

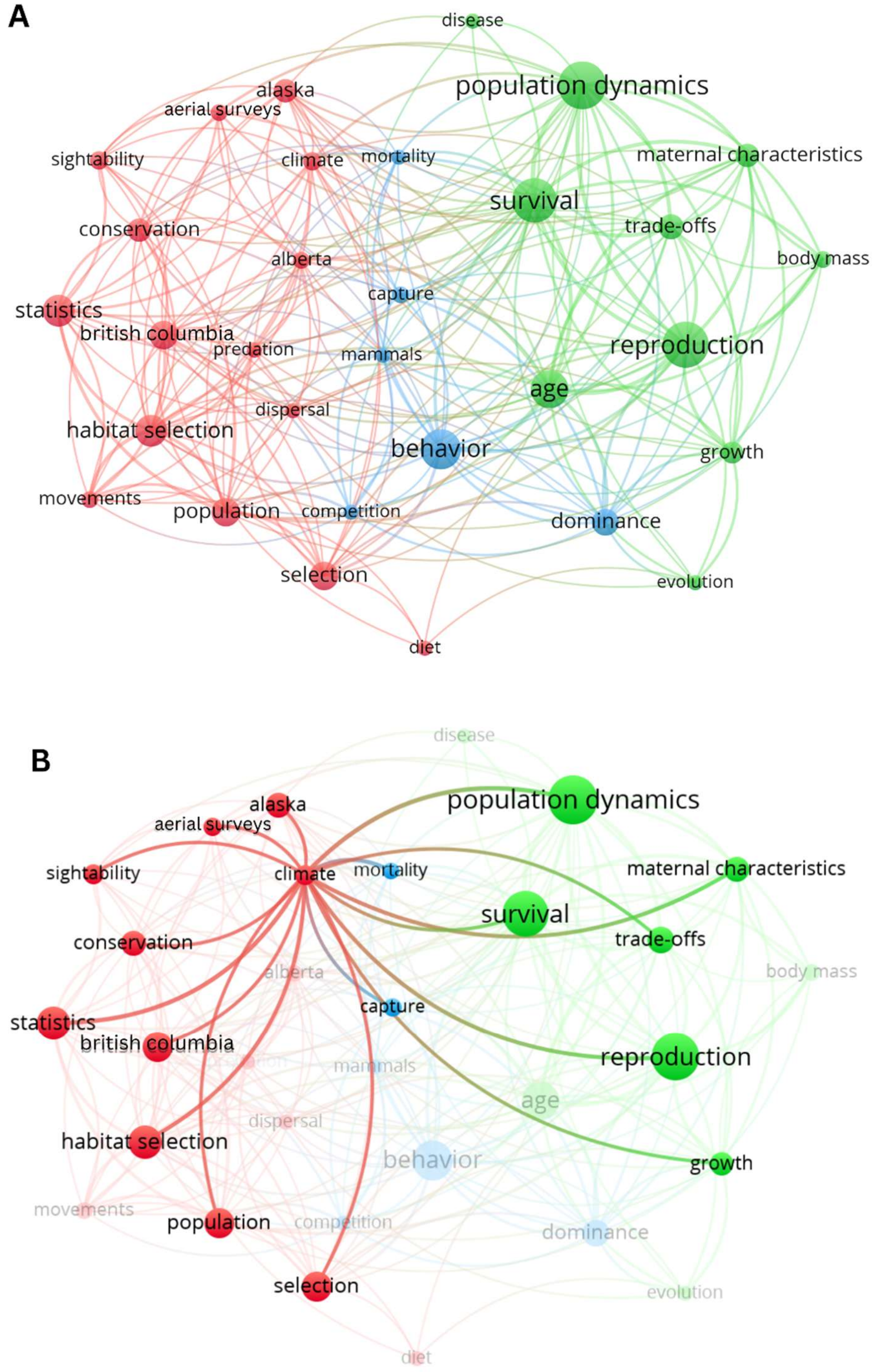

Figure 2.4. Network diagram describing (A) relative proportion and connections between published mountain goat research studies during 1904 – 2023 (n = 258), and (B) relationship linkages between climate and other topic areas. Publications were compiled using a Web of Science literature query using the terms “mountain goat” and “*Oreamnos americanus*” (27 June 2023).

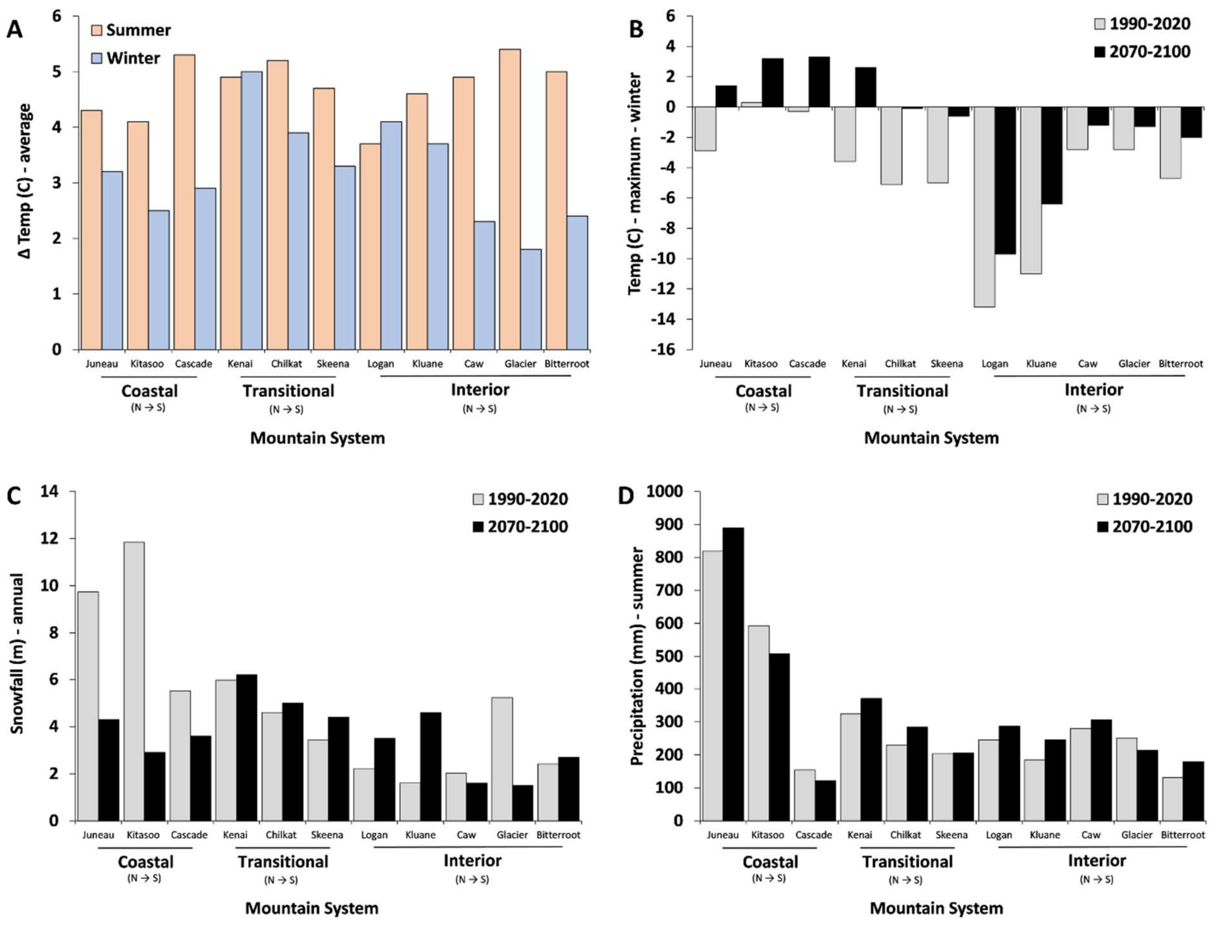

Figure 2.5. Projected change in climate for 11 representative mountain regions (spanning ecotonal and latitudinal gradients; see Appendix for description) inhabited by mountain goats throughout their North American distribution. Baseline historical climate conditions (1990-2020) and estimated future conditions (2070-2100) are summarized for 4 climate variables previously determined to influence mountain goat ecology including: (A) difference in average seasonal temperature between historical baseline and future conditions, (B) observed and projected maximum winter temperature, (C) observed and predicted annual snowfall, and (D) observed and predicted summer precipitation. Simulations are based on an ensemble of 13 General Circulation Models (GCMs) and an intermediate emissions scenario (SSP-370), previously determined to be most suitable for western North America (Wang et al. 2016).

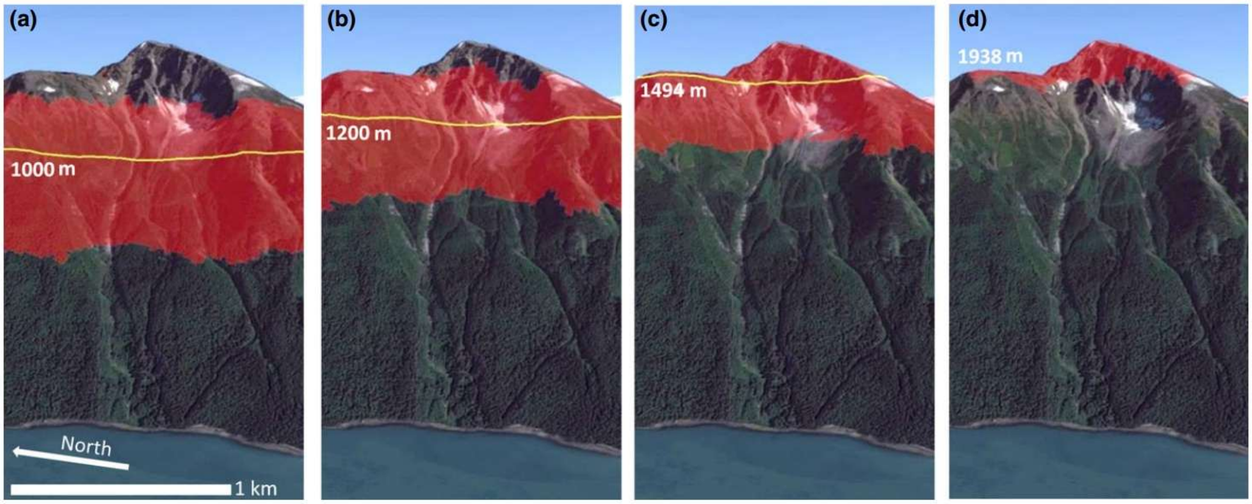

Figure 2.6. Resource selection function modeling output describing predicted changes in mountain goat summer habitat distribution in Lynn Canal, Alaska for four scenarios: (a) current distribution (2005–2015 baseline conditions), (b) year 2085, GCM-GISS-RCP4.5 ("best case scenario"), (c) year 2085, GCM-MRI-RCP8.5/GCM-GFDL-RCP4.5 midpoint ("intermediate scenario), and (d) year 2085, GCM-CCS-RCP-8.5 ("worst case scenario"). Predicted mountain goat summer habitat is shaded in red, and average elevation (observed and projected, based on scenario) is delineated by the yellow line (adapted from White et al. 2018).

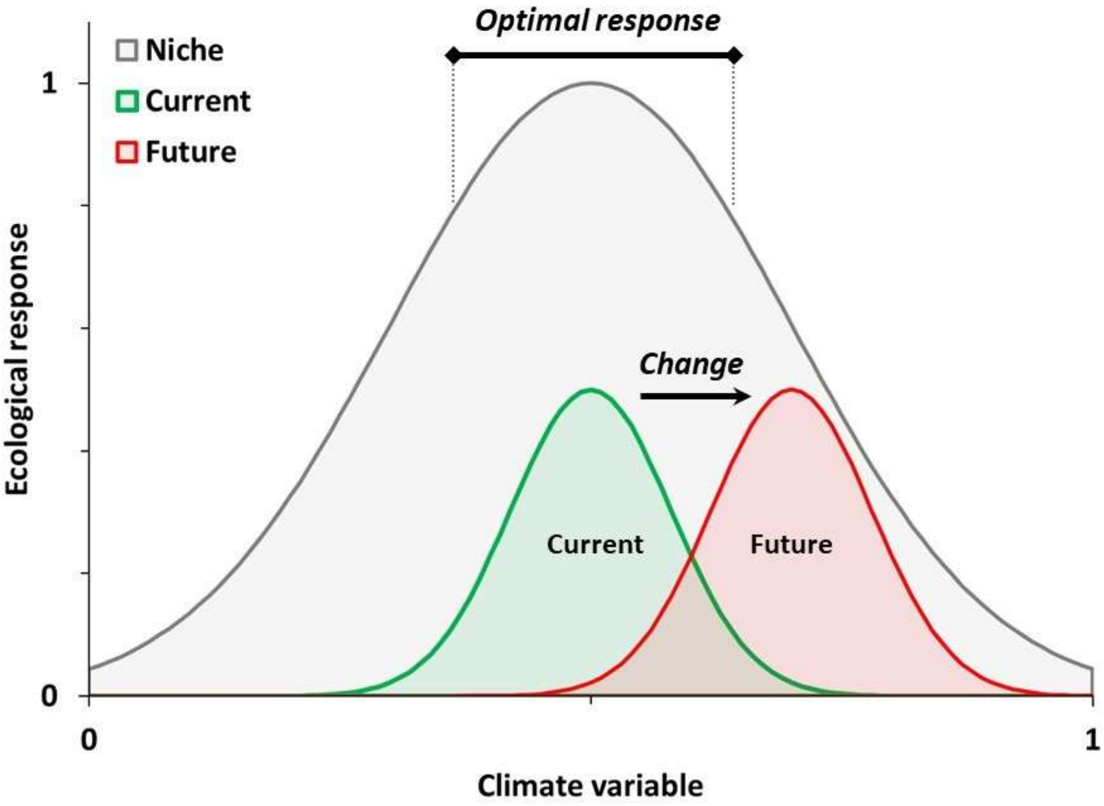

Figure 2.7. Schematic of ecological niche of mountain goats in relation to variation in climate. The current distribution is characterized as an optimal response to current climate conditions. Due to climate change, observed responses may contract and shift toward the extreme of the niche (outside of the optimal zone), which may result in increased stress and reduced performance (adapted from Antão et al. 2022).

Chapter 3. Life-history trade-offs and environmental variability shape reproductive demography in a mountain sentinel

Adapted from: White, K. S., T. Levi, E. Hood, and C. T. Darimont. *In review.* Life-history trade-offs and environmental variability shape reproductive demography in a mountain sentinel. *Journal of Animal Ecology.*

3.1 Chapter Summary

Alpine ecosystems are changing rapidly with implications for the demography of alpine organisms. Here, we studied a sentinel species of mountain environments – the Alaskan mountain goat (*Oreamnos americanus*) – to examine hypotheses about intrinsic and extrinsic drivers of reproductive demography using long-term data collected from individually-marked animals across a broad spatiotemporal extent (n = 180 females, 3 study areas, 17 years). Our analyses reveal the importance of life-history trade-offs and environmental variability on reproductive performance. The cost of reproduction, defined as the impact of reproducing the previous year on current year reproduction, was high, especially for young, largely primiparous females (13-32% reduction) and old, senescing individuals (27-43% reduction); parturition of prime-aged individuals was relatively unaffected by giving birth the previous year (2% reduction). Winter snow accumulation, which alters energetic expenditure and forage availability, exerted strong negative effects on reproduction (20-35% reduction, depending on age). The relationship between temperature during the preceding summer's growing season and parturition window was likewise negative, although weaker and more variable (10-15% reduction).

Demographic modeling provided deeper insights, indicating that snow effects on reproduction likewise exerted stronger impacts on population growth than summer temperature; in part, due to the greater range of observed variability in snow vs temperature. Our analyses further revealed that reproductive performance did not affect subsequent survival of mothers or offspring, suggesting mountain goats employ a 'risk-sensitive', conservative reproductive strategy that prioritizes survival over reproduction. Taken together, these results fill an important knowledge gap by providing novel insights about the interplay between life-history trade-offs and environmental variation, and how they shape the reproductive demography of climate-sensitive mountain ungulates.

3.2 Introduction

Organisms inhabiting extreme environments are particularly sensitive to changes in environmental conditions (Hardie and Hutchings 2010, Berger 2018). Climate is changing more rapidly in mountain regions than surrounding lowland areas (Pepin et al. 2022), which poses pressing conservation challenges (Lynas et al., 2021). Accordingly, more knowledge is needed to understand potential impacts in these sensitive environments. In alpine ecosystems, the study of sentinel species, such as mountain ungulates, can reveal important mechanistic insights about how environmental variation alters species performance (White et al. 2024a) with broad implications for mountain systems as a whole.

Reproduction and survival comprise the principal drivers of population dynamics (Gaillard et al. 2000). While survival typically exerts a stronger influence on population growth, reproduction is often more variable (Gaillard et al. 2000), with the potential to overshadow survival-based contributions in certain contexts (Dulude-de Broin et al. 2020). These demographic components of fitness can be influenced by a variety of factors including disease, predation, malnutrition and anthropogenic impacts (Collins and Kays 2011, Hill et al. 2019). In mountain and high-latitude systems weather and climate can play a central role (White et al. 2011, Berger et al. 2018, Desforges et al. 2021, Harris et al. 2024). Climate-linked effects are typically mediated through nutrition- and energetic-based ecological pathways (Stephenson et al. 2020b, LaSharr et al. 2023a), though direct physical processes such as avalanching snow can also have pronounced demographic impacts (White et al. 2024b). Summer weather conditions are also important, and can, for example, influence forage quality and availability (Bø and Hjeljord 1991, Lenart et al. 2002, John et al. 2023), thermal stress (Mason et al. 2017, Thompson et al. 2020) and insect harassment (Hayes and Berger 2023). These processes can in turn negatively influence the accumulation of endogenous energetic reserves necessary for survival during winter (Parker et al. 2009), with winter snow playing a major role in affecting nutritional intake through burial of forages and increasing energetic costs of locomotion (Dailey and Hobbs 1989, White et al. 2009). Thus, through these mechanisms, variation in seasonal weather conditions is expected to exert strong effects on nutritional condition, reproduction and, ultimately, population performance.

Mountain ungulates contend with often severe and now rapidly changing environmental conditions, raising questions about their viability under such physical challenges. Study of life-history theory and trade-offs may reveal important insights. Life-history theory provides a framework to examine how individuals balance physiological development, reproduction and survival to optimize fitness (Stearns 1998, Hutchings 2021). Life-history strategies characterize how these components are expressed under constraints imposed by physical limitations and trade-offs associated with allocation of nutritional resources (Stearns 1989). The cost of reproduction is a central feature of life-history theory, and relates to how an individual allocates resources to current reproduction relative to ensuring survival (Williams 1966). Long lived, iteroparous species often employ a conservative strategy that favors survival (and the associated opportunity for future reproduction) over investment in current reproduction (Gaillard et al. 2000, Festa-Bianchet and Côté 2008, Hamel et al. 2010).

Such a conservative strategy is expected to be especially beneficial in seasonal environments characterized by substantial environmental stochasticity. Specifically, allocation of protein and energy reserves is expected to be 'risk sensitive' (Bårdsen et al. 2008a) and vary with respect to individual nutritional state, relative to seasonal thresholds, or set points (Renecker and Samuel 1991, Stephenson et al. 2020b). At the individual-level, allocation of resources may be adjusted depending on environmental conditions. For example, during severe winter conditions an individual in poor body condition may restrict allocation of fat and protein reserves to reproduction and conserve stores to ensure survival, resulting in a reproductive pause or reduced litter size (Monteith et al. 2013). Thus, the plasticity of life history traits allows animals to respond to variability in environmental conditions in ways that allow for optimization of fitness (Hutchings 2021).

Mountain goats (*Oreamnos americanus*) are sentinels of change in alpine ecosystems, and due to specialized adaptations for life in cold, alpine environments, they are particularly sensitive to changes in weather and climate (Figure 3.1, White et al., 2024a). The species' distribution spans a wide climatic breadth from the temperate, wet Coast Mountains eastwards to the colder, drier Rocky Mountains, a biogeographic cline that has given rise to behaviorally distinct 'coastal' and 'interior' ecotypes (Herbert and Turnbull 1977, Michaud et al. 2024). Much of our knowledge of the species reproductive ecology comes from detailed studies of the interior ecotype (Festa-Bianchet and Côté 2008, Festa-Bianchet et al. 2019). Previous study in coastal Alaska has documented effects of both winter snowfall and summer temperature on survival (White et al. 2011), but how these factors influence reproduction in coastal systems is not well understood. Examining how reproduction is influenced by weather conditions has important practical applications, given the species' sensitivity to climate (White et al. 2011, 2018, Harris et al. 2024) and human disturbance impacts, including harvest (Hamel et al. 2006, Rice and Gay 2010, Côté et al. 2013). For example, detailed models describing reproductive characteristics can be integrated with existing population models (White et al. 2018, 2021a) to predict outcomes of proposed conservation strategies.

Here, we use long-term (17-yrs) longitudinal data collected from individually-marked mountain goats (n = 180 females) across three coastal Alaska study areas to examine hypotheses about how reproduction is influenced by life-history tradeoffs and environmental conditions. First, because energetic costs of gestation and rearing young can be substantial (Testa and Adams 1998, Parker et al. 2009, Stephenson et al. 2020b), we predicted that individuals would have a higher probability of giving birth if they had not done so the previous year (Hamel et al. 2010, Festa-Bianchet et al. 2019). We further expected that reproductive performance would differ among life stages that vary in relation to physiological maturity and senescence (Lemaître and Gaillard 2017, Festa-Bianchet et al. 2019), such that prime-aged animals would demonstrate lower costs of reproduction than younger and older mothers. We also predicted that survival of mothers and offspring would be similarly affected but that effects would be dampened given the expected prioritization of future survival (and reproductive opportunities) over current reproduction (conservative life-history strategy; Festa-Bianchet et al. 2019). In addition, we predicted that reproductive performance would be reduced following periods of environmental stress (i.e. hot summers and snowy winters), parallelling previously documented effects on adult survival in this and comparable systems (White et al. 2011, Harris et al. 2024). By extension, we expected variation in life-history trade-offs and age-specific reproduction would likewise be modulated by variation in environmental conditions (Parker et al. 2009, Monteith et al. 2014, Lemaître and Gaillard 2017, Stephenson et al. 2020b).

3.3 Methods

3.3.1 Study system

Mountain goats were studied in three areas across a broad geographic range in coastal Alaska (5537 km^2) from 2005-2021 (Figure 3.1a). This area is within the Coast Mountains biogeographic region (Gallant et al. 1995) and is largely characterized by a temperate maritime weather and snow climate (McClung and Schaerer 2006). The region is dominated by coastal temperate rainforest composed primarily of Sitka spruce-western hemlock (*Picea sitchensis-Tsuga heterophylla*) forests at lower elevations (below 450-750 m). At higher elevations, subalpine and alpine habitats dominated by krummholtz forest, low-growing herbaceous meadows and ericaceous heathlands are widespread and persist to elevations of about 1400 m. The geologic terrain is complex and strongly influenced by terrain accretion and uplift processes. Such an arrangement results in a highly fractured landscape dominated by steep and rugged topography that is fragmented by glaciers, icefields, high-volume river systems and marine waters (Stowell 2006). Glacier recession has heavily modified the region, leaving steep, sloping topography. Avalanche paths extend from sea level to 2000 m, and impose an important source of landscape disturbance and habitat heterogeneity.

Mountain goats in this region are widespread and occur at low to moderate densities (0.4 – 1.2/km^2), typical of northern coastal areas inhabited by the species (White et al. 2016, Jessen et al. 2022). Populations exhibit a high degree of local-scale population genetic differentiation, with limited movement among geographically discrete mountain complexes (Shafer et al. 2011, 2012, White et al. 2021a). Mountain goats are habitat specialists and select steep, rugged terrain in close proximity to cliffs and exhibit seasonal variation in altitudinal distribution (White et al. 2012, Shafer et al. 2012, White and Gregovich 2017). The study populations were partially migratory, with some individuals, depending on study area, residing in alpine and subalpine habitats throughout the year (White and Gregovich 2018, Shakeri et al. 2021). However, most individuals conduct short-distance (5-10 km), seasonal migrations involving annual movements between high-elevation alpine summer habitats and forested, low-elevation wintering areas (White et al. 2012, White and Gregovich 2018, Shakeri et al. 2021). Downslope migrations tend to correspond with the first major snowfall events at high elevation (i.e., mid-October), while upslope migrations are timed with onset of snow ablation and the pre-parturition period (i.e. early-May)(White et al. 2012). Impacts of human development and activity in the study area are, generally, minimal. Nonetheless, low-intensity or localized activities include regulated hunting, ground- and air-based recreational tourism, timber harvest and mining (White and Gregovich 2017, 2018, White et al. 2021a). The large mammal predator-prey communities in this area are intact and, in addition to mountain goats, key species include: moose (*Alces alces*), Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), wolves (*Canis lupus*), coyotes (*Canis latrans*), black bears (*Ursus americanus*), brown bears (*Ursus arctos*) and wolverines (*Gulo gulo*); though local variation occurs relative to species distribution and abundance (MacDonald and Cook 1996, White et al. 2012).

3.3.2 Mountain goat monitoring

Mountain goats were captured using standard helicopter darting techniques (White et al. 2021b). During handling all animals were fitted with mortality sensing very high frequency (VHF) and/or global positioning system (GPS) radio-collars (Telonics Inc., Mesa, AZ). Age of animals was determined by counting horn annuli (Brandborg 1955, Smith 1988), and, in some cases, cross validated by examination of tooth eruption patterns (for young animals) and/or cementum analysis of incisors (for deceased animals; Matson's Laboratory, Milltown, MT). Capture and handling procedures were reviewed and approved by the Alaska Department of Fish and Game Institutional Animal Care and Use Committee (protocols 05-11, 2016-25, 0078-2018-68, 0039-2017-39) and followed American Society of Mammalogists guidelines (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

Following capture, animals were typically monitored at least once per month (often multiple times per month) via aerial telemetry to determine whether animals were alive or dead. Kidding rates and subsequent survival were estimated by monitoring individual study animals during monthly surveys using fixed-wing aircraft (usually a Piper PA-18 Super Cub) equipped for radio-telemetry tracking or via ground-based observations. During surveys, radio-collared adult female mountain goats were observed (typically using 14X image stabilizing binoculars) to determine whether they gave birth to kids and, if so, whether they survived until September. Monitoring kid production and survival was only possible during the non-winter months when animals could be reliably observed in open, alpine habitats. Consequently, we were only able to assess kid survival during the summer period (May-September). Cases in which kid status assessments were equivocal were not used for subsequent estimates.

3.3.3 Winter and summer climate data

We compiled regional climate data from reference weather stations located in the vicinity of Juneau, AK, a geographically central location within 40-100 km of study animals for which weather data are continuously recorded (National Weather Service, Juneau, AK). Following White et al. (2011), temperature measurements were recorded at the Juneau International Airport National Weather Service station and adjusted using the environmental lapse rate (-6.58 C/1,000 m; Barry and Van Wie 1974) to represent the mean elevation (910 m) used by mountain goats in the study region during summer. Summer temperature was expressed as mean temperature (C) during July-August. During the study period, summer temperature averaged 7.89 C (range = 6.00 – 9.34 C). Snow measurements were recorded at Eaglecrest, Alaska, a mid-elevation site (366 m) located 9.9 km south of the Juneau Airport, and representative of elevations commonly used by mountain goats in the study region during winter. Snow conditions are expressed as mean snow depth (m) during late-winter (March-April). During the study period, snow depth averaged 1.24 m (range = 0.01 – 2.64 m).

3.3.4 Data Analyses

We used generalized linear mixed effects models (Bolker et al. 2009) to examine the effects of previous reproductive success and environmental conditions (and their interaction) across different life-stages on parturition success, offspring survival during summer, and annual survival of adult females. Analyses were conducted separately for each response variable and used reduced subsets of the total data set for which complete longitudinal records were available. In the case of parturition, for example, only cases where previous year and current year parturition were known for a given individual during a given paired year combination comprised a complete record. Incomplete data largely occurred during the year when a female was captured, and knowledge about previous year parturition was unknown or individuals were otherwise not monitored from the beginning of the biological year. Parturition was defined as a binary response variable, as our goal was to estimate probability of parturition. In practice, such estimates closely match fecundity given twinning is very rare (1.5%, 6/405 cases; White *unpublished data*). Survival was also defined as a binary response variable with coding dependent upon whether an adult female survived from June until the following May (termed annual survival) or, in the case of offspring from parturition, until September (termed summer survival). Life stages were indexed based on age and encompassed biologically relevant *a priori* categories spanning primiparous (age: 3 yrs, age: 4 yrs, age: 5 yrs), prime-aged (age: 6-10 yrs) and senescent (age: 11-13 yrs, age: 14-16 yrs) stages. Overall, each age category was coded manually as a dummy variable to simplify examination of age-specific interactive effects (i.e. assessment of whether parturition in a given age category was affected differently by a given covariate, as compared to other age categories). A principal goal of our modeling efforts was to understand and parameterize how reproduction and survival varied in relation to age (life-stage) and, ultimately, whether the effect of other intrinsic and extrinsic covariates on reproduction or survival was age-dependent. Thus, we included age (i.e. all age categories) in each model considered; though age categories were collapsed, in some instances, if sample sizes precluded adequate parameterization. Overall, we examined hypothesized additive and interactive relationships between parturition (and offspring and adult survival, in separate analyses) and age along with reproductive status, summer temperature and winter snow depth during the biological year preceding parturition (i.e. during the gestation period). In the case of adult female survival, however, summer and winter covariate conditions coincided with the current year.

Our modeling approach involved initial examination of random effects considered to be plausible *a priori*, and included individual identification and site, as well as a term for nesting individual identification within site. However, we included individual identity as a random effect in all models due to repeated measures among individuals across years. We assessed importance of each random effect by contrasting a global (termed null) model, comprised of only fixed effects terms (GLM), with nested models that included additive effects of each random effect using a generalized linear mixed model framework (logit-link function and binomial error distribution). We assessed the importance of random effects using a AICc and likelihood ratio tests, based on maximum likelihood estimation (Bolker et al. 2009). Unlike linear mixed models, restricted maximum likelihood (REML) cannot be used for assessing random effects in generalized linear mixed models; Fieberg 2022). Once the appropriate random effect structure was determined, we used generalized linear mixed models to systematically examine candidate models that *a priori* represented the hypothesized relationships of interest. We determined the top model(s) by examining the weight of evidence for each model using AICc and by determining whether 95%

confidence intervals of β coefficient estimates encompassed zero (Burnham and Anderson 2010). If AICc weights were similar among top models, we considered both models including the more complex and informative models, provided an added parameter(s) was deemed informative per established criteria (*sensu* Arnold 2010, Sutherland et al. 2023). We examined model classification and predictive performance by deriving a receiver operating characteristic curve (ROC) and calculating the area under the curve (AUC). We considered AUC values >0.8 to indicate excellent discrimination, 0.7–0.8 to indicate acceptable discrimination, 0.5–0.7 to indicate low discrimination, and<0.5 to indicate poor discrimination (Hosmer and Lemeshow 2000). We also evaluated the fit between observed vs expected values (QQ plot, K-S and dispersion tests), and residual plots examining calculated residuals vs predicted values across a range of quantiles. Generalized linear mixed modeling analyses were conducted using *lme4* in R version 4.3.1 (Bates et al. 2014, R Core Team 2023).

3.3.5 Sensitivity analyses – climate effects on parturition

We used a population modeling approach to conduct simulations and assess the relative importance of summer vs winter conditions on reproductive performance and ultimately population growth. Specifically, we used a post-breeding, sex- and age-structured (20 age classes) population model previously described by White et al. (2018, 2021b). Briefly, the model is parameterized using sex- and age-specific survival estimates statistically derived using a spatially and temporally extensive, 44-year (1977-2021) known-fates data set collected from mountain goats throughout coastal Alaska (n = 14 study sites, 600 individuals, 1,910 mountain goat yrs; White et al. 2011, 2018, 2021, this study). Neonate survival was parameterized following Rice and Gay (2010), as described in White et al. (2018). Age-specific fecundity was estimated based on direct observations of radio-marked females using a subset of the data set, as described above.

The original implementation of the model (i.e. White et al. 2018) involved simulating the effects of climatic variability on survival and, ultimately, population growth using average age-specific fecundity values. In the current analyses, we instead calculate population growth by simulating the effects of variation in summer and winter weather conditions on fecundity, while using average sex- and age-specific survival estimates. Specifically, we examined three scenarios for each weather variable (min, mean, max) and ran 10,000 simulations (30 yr time period) for each scenario. For a given scenario, we adjusted the input for the focal climate variable (i.e. winter snow or summer temperature) and held all other inputs at their mean level. To reduce initial transient effects, we initialized each model run based at the stable age distribution holding all climate variables at their mean level. To account for uncertainty, we sampled from within the error distribution of beta coefficients (i.e. sex- and age-specific survival) accounting for covariance structure among coefficients using the RMark package in R (Laake 2013). We also modeled interannual variation in annual fecundity as a lognormally distributed random variable. The standard deviation of the distribution was parameterized using the observed variance across the range of interannual fecundity estimates (SD = 0.106, n = 16 years, 2006 – 2021; data described above). This approach enabled us to simulate demographic stochasticity using empirical data collected in our study system.

Overall, our simulation approach enabled us to estimate the mean annual change in population size (λ), and its associated distribution, for each scenario (i.e. isolating each climate-linked reproductive effect on population growth). We then calculated the difference in predicted population growth across the range of variation for winter snow and summer temperature per each scenario. Ultimately, this enabled determination of the relative strength of each climate driver on population growth due to parturition.

3.4 Results

3.4.1 Descriptive summary

Overall, we monitored 180 individually marked females across 3 study areas during 2005-2021. We determined annual parturition status on 640 occasions (mean = 3.5 events/individual) among individuals that ranged from 1 – 16 years of age. Individuals were observed with offspring in 405 cases, including 6 instances of twins (1.5% of all parturition events). The proportion of females observed with offspring during the parturition period varied in relation to age. Of parturient females subsequently monitored until autumn (n = 311 cases), 84±2% were observed with their offspring at heel. In 24 instances, we commenced monitoring of females between ages 1 – 3 years old and subsequently monitored animals annually (4.6 ± 0.4 years/individual, on average) during the parturition period to determine age of primiparity. We did not detect any instances of parturition among 1- or 2-year old females (Fig 2), with the earliest age of reproduction occurring at 3 years (21%, 5/24 cases). Most females did not give birth until 4 years (54%, 13/24 cases) with the remainder occurring at 5 years (21%, 5/24 cases) and 6 years (4%, 1/24 cases) of age. Overall, age of primiparity occurred at 4.1 ± 0.2 (n = 24) years of age, on average (Figure 3.2).

3.4.2 Modeling age, climate and life-history trade-offs

Parturition – To examine effects of previous year reproduction and weather conditions on parturition, we examined 13 candidate models describing *a priori* hypothesized relationships, including relevant interaction terms (Table B1); all models retained individual identity as a random effect. Model selection revealed two top models with near identical AICc weights (Table B1). The top model (AICc $w_i = 0.28$) included fixed effects for age, previous year reproduction (including a separate interactive effect for prime-aged animals versus all other age categories) and winter snow. The 2nd best model had near equivalent performance (AICc $w_i = 0.27$) and was identical except for also including the summer temperature effect. As a consequence, we considered both models but used the more biologically informative, 2nd best model to express relationships between probability of parturition and the full suite of informative fixed effect parameters.

Specifically, we determined that parturition varied with respect to age, with reproduction being lowest for primiparous and senescent individuals, and highest for prime-aged animals (Table 3.1a, Figure 3.3). We also documented a strong negative relationship between parturition and the presence of an offspring the previous year (Table 3.1a, Figure 3.3). This relationship applied to all age categories consistently, with the exception of prime-aged individuals. Specifically, parturition of prime-aged animals was not influenced by giving birth to offspring during the previous year. In addition, we detected a strong negative relationship between parturition and snow depth that consistently affected all age categories (Table 3.1a, Figure 3.4). Evidence for an effect of summer temperature on reproduction was also negative but was considered modest in comparison to effects of age, winter snow and previous year reproductive status with the upper confidence interval of the β coefficient estimate marginally overlapping zero (sensu Sutherland et al. 2023)(Table 3.1a, Figure 3.5). The area under the ROC curve was 0.87, and indicates excellent model discrimination. Further analyses of residuals indicated correspondence between predicted and observed values (Kolmogorov-Smirnov test, = 0.55, dispersion test = 0.48).

Sensitivity analyses – climate effects on parturition – We used a sex- and age-structured matrix population model to simulate the relative effect of summer versus winter conditions on mountain goat reproduction and ultimately population growth. Our analyses revealed that variation in winter snow exerts a substantially stronger influence on population growth than summer temperature (Figure 3.6). For example, when all other input parameters were held at the mean value, winter snow had the potential to alter reproductive rates and change annual population growth rate (λ) by 6.8%, whereas equivalent assessment of summer temperature revealed a change in λ of 3.0%, across the full range of observed conditions. Overall, these differences were attributed to the stronger effect of snow, as compared to summer temperature, on probability of parturition (see above) as well as the greater range of variation in observed snow depth (min = 0.01 m, mean = 1.21 m, max = 2.64 m) vs summer temperature (min = 6.00, mean = 7.88 C, max = 9.34) during the 17 year study period (2005 – 2021).

Adult female survival – To examine effects of previous year reproduction and weather conditions on annual survival of adult females, we examined 16 candidate models describing *a priori* hypothesized relationships, including relevant interaction terms (Table B2); all models retained individual identity as a random effect to account for repeated measures of individuals across years. We used a reduced subset (n = 135 individuals, 343 animal-years) of our original data set because the requirement of having information about current year kid status and complete known-fate survival data for a given year per individual female. We initially considered our original 6-age category design but also examined structures including 3-age categories, due to the reduced sample size and associated statistical power to parameterize relationships.

The top model (AICc w_i = 17.1) revealed that adult female animal survival varied with respect to age and winter snow depth (Table B2). Specifically, survival was highest among young (age = 3-5 yrs), intermediate for prime-aged (age = 6-10 yrs) and lowest for old (age = 11-16 yrs) females (Table 3.1b). Late-winter snow depth exerted a consistent, negative effect on survival across all age categories. The area under the ROC curve was 0.67, indicating acceptable model discrimination. Further analyses of residuals indicated correspondence between predicted and observed values (Kolmogorov-Smirnov test, = 0.46, dispersion test = 0.93). We did not document strong support for effects of previous reproduction or summer temperature on adult female survival. The 2nd best model (AICc w_i = 10.1) was identical to the top model but included previous reproduction. However, the confidence intervals of the β coefficient estimate for this variable overlapped zero.

Offspring survival – To examine effects of previous year reproduction and weather conditions on offspring survival, we examined 13 candidate models describing *a priori* hypothesized relationships, including relevant interaction terms (Table B3); all models retained individual identity nested within area as a random effect (i.e. because individuals only occurred within a given study area). We used a reduced subset (n = 241 offspring, 116 adult females) of our original data set because the requirement of having information about previous year as well as current year offspring status for individual females. We initially considered our original six age category design but also examined structures including three age categories, due to the reduced sample size and associated statistical power to parameterize relationships.

Model selection revealed two competitive top models (Table B3). The top model (Model 3, AICc w_i = 0.23) indicated summer kid survival differed between young/prime-aged (3-10 yrs) mothers and old (age 11-16 yrs) females (Table 3.1c). Specifically, the probability of kid survival during summer was lower for old mothers ($\hat{S}$ = 81.1, CI = 53.4 - 94.6) as compared to young/prime-age females ($\hat{S}$ = 90.1, CI = 72.1 - 97.0). The area under the ROC curve was 0.84, indicating excellent model discrimination. Further analyses of residuals indicated correspondence between predicted and observed values (Kolmogorov-Smirnov test, = 0.27, dispersion test = 0.51). The 2nd best model (Model 10, AICc w_i = 0.16) included the same age effect but also an additive effect of snow depth. This model suggested a negative effect of previous winter snow depth on offspring survival during the following summer; but the effect was weak, with confidence intervals overlapping zero. The area under the ROC curve was 0.72, indicating acceptable model discrimination. Further analyses of residuals indicated correspondence between predicted and observed values (Kolmogorov-Smirnov test, = 0.11, dispersion test = 0.49).

3.5 Discussion

Knowledge about how vital rates are influenced by variation in environmental conditions and life-history trade-offs is important for understanding mechanisms underlying population dynamics. This is especially true for climate-sensitive mountain species that are vulnerable to the rapid environmental changes currently occurring in alpine ecosystems (Jacobson et al. 2004a, Sandercock et al. 2005, White et al. 2024a). In this study, we used long-term longitudinal data spanning a broad spatiotemporal extent and extensive environmental variation to elucidate how mountain ungulate reproduction varied in response to age, life-history trade-offs, and changes in summer and winter weather conditions. We found that reproductive performance was sensitive to previous reproductive investment and variation in seasonal weather conditions (especially during winter). Costs of reproduction however did not affect maternal survival highlighting a conservation reproductive strategy. Together with previous work conducted on interior mountain goats (Festa-Bianchet and Côté 2008, Hamel et al. 2010, Festa-Bianchet et al. 2019), our study, the first focused on the coastal ecotype of the species, offers a comprehensive understanding of the species' reproductive ecology across a range of conditions and advances our capacity to address conservation challenges faced by the species.

Life-history trade-offs – Reproduction is energetically costly and can invoke trade-offs dependent on life-stage and physical development. Adapted to extreme environmental conditions, mountain goats have slow growth rates and a late age of primiparity, leading to a high cost of reproduction among young animals. In this regard, our findings were similar to other long-term studies of mountain goats and bighorn sheep that demonstrated that young females had a lower probability of parturition if they had previously given birth, as compared to nulliparous females (Hamel et al. 2010, Festa-Bianchet et al. 2019). Such reproductive costs did not occur among prime-aged individuals, but they were increasingly evident as females entered older, senescent age classes. Similar evidence of reproductive senescence and increased costs of reproduction among older age classes has previously been documented in other northern ungulate populations (Clutton-Brock et al. 1983, Ericsson et al. 2001, Morin et al. 2016, Boertje et al. 2019). However, in other instances, including mountain goats, costs of previous year reproduction among older animals is not clearly evident (Clutton-Brock 1984, Hamel et al. 2010). Consistent with the ‘terminal investment hypothesis' (sensu Pianka and Parker 1975, Clutton-Brock 1984), such work suggests that as animals age investment in reproduction increases due to otherwise declining reproductive value. Among mountain goats, Hamel et al. (2010) suggested that sociality may play a key role in reduced costs of reproduction among older animals, given such individuals often have higher social rank, larger body mass and greater capability to recover from reproductive events. Differences in population density and resulting impacts on sociality may explain differences between the higher density population studied by Hamel et al (2010) and the generally lower density and more geographically expansive populations monitored in this study. Despite this nuanced difference in stage-specific reproductive costs, the general patterns of reproduction including late age of primiparity, very low incidence of twins and frequency of reproductive pauses are consistent among both long-term studies and provides further empirical evidence of the species’ conservative reproductive strategy (Festa-Bianchet and Côté 2008).

Given the relatively high energetic cost of reproduction, employing a life-history strategy that prioritizes survival over reproduction is likely a central adaptation for ‘capital’ breeders (Festa-Bianchet et al. 1998, 2019), that inhabit extreme environments with short growing seasons and unpredictable, often severe, winter conditions. Previous work among northern and mountain ungulates further elucidates these dynamics and suggests that reproduction, by competing with nutritional resources needed for survival, leads to ‘risk sensitive’ reproductive allocation, especially in variable environments (Bårdsen et al. 2008b). Our results are consistent with these expectations, revealing that mountain goat reproductive investment and performance is indeed sensitive to variation in environmental conditions and previous parturition success. Whereas annual survival of females was not affected by giving birth the previous year. Similar to previous studies among mountain goats (Hamel et al. 2010, Festa-Bianchet et al. 2019), these findings indicate that adult females adopt a conservative reproductive strategy that favors their own survival over investment in offspring.

Maternal costs of reproduction may also impact performance and survival of offspring (Feder et al. 2008, Hamel et al. 2010, Festa-Bianchet et al. 2019). We expected that offspring born to females that had also given birth the previous year would have lower over-summer survival than those born to females that were barren during the previous year. However, we did not document evidence of this relationship. Specifically, while we documented a clear cost of reproduction on the future probability of parturition, we determined that such effects did not extend to reducing survival of offspring during their first summer. Similar to findings in interior mountain goat populations (Hamel et al. 2010), this likely occurs because nutritional constraints are relaxed during the vegetative growing season and effects of reproduction on offspring vitality and survival are not likely to be manifested until the winter season when nutritional deprivation and physiological stress are more pronounced.

Weather and climate effects – Mountain goat demography is sensitive to variation in climate conditions. Previous research has documented negative effects of warm summer temperature and deep winter snow on mountain goat survival (White et al. 2011, Harris et al. 2024). Our analyses of reproductive performance revealed parallel relationships. Specifically, the probability of parturition declined 10-15% following the warmest summer conditions, as compared to the coolest. Effects were more pronounced with winter snow depth; we observed a 25-30% decline in parturition following severe vs mild winters. Translated to population dynamics, our sensitivity analyses indicated that variation in reproduction across the range of observed winter snow depth conditions had greater potential to elicit change in population growth rate (λ, range = 0.972 – 1.041), as compared to variation in observed temperature during the summer growing season (λ, range = 1.001 – 1.031; Figure 3.6). Consequently, across the range of conditions observed, winter conditions exerted a stronger effect (in both statistical and absolute terms) on parturition than summer temperature. A similar, winter dominant pattern was observed in earlier, extensive study of winter snow and summer temperature effects on survival of adult mountain goats in coastal Alaska (White et al. 2011). These results suggest similar ecological and physiological mechanisms underlie climate-linked variation in both reproduction and survival among mountain goats. For example, summer and winter weather are expected to principally influence reproductive performance and survival through nutritional pathways that modulate gain and expenditure of endogenous nutritional reserves (Parker et al. 2009). Specifically, during the summer growing season environmental conditions influence the nutritional characteristics and availability of forage resources and, ultimately, assimilation of energy and protein reserves necessary for survival during winter (Lenart et al. 2002, Pettorelli et al. 2007, Parker et al. 2009, Monteith et al. 2014, John et al. 2023); a period when animals experience a negative energy balance due to reduced forage quality, accessibility and increased energetics costs of locomotion (Dailey and Hobbs 1989, White et al. 2009, Stephenson et al. 2020b).

That summer and winter weather affect both mountain goat reproduction (this study) and survival (White et al. 2011) in similar ways suggest longer-term projections regarding climate change impacts on mountain goat population dynamics in coastal Alaska are likely to remain a subject of conservation concern. Specifically, previous survival-based population modeling simulations indicated the deleterious projected increase in summer temperature was expected to outweigh beneficial declines in winter snowfall and result in long-term population declines, across a range of general circulation model (GCM) and emissions scenarios (White et al. 2018). This occurs because future climate projections indicate summer temperature and associated effects will continue to increase over time (and extended beyond current observed conditions), whereas change in winter snowfall and associated negative reproductive effects will decrease (Shanley et al. 2015, White et al. 2018). Thus, given the similar directionality among responses of reproduction and survival to summer and winter weather conditions, projected outcomes of climate change on coastal mountain goat populations dynamics are expected to remain consistent with, or strengthened, relative to previous simulations.

Ecotypic similarities and conservation implications – Phenotypic traits can vary across geographic gradients within a species distribution giving rise to distinct ‘ecotypes’ (Lomolino et al. 2017). Among mountain goats, coastal-interior gradients that track variation in climate and habitat conditions have led to suggestion that population performance may likewise differ between coastal and interior regions within the species North American distribution (Herbert and Turnbull 1977, Rice et al. 2022) – yet empirical evaluation has been limited. Long-term studies of individually marked animals provide an important opportunity to understand life-history and reproductive ecology in detail and examine proposed biogeographic relationships. Comparative evidence from long-term studies of the species in interior (Caw Ridge, Alberta; Festa-Bianchet et al. 2019) and coastal systems (this study) reveal similar reproductive characteristics, suggesting such adaptations are conserved across their range. Thus, relative to other northern ungulate species, mountain goats have low reproductive productivity and thus high sensitivity to population perturbations – both natural and anthropogenic. This finding has important conservation implications given recent work suggesting, based on indirect evidence of age at primiparity, that coastal populations have higher reproductive capacity than interior populations and thus capable of sustaining higher harvest rates (Rice et al. 2022). Our results make clear, instead, that increasing harvest rates of coastal populations is not supported on the basis of reproductive performance, as meaningful differences between areas are not evident based on direct observation (Figure B1). This is an important issue for a species, such as mountain goats, at the slow end of the life-history continuum (sensu Bielby et al. 2007, Healy et al. 2019) that are only capable of sustaining minimal harvest rates (1-4%; Hamel et al. 2006, Rice and Gay 2010, White et al. 2021a). While ecotypic variability is evident in some aspects of the species behavior and ecology (Michaud et al. 2024), extensive evidence from long-term field studies indicates such differences do not translate equivalent variability in reproductive performance.

Species inhabiting extreme environments are particularly sensitive to environmental change and stochastic events, often occur in small, isolated populations and are disproportionately vulnerable to localized declines or extinctions (Berger 1990, O'Grady et al. 2004, Turgeon et al. 2024). As such, implementation of quantitative modeling approaches offers an important tool for understanding population dynamic processes, monitoring population performance and evaluating proposed conservation strategies (Shenk and Franklin 2001, Johnson et al. 2010, Mills 2013).

Development of models for species, such as mountain goats, that inhabit difficult mountain environments, with long-term, high-quality data is logistically challenging, but critically needed. Our study provides an important contribution by enabling climate varying parameterization of reproductive components for mountain goat population models in the coastal portion of their range. This approach, for example, revealed important insights about the relative effects of summer vs winter weather on mountain goat population growth. More broadly, our analyses and modeling framework advance our capacity for attaining a more comprehensive mechanistic understanding of mountain goat population dynamics in coastal systems. Given the species' sensitivity to climate change and anthropogenic impacts, strengthening analytical tools needed to address conservation challenges represents a promising pathway for ensuring the species productivity and persistence into the future.

Table 3.1 Effects of age, previous reproductive status and climate on the probability of mountain goat: a) parturition, b) adult female annual survival and c) offspring summer survival in coastal Alaska during 2005-2021.

a) Probability of parturition

Parameter	β	SE	Confidence Intervals		Z-value	P-value
			Lower	Upper		
Intercept	0.993	1.463	-1.874	3.859	0.679	0.497
Age (4)	1.693	0.844	0.038	3.348	2.005	0.045
Age (5)	3.499	0.927	1.682	5.317	3.773	0.000
Age (6-10)	3.023	0.869	1.320	4.725	3.480	0.001
Age (11-13)	3.264	0.939	1.424	5.105	3.476	0.001
Age (14-16)	2.382	1.038	0.347	4.416	2.295	0.022
Repro_{t-1}	-1.386	0.502	-2.370	-0.401	-2.759	0.006
Snow	-0.680	0.187	-1.046	-0.313	-3.635	0.000
Temp	-0.205	0.144	-0.488	0.077	-1.423	0.155
Repro_{t-1} × age (6-10)	1.270	0.569	0.154	2.386	2.230	0.026

b) Probability of adult female annual survival

Parameter	β	SE	Confidence Intervals		Z-value	P-value
			Lower	Upper		
Intercept	3.315	0.577	2.183	4.446	5.743	0.000
Age (6-10)	-1.164	0.546	-2.234	-0.093	-2.131	0.033
Age (11-16)	-2.127	0.582	-3.267	-0.987	-3.658	0.000
Snow	-0.392	0.185	-0.754	-0.030	-2.123	0.034

c) Probability of offspring summer survival

Parameter	β	SE	Confidence Intervals		Z-value	P-value
			Lower	Upper		
Intercept	2.206	0.640	0.951	3.460	3.446	0.001
Age (11-16)	-0.703	0.398	-1.484	0.077	-1.766	0.077

Notes: Age categories are coded as dummy variables with corresponding ages (yrs) in parentheses. Age categories were combined in some instances to optimize model fit and accommodate sample size limitations. Repro_{t-1} represents parturition status during the previous year. Snow represents average daily snow depth during late-winter (April – May). Temp represents average daily summer temperature during mid-summer (July – Aug). Intercepts correspond with: a) 3 yr old females without an offspring the previous year, b) 3 – 5 yr old females, and c) offspring with mothers aged 3 – 10 yrs.

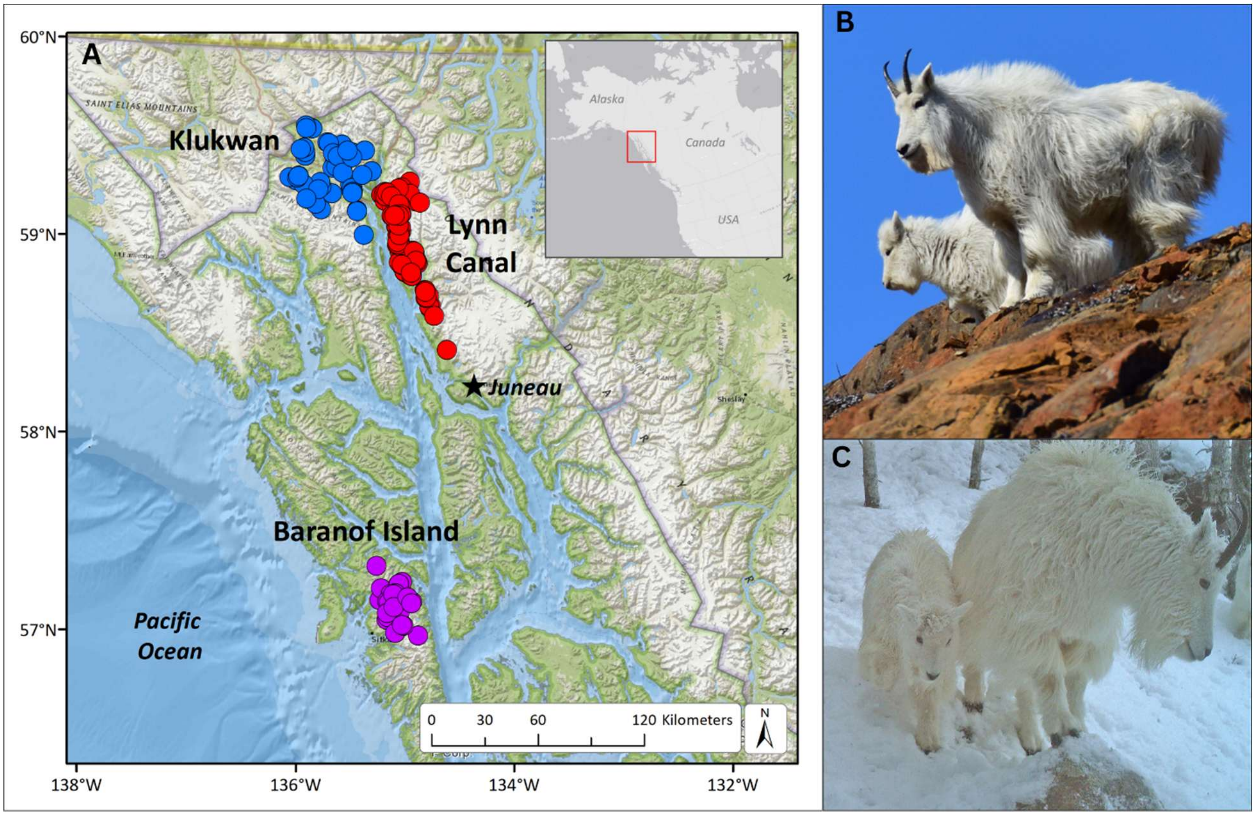

Figure 3.1. Study system. (A) Map depicting locations where radio-marked female mountain goats and their offspring were studied during 2005 – 2021 in three study areas located in coastal Alaska. (B) Female mountain goat (*Oreamnos americanus*) and offspring during early-spring, experiencing snow-free conditions following a mild winter. (C) Female mountain goat and offspring in forested winter range during mid-winter, Takshanuk Mountains, Alaska.

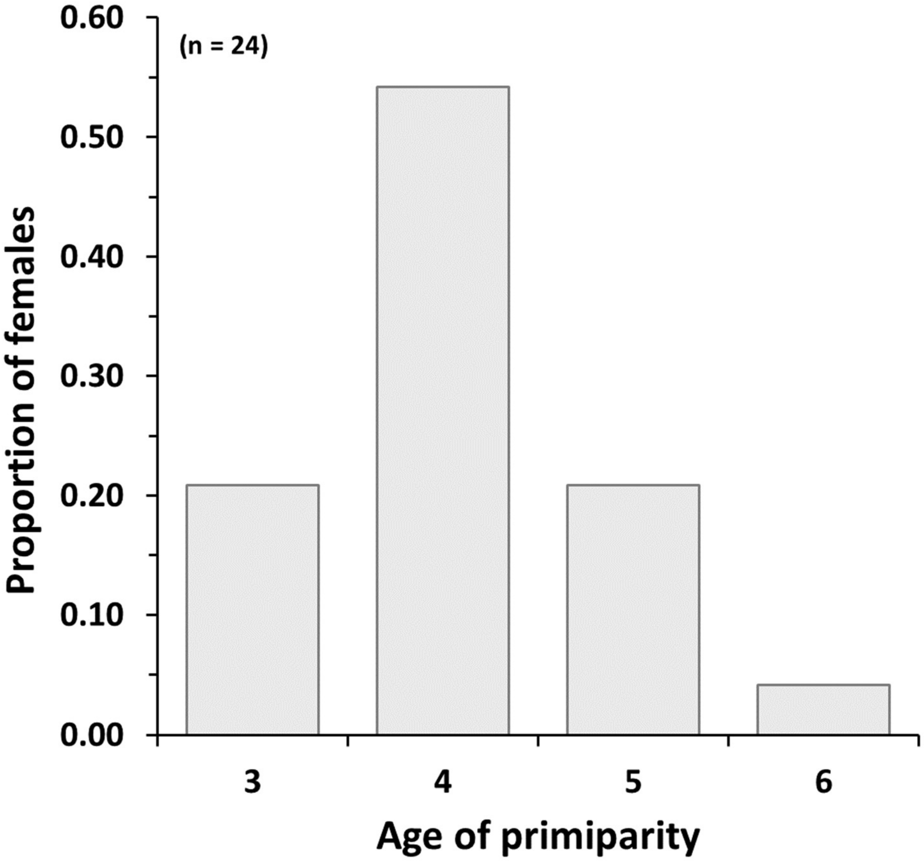

Figure 3.2. Age of primiparity among radio-marked female mountain goats (n = 24) in coastal Alaska during 2005-2021. Estimates based on the subsample of females for which monitoring began at age ≤ 3 years old.

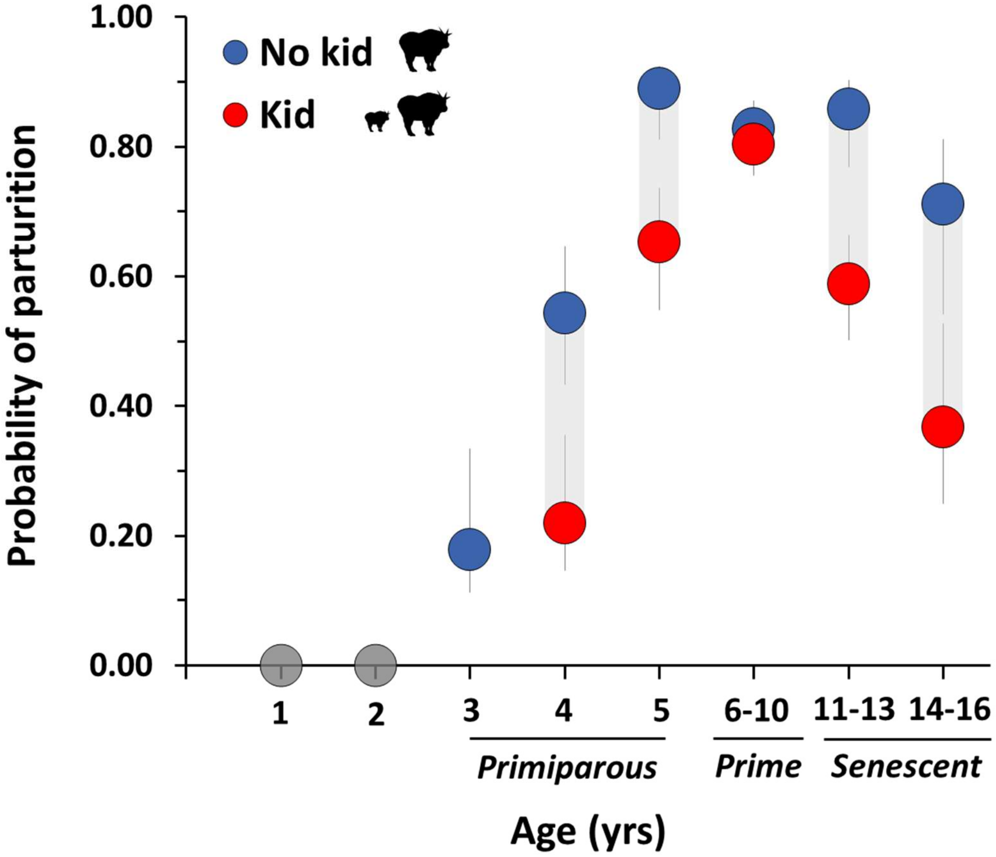

Figure 3.3. Cost of reproduction in relation to age and previous reproductive performance for mountain goats (n = 180 females, 640 female-years) in coastal Alaska during 2005-2021. Probability of parturition was significantly reduced following successful reproduction for primiparous (age = 3-5 years) and senescent (age = 11-16 years) female mountain goats. A cost of reproduction was not evident for prime-aged (age = 6-10 years) individuals. Estimates presented for average winter conditions (snow depth, March-April = 1.29 m).

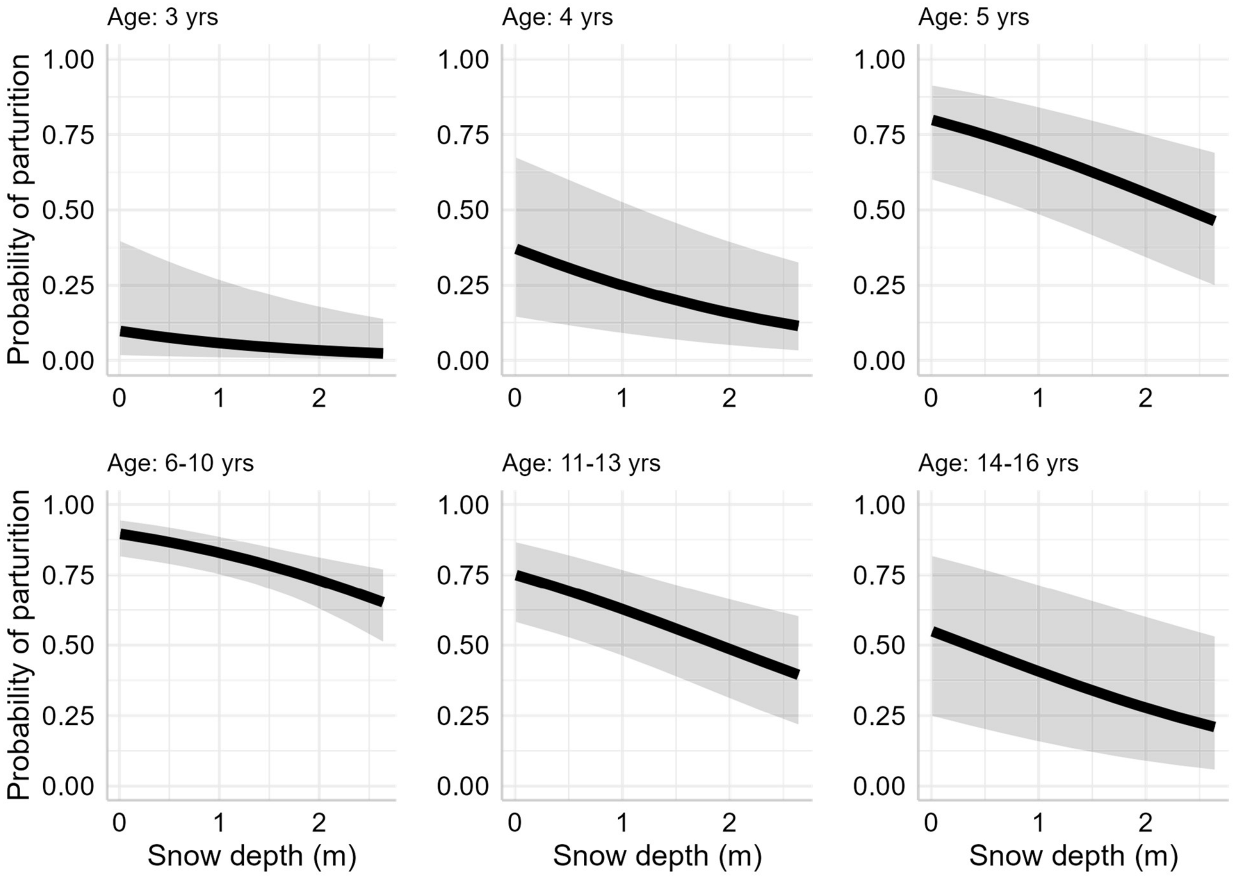

Figure 3.4. Effect of previous winter snow on age-specific reproduction for mountain goats in coastal Alaska during 2005-2021. Estimates are presented for individuals that successfully reproduced the previous year. Snow conditions are expressed as mean snow depth (m) during late-winter (March-April). Snow measurements were recorded at Eaglecrest, Juneau, Alaska, a mid-elevation site (1200 ft) representative of elevations used by mountain goats in the study region.

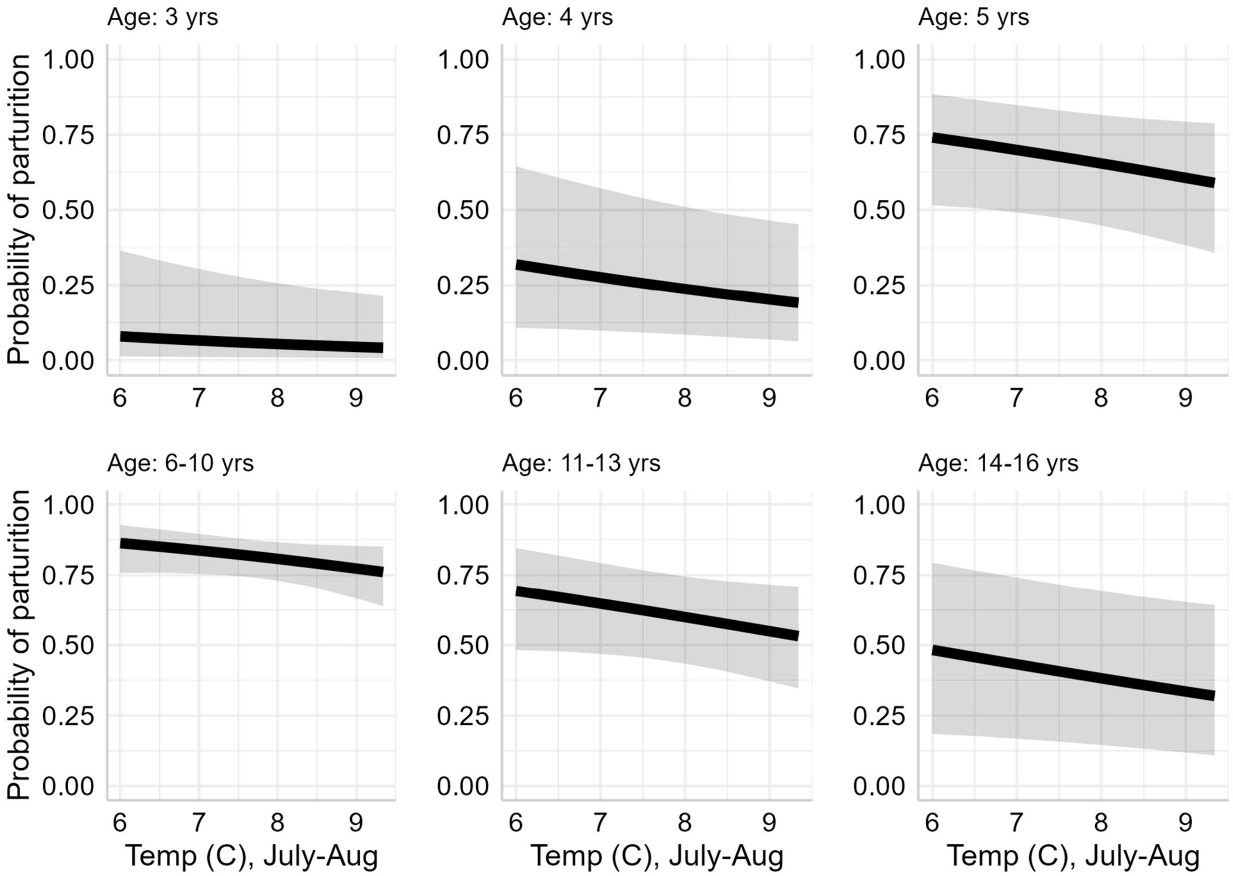

Figure 3.5. Effect of previous summer temperature on age-specific reproduction for mountain goats in coastal Alaska during 2005-2021. Estimates are presented for individuals that successfully reproduced the previous year, and based on average winter snow depth (1.29 m). Summer temperature is expressed as mean temperature (C) during July-August. Following White et al. (2011), temperature measurements were recorded at the Juneau Airport National Weather Service station and adjusted using the environmental lapse rate to represent the mean elevation (910 m) used by mountain goats in the study region during summer.

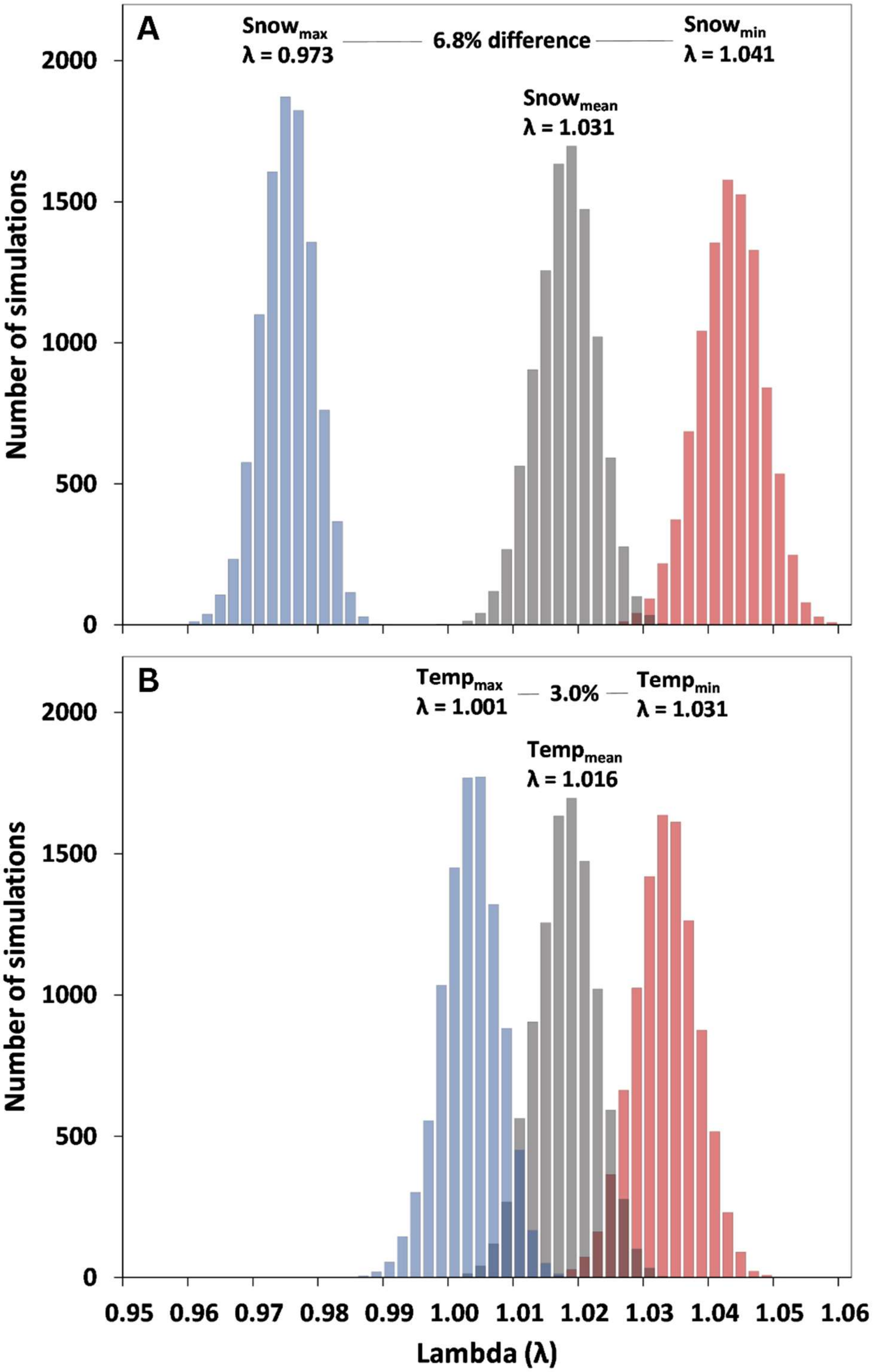

Figure 3.6. Variation in population growth (λ) based on simulated effects of winter snow depth and summer temperature on reproduction across the range of observed climatic conditions. Simulations (n = 1000 per scenario), conducted using a sex- and age-specific population model, spanned a 30 yr period and based on specifying the climate pattern of interest and holding all other input parameters at the mean value.

Chapter 4. Snow avalanches are a primary climate-linked driver of mountain ungulate populations.

Adapted from: White, K. S., E. Hood, G. J. Wolken, E. H. Peitzsch, Y. Bühler, K. Wikstrom Jones, and C. T. Darimont. 2024. Snow avalanches are a primary climate-linked driver of mountain ungulate populations. Communications Biology, 7: 423.
https://www.nature.com/articles/s42003-024-06073-0

4.1 Chapter Summary

Snow is a major, climate-sensitive feature of the Earth’s surface and catalyst of fundamentally important ecosystem processes. Understanding how snow influences sentinel species in rapidly changing mountain ecosystems is particularly critical. Whereas effects of snow on food availability, energy expenditure, and predation are well documented, we report how avalanches exert major impacts on an ecologically significant mountain ungulate - the coastal Alaskan mountain goat (*Oreamnos americanus*). Using long-term GPS data and field observations across four populations (421 individuals over 17 years), we show that avalanches caused 23-65% of all mortality, depending on area. Deaths varied seasonally and were directly linked to spatial movement patterns and avalanche terrain use. Population-level avalanche mortality, 61% of which comprised reproductively important prime-aged individuals, averaged 8% annually and exceeded 22% when avalanche conditions were severe. Our findings reveal a widespread but previously undescribed pathway by which snow can elicit major population-level impacts and shape demographic characteristics of slow-growing populations of mountain-adapted animals.

4.2 Introduction

Climate change is occurring rapidly in mountain environments (Hock et al. 2019, Pepin et al. 2022), imposing profound changes to sensitive ecological communities and processes. Multiple and novel stressors can harm species such as alpine ungulates, which have specialized adaptations and narrow biophysical niches (Parmesan 2006, Natori and Porter 2007, White et al. 2018). Questions remain, however, about potential demographic implications and their underlying mechanistic drivers (White et al. 2018, Lovari et al. 2020). Seasonal snow conditions might play a central role, and can act as a primary influence on ungulate population dynamics (Penczykowski et al. 2017, Boelman et al. 2019). Identified mechanisms are largely ecological and physiological, with changes in snow depth and distribution altering energetic costs of locomotion, vulnerability to predation, and accessibility and quality of forage in both summer and winter (Dailey and Hobbs 1989, Jędrzejewski et al. 1992, Pettorelli et al. 2007, Berger et al. 2018). We take a different focus, showing here how snow avalanches act as a direct, physical process that cause high levels of mortality and strongly influence demography in mountain wildlife populations.

Mountain ungulates are behaviorally predisposed and morphologically adapted to steep, rugged terrain to avoid the risk of predation (Figure C1) (Sarmento and Berger 2020). Such specialization, however, may carry other risks. Specifically, slopes that provide effective refugia from predators are also subject to frequent avalanching. Indeed, avalanche mortalities have been described for several ungulate species (Jonas et al. 2008b, White et al. 2011, Conner et al. 2018, Skladanowski et al. 2021). However, the difficulties associated with systematically documenting avalanche fatalities, which requires marking and long-term monitoring of individuals across broad geographies in dangerous mountain conditions, have precluded a definitive demographic assessment. To address this gap, we combined an extensive, individual-based mountain goat field monitoring data set with spatially explicit avalanche terrain data to quantify how avalanches influence the population ecology of mountain wildlife.

We collected data on mountain goats and their environment in southeastern Alaska, USA. The area's Coast Mountains are characterized by steep, rugged topography, with avalanche activity observed across the full vertical range of habitat occupied by mountain goats (0 to >1500 m). To quantify mountain goat exposure to and mortality from avalanches, we affixed global positioning system (GPS) and very high frequency (VHF) radio-collars to 421 animals from four populations over a 17-year period (*n* = 1218 mountain goat years). The four populations inhabit a ~500 km domain characterized by a broad range of biogeographic settings (Figure 4.1A).

4.3 Methods

4.3.1 Study system

Mountain goats were studied in four separate areas across a broad geographic range in coastal Alaska (5537 km^2; Figure 4.1 and Table C1) from 2005-2022. This area is within the Coast Mountains biogeographic region (Gallant et al. 1995). Mean monthly temperatures range from -2 to 14°C and mean annual precipitation is 1400 mm in Juneau (Fellman et al. 2014), the area's most populous city. Across the region, annual precipitation ranges from 1 to >8 m and winter snowfall ranges from 0.5 to > 3 m of snow water equivalent (Shanley et al. 2015). During the study period, annual snowfall at sea level in Juneau averaged 233 cm with a range of 89-501 cm.

The region is part of the world’s largest contiguous coastal temperate rainforest and composed primarily of Sitka spruce-western hemlock (*Picea sitchensis-Tsuga heterophylla*) forests at lower elevations (below 450-750 m). At higher elevations, subalpine and alpine habitats dominated by krummholtz forest, low-growing herbaceous meadows and ericaceous heathlands are widespread and persist to elevations of about 1400 m. The geologic terrain is complex and strongly influenced by terrain accretion and uplift processes (Stowell 2006). The resulting landscape is highly fractured and dominated by steep, rugged topography that is fragmented by active glaciers, icefields, high-volume river systems and marine waters (Stowell 2006). The avalanche paths in this study extend from sea level to 2000 m and include a variety of aspects as a result of the complex topography of the Coast Mountains.

Mountain goats in this region are widespread and occur at low to moderate densities, typical of northern coastal areas inhabited by the species (White et al. 2016, Jessen et al. 2022). Populations exhibit a high degree of local-scale population genetic differentiation, with limited movement among geographically discrete mountain complexes (Shafer et al. 2011, 2012, White et al. 2021a). Mountain goats are habitat specialists and select steep, rugged terrain in close proximity to cliffs and exhibit seasonal variation in altitudinal distribution (White et al. 2012, Shafer et al. 2012, White and Gregovich 2017). Mountain goats are partially migratory, with some individuals, depending on study area, residing in alpine and subalpine habitats throughout the year (White and Gregovich 2018, Shakeri et al. 2021). However, most individuals conduct short-distance (5-10 km), seasonal migrations involving annual movements between high-elevation alpine summer habitats and forested, low-elevation wintering areas (White et al. 2012, White and Gregovich 2018, Shakeri et al. 2021). Downslope migrations tend to correspond with the first major snowfall events at high elevation (i.e., mid-October), while upslope migrations are timed with onset of the spring snow ablation and pre-parturition period (i.e. early-May) (White et al. 2012). Individuals in Lynn Canal are highly migratory and, like mountain goats on the Cleveland Peninsula, primarily use low elevation forested habitat during winter months, while individuals in Klukwan and Baranof more frequently employ mixed-migration strategies, more often utilizing higher-elevation subalpine and alpine habitats where avalanche exposure is greater (Smith and Raedeke 1982, White et al. 2012, White and Gregovich 2018)(Figure C5). Impacts of human development and activity in the study area are, generally, minimal. Nonetheless, low-intensity or localized activities do occur and include regulated hunting, ground- and air-based recreational tourism, timber harvest and mining (White and Gregovich 2017, 2018, White et al. 2021a). The large mammal predator-prey communities in this area are intact and, in addition to mountain goats, key species include: moose (*Alces alces*), Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), wolves (*Canis lupus*), coyotes (*Canis latrans*), black bears (*Ursus americanus*), brown bears (*Ursus arctos*) and wolverines (*Gulo gulo*); though local variation occurs relative to species distribution and abundance (MacDonald and Cook 1996, White et al. 2012).

4.3.2 Mountain goat monitoring

Adult male and female mountain goats were captured using standard helicopter darting techniques (White et al. 2021b). During handling all animals were fitted with mortality-sensing very high frequency (VHF) and/or global positioning system (GPS) radio-collars (Telonics Inc., Mesa, AZ). GPS radio-collars were programmed to acquire a GPS location at 6-hr intervals; ancillary activity sensor and temperature measurements were collected over a 15-min evaluation period commencing at the initiation of the GPS location acquisition attempt. Age of animals was determined by counting horn annuli (Brandborg 1955, Smith 1988) and, in some cases, cross validated by examination of tooth eruption patterns (for young animals) (Brandborg 1955) and/or cementum analysis of incisors (for deceased animals; Matson's Laboratory, Milltown, MT). Capture and handling procedures complied with all relevant ethical regulations for animal use and were approved by the Alaska Department of Fish and Game Institutional Animal Care and Use Committee (protocols 05-11, 2016-25, 0078-2018-68, 0039-2017-39) and followed American Society of Mammalogists guidelines (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

Following capture, animals were typically monitored at least once per month (often multiple times per month) via aerial telemetry to determine whether animals were alive or dead. Survival status was also determined via examination of GPS radio-collar location, activity and temperature sensor data, an approach that often enabled temporal determination of death to within a 6-hr time window. In cases where animals were determined to have died, an initial fixed-wing aerial reconnaissance of the site was conducted and followed up with a ground-based examination to determine context and causes of death, to the extent possible. Due to safety and logistic considerations, ground-based examinations were typically conducted after initial aerial reconnaissance and determination of death. Due to the delay, it was not always possible to definitively distinguish between non-avalanche related causes of death (i.e. due to scavenging of carcasses). However, avalanche-caused mortality determinations were definitive and associated with carcasses being buried under, or associated with, avalanche debris and located within active avalanche paths.

4.3.3 Avalanche simulations and mapping

Avalanche hazard indication maps were developed from terrain analysis, downscaled climate model reanalysis, and numerical simulations of avalanche runout dynamics. Object-based image and terrain analyses were used with a digital terrain model (DTM; 5-m resolution) to determine avalanche potential release areas outside of closed canopy, conifer forest areas (Bühler et al. 2018a, 2018b). Dynamically downscaled climate reanalysis (4-km resolution)(Lader et al. 2020) was used to calculate the maximum snow depth increase over three days in the 1981-2010 climatology, which was used to determine the avalanche release depth for each potential release area. We recognize that biologically meaningful avalanche activity can occur within closed-canopy forests but maintain that such events are very uncommon in southeast Alaska relative to avalanche activity in alpine areas. As such, for this large-scale approach we assumed that closed canopy, conifer forest areas were not prone to significant avalanche activity and restricted our automated mapping of potential release areas to landcover types outside this designation. Potential release areas and release depths were then used in the numerical dynamic avalanche model Rapid Mass Movement Simulations (RAMMS)(Christen et al. 2010) to simulate millions of individual avalanches within the study areas and map avalanche hazard following the large scale hazard indication modelling approach developed by Bühler et al. (2022)(Bühler et al. 2022). Mapped avalanche hazard zones were further used to confirm that all mortalities classified as avalanche-related were located in avalanche hazard zones.

4.3.4 Mountain goat spatial analyses

Mountain goat GPS radio-collar location data were compiled and subsequently filtered, using methods described by D'Eon et al. (2002)(D'Eon et al. 2002) and D'Eon and Delparte

(2005)(D'Eon and Delparte 2005), to ensure geolocational accuracy. Using a geographical information system (GIS), mountain goat GPS location data were intersected with avalanche hazard indication maps to determine relative proportion of time each individual mountain goat spent in avalanche terrain during months when avalanche mortalities occurred (Oct-May). We defined avalanche terrain as avalanche potential release areas and runout paths combined, as both features comprised equivalent risk to mountain goats. Proportional use of avalanche terrain was calculated for each individual and coded based on whether the individual did or did not die in an avalanche. Monthly and seasonal differences in proportional use avalanche terrain was analyzed in relation to fate using paired students t-tests, with $P < 0.05$ denoting statistical significance.

4.3.5 Mountain goat mortality and survival estimation

As described above, causes of mortality were ascertained for every deceased individual. All causes of mortality were summarized as either being caused by an avalanche or other, non-avalanche related cause(s), including unknown (Table C3). Cause-specific mortality was summarized for each population across all years of study as well as by month and study area. Survival of radio-collared animals was calculated for the annual cycle (June-May), at monthly time steps, using the Kaplan-Meier estimator (Pollock et al. 1989). This method allows for staggered entry and exit of newly captured or deceased animals, respectively. While post-capture effects were not evident in our study, we implemented a conservative approach and excluded mountain goats for survival analysis for three days after capture (following Wagler et al. 2022)(Wagler et al. 2022). Survival was estimated using only avalanche-caused mortality cases in order to determine the proportion of radio-marked animals that died due to avalanches (i.e. population-level mortality) for each year and study area. To ensure our sample was representative of the overall adult population, we conducted annual capture events to compensate for mortality losses, and maintain balanced sex and age classes in our sample of marked individuals (Prichard et al. 2012). On average, 11% of study populations were marked and monitored each year (based on mark-resight aerial survey sightability estimation)(White et al. 2016); a large proportion and overall sample size (n = 421 individuals) for deriving reliable estimates of avalanche-related survival (Murray 2006).

4.4 Results

4.4.1 Avalanche mortality in mountain goats

To determine cause of mortality, we intensively monitored survival status and identified the timing and location of mortality events. We found that avalanches comprise a major source of mortality, accounting for 23 to 65% (mean = 36%; n = 93) of average annual mortality, depending on population (n = 258; Figure 4.1B). Avalanches were a more common cause of mortality for females (41%, n = 39) compared with males (33%, n = 54). These mortalities predominantly (61%) comprised prime-aged (4-9 yrs old) individuals for both females (54%) and males (67%), age classes that otherwise have the highest survival rates and reproductive contribution (Figure C2, C3) (Mainguy et al. 2009, White et al. 2011, 2018). Avalanche mortality varied spatially and temporally across populations in relation to geographic, climatic, and ecological characteristics of regional study areas, being highest on Baranof Island (65%, n = 51), relative to Klukwan (39%, n = 71), Cleveland Peninsula (29%, n = 7), and Lynn Canal (23%, n = 129; Figure 4.1B). Avalanche mortalities occurred across nine months of the year, and peaked when snow conditions were most unstable during early season snowpack development (October and November) and the spring melting period (April and May; Figure C4).

The high levels of mortality highlight the challenges mountain ungulates face in mitigating avalanche risk. Avalanche formation involves the interaction among meteorological conditions, snowpack, and terrain. Exposure to avalanche hazard depends largely on topography and the prevalence of structural weaknesses in the snowpack that vary in space and time (Schweizer et al. 2003). While we did not explicitly test whether mountain goats select specific terrain types to avoid avalanches during risky periods, the complex and dynamic physical interactions that create avalanche vulnerability are likely difficult to detect among wildlife, minimizing opportunity for development of behavioral strategies to avoid avalanche hazards in areas and periods of snowpack instability. Thus, compared to mortality mechanisms such as predation (for which most attempts end in prey escape) and winter starvation that can be mitigated by learning and behavioral adaptations, avalanches may represent a 'wicked problem'; that is, there are limited opportunities for trial-and-error learning due to the catastrophic outcomes that follow initial exposure (Hogarth et al. 2015, Fisher et al. 2022). By extension, opportunities for and pace of fine-scale behavioral adaptation may be constrained because risk perception of such cryptic and stochastic processes is likely weak and not strongly linked to heritable variation of behavioral responses (Endler 1986).

4.4.2 Costs of living dangerously

We hypothesized that putatively stochastic avalanche mortality events would be linked, in aggregate and across populations, with the amount of time mountain goats spend in avalanche terrain during months with snow cover. Accordingly, we modelled the potential release area locations (Bühler et al. 2018b) and the maximum spatial extent of simulated individual avalanches within the geographic range of the study populations using Rapid Mass Movement

Simulation (RAMMS), a numerical dynamic avalanche simulation model (Christen et al. 2010). Delineating avalanche hazard zones allowed us to quantify prevalence and use of avalanche terrain in winter for individual mountain goats, assess the physical setting of avalanche mortality sites, and, in some cases, track the precise locations of avalanche entrainment and burial of killed individuals (Figure 4.2). We then evaluated whether exposure to avalanche hazard varied seasonally by intersecting temporally referenced GPS radio-collar locations (n = 801,410 locations, 367 individuals) with the avalanche hazard spatial data layer (Figure 4.2).

Mountain goat use of avalanche terrain was widespread and linked to mortality. Avalanche release areas and paths constitute most (62%) of the alpine and subalpine footprint across the winter range. There was little variability in the proportion of avalanche terrain in the three largest study areas, which ranged from 57% in Lynn Canal to 67% in Klukwan; however, in the smallest study area, Cleveland Peninsula, avalanche terrain comprised only 17% of the wintering area (Table C1). Across all months and populations, mountain goats that died in avalanches exhibited significantly higher use of avalanche terrain (67±3%, n = 85) than those that did not die in avalanches (54±2%, n = 282, t =3.643, $P < 0.01$), a pattern that we likewise observed in finer-scale temporal analyses (i.e., for each individual month during the snow period; Figure 4.3, Table C2). Use of avalanche terrain varied substantially among populations, helping to explain observed spatial differences in avalanche mortality. Lynn Canal and Cleveland Peninsula, where animals used avalanche terrain less than 40% of the time in winter months, had the lowest proportion of avalanche mortalities. The Klukwan and Baranof populations, where animals occupied avalanche terrain more than 70% of the time in winter, had avalanche mortality rates roughly double those of the other areas (Figure 4.1B, C5).

4.4.3 A new view of snow and mountain ungulate population dynamics

Avalanche mortality patterns scaled up to reveal population-level implications. Estimated from radio-marked individuals, the proportion of the population that died from avalanches averaged 8% annually over the study (n = 43 population-years) and showed substantial spatial and temporal variation (Figure 4.4). Three populations had at least one year where more than 15% of the population died in avalanches, with peak annual avalanche mortality of over 22% of the Baranof population. Yet, we also documented years without avalanche mortalities in all four populations. Such variation suggests a complex relationship between snow and ungulate population ecology. In particular, the prevailing ecologically-focused view that snow depth and coverage is the primary snow-related control on ungulate fitness (Penczykowski et al. 2017) may not hold true for populations exposed to substantial avalanche hazard. Instead, intra-seasonal variability in winter weather, which controls the amount of snowfall and the formation of weak layers in the snowpack (Schweizer et al. 2003), may serve as a key physical driver of population-level mortality.

That population-level mortality from avalanches can exceed 20% in a single year highlights the role of stochastic environmental processes in the viability of inherently vulnerable alpine wildlife. Stochastic predation events in mountain bighorn sheep, for example, can precipitate acute population declines resulting in demographic restructuring and long recovery times (Festa-Bianchet et al. 2006). Avalanches may have similar implications for mountain goats. Growth rates of mountain goat populations are particularly low. For example, modeling from this and other areas – that has not incorporated the higher end of variation in annual mortality reported here – suggests that populations are able to sustain only limited annual removals such as by harvest (1-4% annually) (Hamel et al. 2006, Rice and Gay 2010, White et al. 2021a). In this context, avalanche-driven mortality, which is dominated by prime aged individuals (Figure C2), is capable of eliciting major demographic impacts and may underlie previously documented population declines and extirpation events in fundamentally tenuous mountain ungulate populations (Jacobson et al. 2004b, Hamel et al. 2006, Rughetti et al. 2011, DeCesare and Smith 2018, White et al. 2021a).

4.5 Discussion

Understanding mountain goat use of dangerous, avalanche-prone terrain requires broader consideration of how avalanches might influence multiple components of fitness. Mountain goats utilize steep terrain to mitigate predation-risk, with optimally selected slope angles (36-58°) (White and Gregovich 2017) closely corresponding with the most avalanche prone slopes (30-45°) (McClung and Schaerer 2006) (Figure C1). Additionally, scouring by avalanches provides nutritional benefits by generating and maintaining accessibility of forage rich, early-successional habitats during winter and spring (Figure 4.5) (Rixen et al. 2007, O'Leary et al. 2020). Yet, given sufficient exposure, avalanche terrain might manifest as a form of ecological trap. Ecological traps have traditionally been described in contexts where rapid and direct human-induced landscape change (i.e., habitat modification) results in ecological and evolutionary mismatch such that animals, in apparent error, select certain habitats associated with low fitness (Hale and Swearer 2016a). Avalanches may thus represent a novel form of ecological trap that is linked to similarly imperceptible seasonal changes in the structure of snow cover blanketing mountain environments. Whether and how climate change might lurk behind the pronounced avalanche-caused mortality we observed is unknown. If mountain goats evolved with similar snow conditions, the benefits of using avalanche-prone terrain must be extraordinarily high for populations to offset such high mortality (in proportion and magnitude).

Population-level variability in avalanche mortality highlights the role of migratory and wintering strategies in exposing mountain ungulates to avalanche hazard. Mountain goats in Lynn Canal are highly migratory and primarily use low elevation forested habitat during winter months, while individuals in Klukwan and Baranof employ mixed-migration strategies, often remaining at higher-elevation during winter to forage in subalpine habitats and on wind-scoured alpine ridges (Figure C5, "Methods – Study System"). Other mountain ungulate species exhibit comparable variation in partially migratory behavior, with a fraction of individuals residing year-round at high elevation while others migrate to low-elevation ranges during winter (Spitz et al. 2018, Lowrey et al. 2020). Partial migration is taxonomically widespread, especially among ungulates (Berg et al. 2019). Accordingly, our findings have broad implications, given that selection imposed by avalanches may reduce the prevalence of risk-prone higher-elevation resident strategies. Over time, climate-driven variation in avalanche hazard (Peitzsch et al. 2021) may alter fitness trade-offs among migratory phenotypes and, ultimately, the occurrence of partial migration in mountain systems.

Regardless of details yet unknown, climate change impacts on snow characteristics will loom large in the future of mountain ungulates. It will shift the spatial and temporal occurrence of avalanches (Ballesteros-Cánovas et al. 2018, Giacona et al. 2021), with implications for exposure and entrapment. Warming will intensify extreme precipitation during winter (Tabari 2021) and increase the occurrence of rain-on-snow events (Beniston and Stoffel 2016, Musselman et al.

2018), both of which contribute to snowpack instability and avalanche release (Hägeli and McClung 2003). Avalanche character will also shift from dry-snow dominated to wet slides (Ballesteros-Cánovas et al. 2018), with potentially increased avalanche mortality rates (Strapazzon et al. 2021). At the same time, future increases in snowline elevation in mountain environments may decrease avalanche hazard at lower altitudes (*43*). Yet, the demographic influence of avalanches on mountain ungulate populations is likely to persist into the future because both avalanche hazard (Giacona et al. 2021) and mountain ungulate ranges (Büntgen et al. 2017, White et al. 2018) are expected to shift upward in elevation as climate warms.

The high rates of avalanche mortality we document might be widespread among mountain wildlife, and if so carry important cultural and ecological implications. Mountain environments with avalanche hazard currently cover about 6% of Earth's land area and occur on all continents (Glazovskaya 1998), with 32 mountain ungulate species across 70 countries inhabiting a substantial fraction of this range (Shackleton 1997). Ungulate carcasses provide critical nutritional benefits to a diversity of avian and mammalian scavenging specialists (Figure C6) (Wilson and Wolkovich 2011, Prugh and Sivy 2020), and are particularly important in mountain food webs characterized by low ungulate biomass (*52)*. Moreover, Indigenous hunters have relied on mountain ungulate populations for millennia, a relationship involving important subsistence and cultural traditions including use of wool for weaving ceremonial robes and other regalia (Rofkar 2014, Tepper et al. 2017, Jessen et al. 2022). Mountain ungulates are also highly regarded among contemporary sport hunters and recreational wildlife-viewers worldwide. Thus, recognition that the persistence of ecologically and culturally important mountain ungulate populations relates to climate-linked phenomena in more diverse ways than previously acknowledged has far-reaching conservation and cultural implications for mountain ecosystems and people.

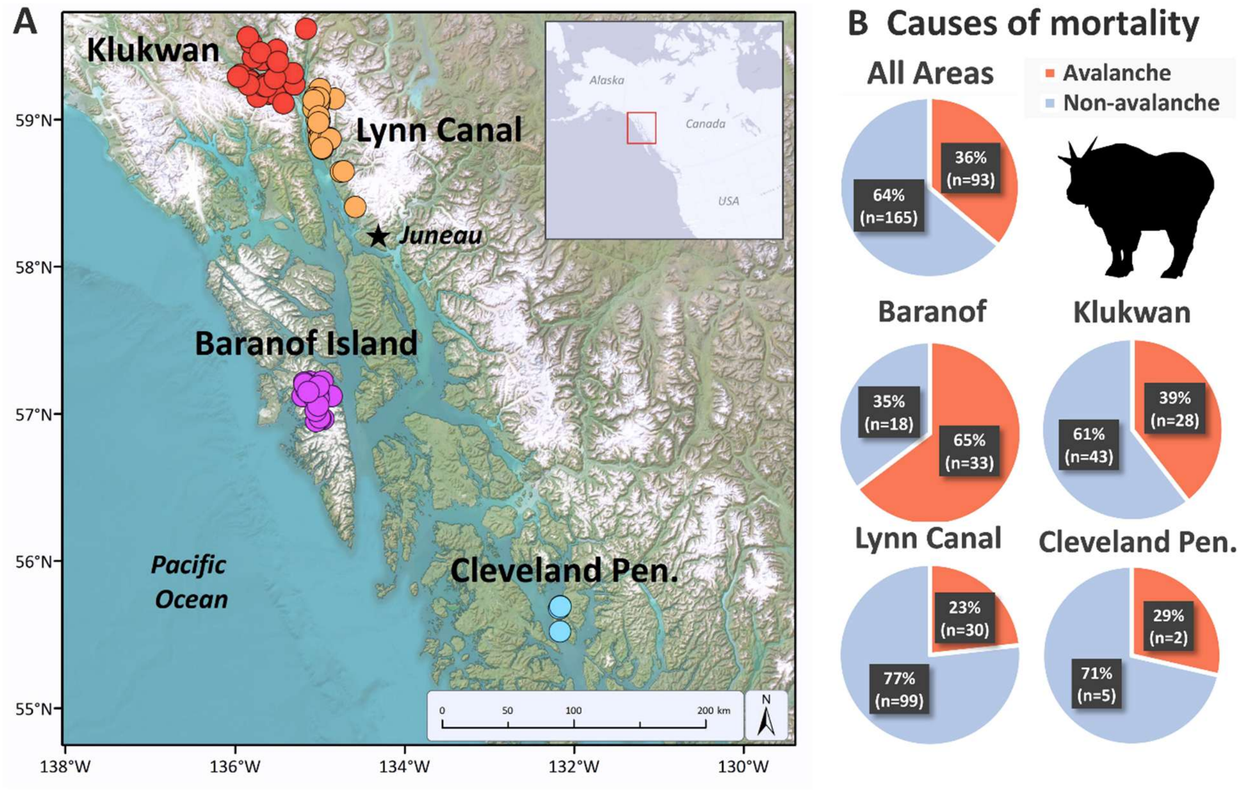

Figure 4.1. Avalanche mortality across populations. (A) Map depicting locations where radio-marked mountain goats died in avalanches during 2005 – 2022 in four study areas in southeastern Alaska. (B) The proportion of collared mountain goats that died from avalanches (n = 93) vs. non-avalanche related causes (n = 165) by study area and summarized across the region.

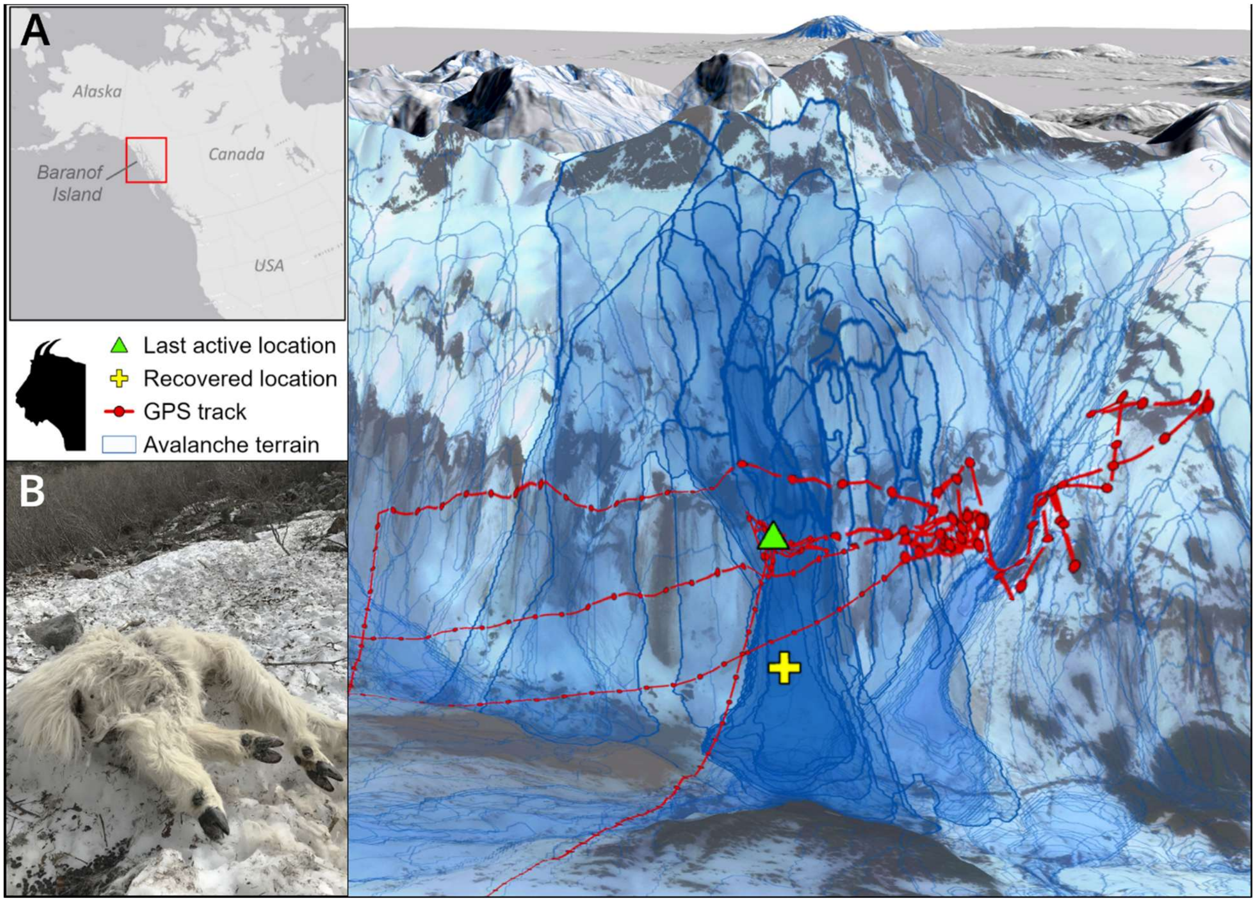

Figure 4.2. Estimation of mountain goat use of avalanche terrain. (A) Mountain goat study location where (B) GPS radio-collar location data were intersected with large-scale avalanche hazard indication maps to quantify individual mountain goat exposure to avalanches. The example 3D image illustrates typical winter use of avalanche terrain by an adult female mountain goat (BG041) that was caught (triangle) and subsequently buried (cross) by an avalanche in the Baranof Island study area in January 2016. Simulated avalanches that swept through the mountain goat mortality site are delineated (thick blue outlines), as well as all other avalanches in the area (light blue outlines). (C) A mountain goat (KG034) carcass partially buried in avalanche debris, near Klukwan, Alaska in May 2017. The animal suffered a depressed skull fracture among other critical injuries.

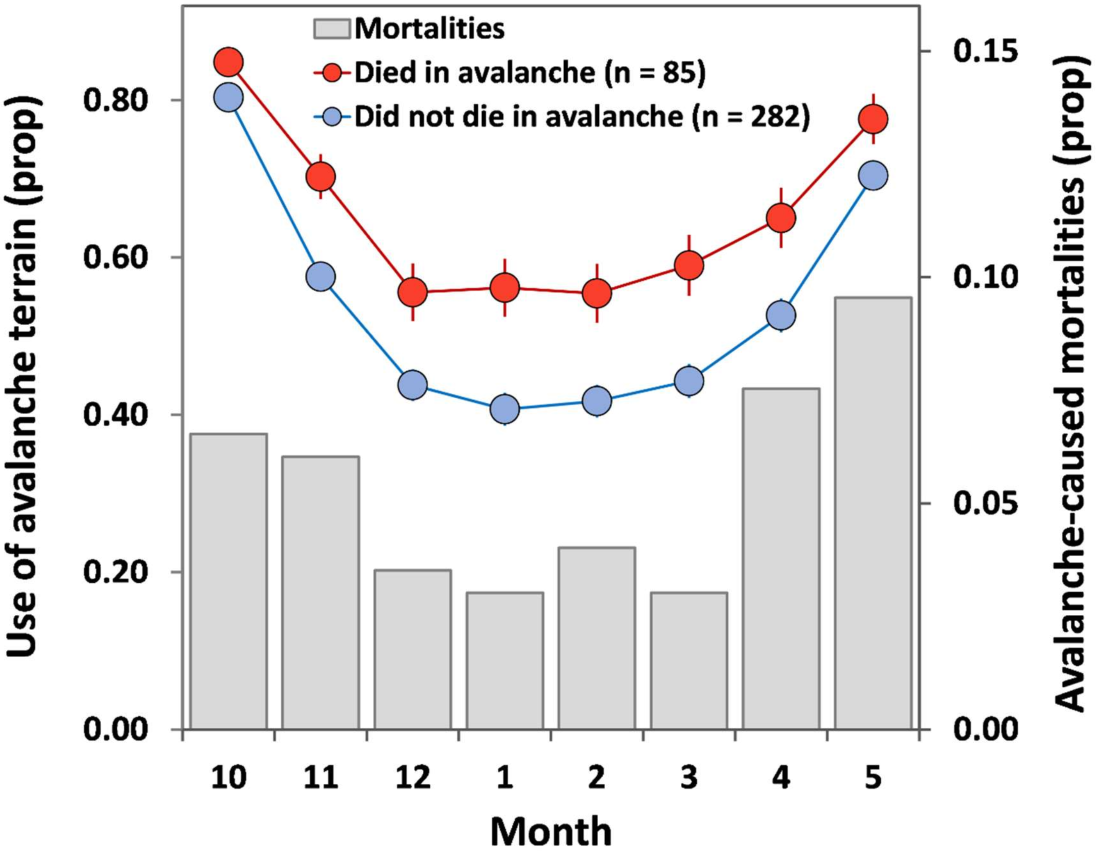

Figure 4.3. Mountain goat use of avalanche terrain and survival. GPS radio-collared mountain goats that died in avalanches (red circles, n = 85) used significantly more avalanche terrain each month relative to individuals that did not die in avalanches (blue circles, n = 282; $P<0.05$ for all months). Error bars represent 95% confidence intervals. Proportion of mortalities caused by avalanches is summarized by month for the months with snow (grey bars, secondary y-axis) and includes all GPS plus VHF radio-monitored animals (total avalanche mortalities, n = 93). Data were collected in four study areas in southeastern Alaska during 2005-2022. GPS radio-collar location data was collected from a subset (87%) of the total individuals monitored (n = 421). Avalanche terrain includes non-forested predicted avalanche release areas and avalanche paths derived using the RAMMS avalanche simulation model.

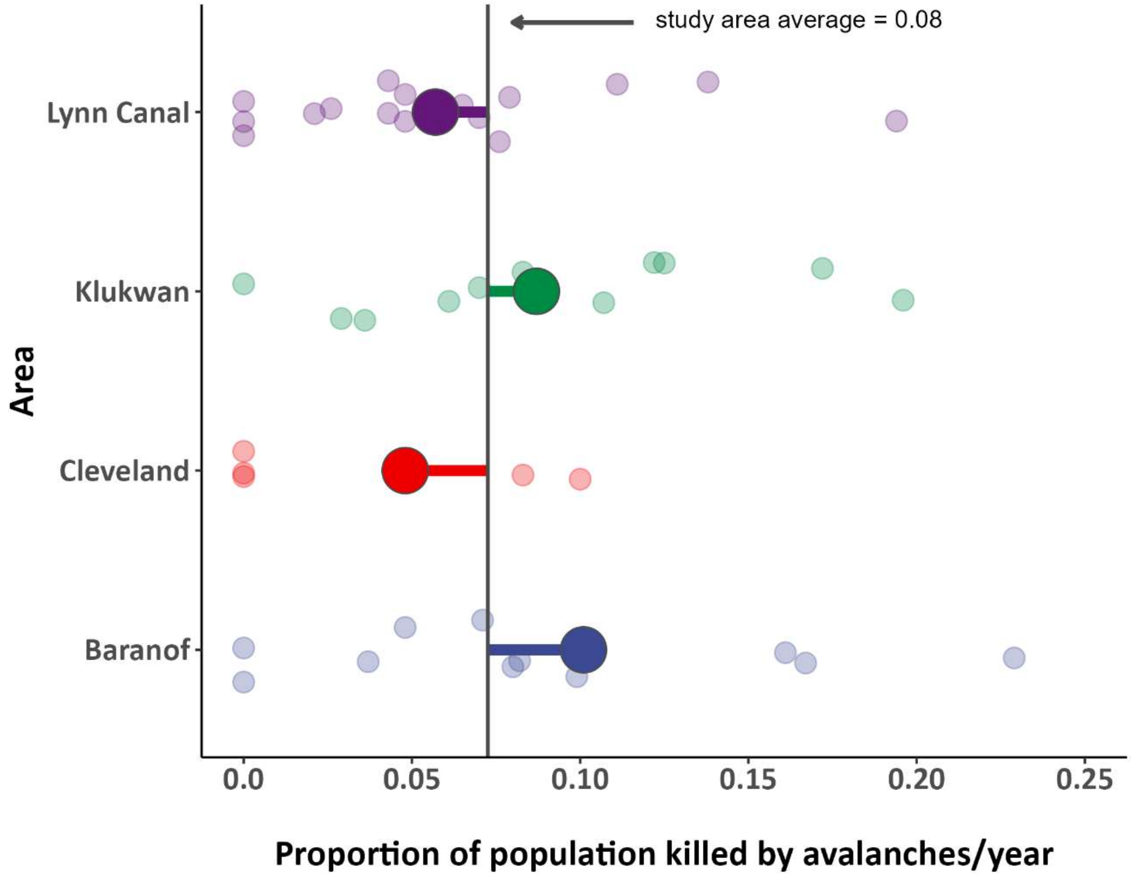

Figure 4.4. Spatiotemporal variation among populations in avalanche-caused mortality. Proportion of radio-marked mountain goats that died due to avalanches in a given year for each southeastern Alaska study area during 2005 - 2022. Average estimates are depicted by the large colored circles, and small circles represent annual study area estimates. The black vertical line delineates the average across all four study areas and years.

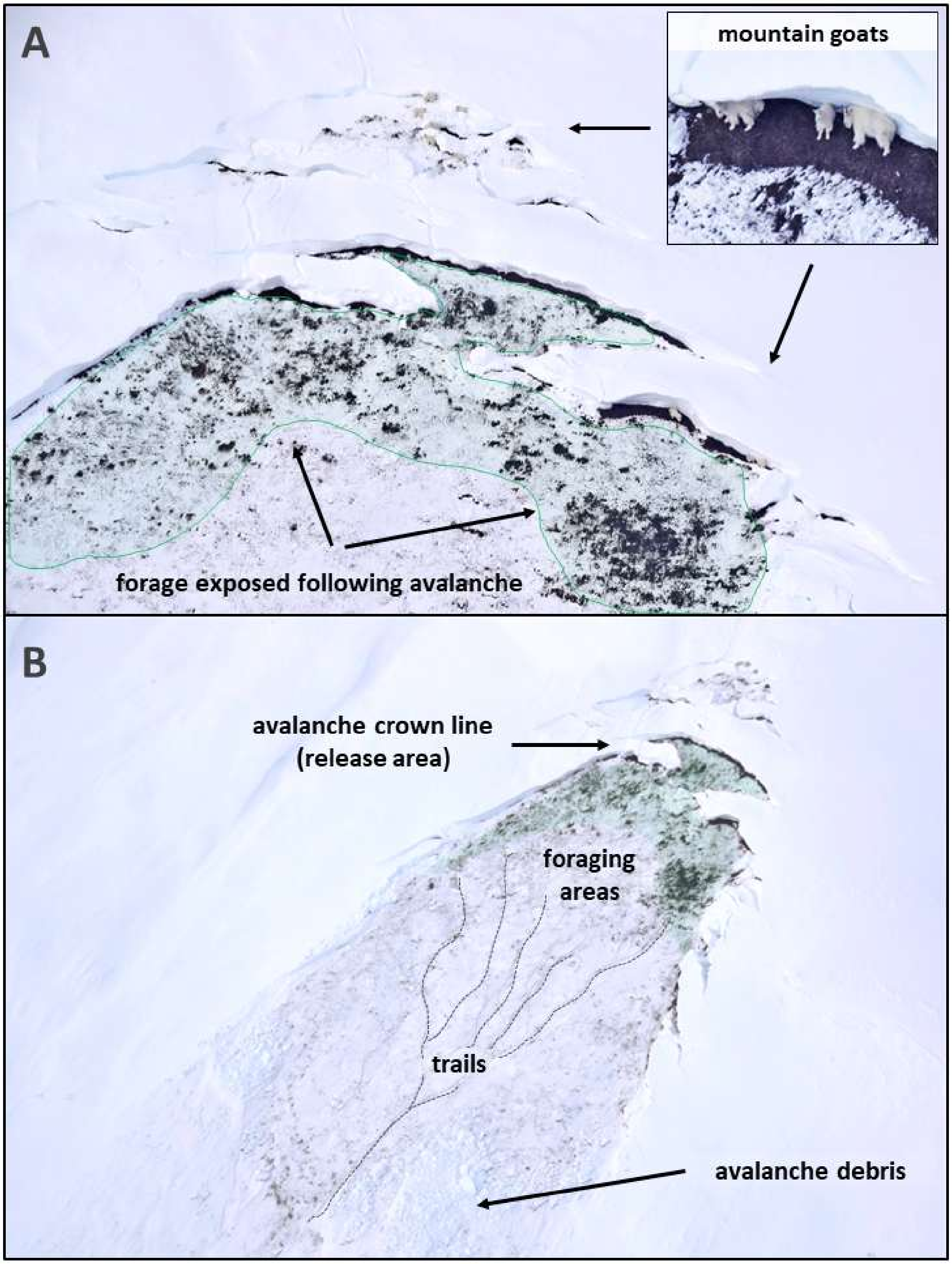

Figure 4.5. Avalanches and winter habitat use. (A) Photograph depicting mountain goat foraging following a glide avalanche, Summit Creek, Klukwan, Alaska, February 2021. Glide avalanches extend across the full depth of the snowpack and scour the landscape to expose underlying vegetation (primary foraging area highlighted in light green). Here, two groups of mountain goats used separate locations along the fractured crown line (black arrows). (B) Extensive tracks, visible in the image, indicate foraging activity on the newly exposed, vegetated slope.

Chapter 5. Snow avalanches and the impact of climate-linked extreme events on mountain wildlife population dynamics and resilience

Adapted from: White, K. S., T. Levi, E. Hood, and C. T. Darimont. *In review.* Snow avalanches and the impact of climate-linked extreme events on mountain wildlife population dynamics and resilience. *Global Change Biology*.

5.1 Chapter Summary

Climate is changing rapidly in mountain environments, giving rise to increasing variability in weather, incidence of extreme events and alteration of the cryosphere. Natural hazards, such as snow avalanches, and the ecological communities they impact may be particularly sensitive to such change. While avalanches may impose both ‘good’ and ‘bad’ effects on mountain ecosystems, the direct impacts that lead to mortality have particularly important implications for future viability and resilience of slow-growing alpine wildlife populations. Here, we studied a sentinel species of mountain environments – the coastal Alaskan mountain goat (*Oreamnos americanus*) – using long-term field data from individually marked animals (600 individuals over 44 years) in a quantitative modeling framework to understand of how avalanches influence demographic processes. Specifically, we developed and parameterized a sex- and age-specific population modeling approach to simulate the effects of avalanche-caused mortality on population growth rate (λ). We examined a range of ecologically relevant scenarios based on empirically-observed states of avalanche-caused mortality. During years when avalanche impacts are severe, populations can experience significant additive mortality and population declines (up

to 15%). Due to low reproductive rates, such impacts can lead to long demographic recovery times (up to 11 years, or ~1.5 mountain goat generations). Thus during the course of a typical mountain goat lifetime significant avalanche-linked perturbations can be expected to occur, suggesting that meaningful demographic signatures of avalanche impacts are generationally recurrent and routinely imbedded in population histories. From a conservation perspective, such impacts are striking, and highlight the utility of employing a quantitative modeling approach to predict possible effects of avalanches, and extreme events more broadly, on mountain ungulate population dynamics and viability. Our work explicitly builds upon recent findings about the importance of avalanches on mountain-adapted animal populations and has implications for the cultural and ecological communities that depend on them.

5.2 Introduction

Environmental change plays an important role in driving population dynamics and patterns of biodiversity (Ozgul et al. 2010, Bellard et al. 2012, Mills 2013, Gilbert et al. 2020). Increasingly, such dynamics are influenced by variation in weather conditions and linked to longer-term processes of climate change (Bellard et al. 2012, Harris et al. 2018). Of principal concern is the increasing occurrence of extreme events that may have catastrophic, long-lasting effects on populations and ecological systems (Smith 2011b, Ummenhofer and Meehl 2017, Sergio et al. 2018, Walsh et al. 2020). Such impacts may shift ecological baselines and hold potential compromise viability and even extirpate species, particularly specialists with narrow biophysical niches (Smith 2011a, Urban 2024). Despite such extraordinary impacts, our understanding of how extreme events affect populations is limited by the requirement to monitor populations for long periods of time to allow for the impact of rare events to be accurately quantified (Maxwell et al. 2019). Whereas important theoretical and empirical progress has been made, knowledge gaps remain (Smith 2011b, Ummenhofer and Meehl 2017).

Alpine ecosystems deserve special attention. Mountain environments comprise 25% of Earth's terrestrial surface, harbor a disproportionate fraction of global biodiversity, and are particularly sensitive to shifts in atmospheric conditions, including extreme events (Hock et al. 2019, Rahbek et al. 2019, Pepin et al. 2022, Urban 2024). Existing evidence indicates that climate is changing rapidly in mountain areas, altering snow and temperature regimes in significant ways and catalyzing impacts on sensitive ecological communities and processes (Pepin et al. 2022, Schmeller et al. 2022, Eckert et al. 2024). In these systems, effects of climate change may be more strongly influenced by increases in the frequency of extreme events than by changes to average conditions. Snowcover in mountain regions, for example, is sensitive to shifts in weather and climate patterns due to changes in water vapor advection and air temperature lapse rates (Gultepe 2015). Specifically, due to orographic effects, mountains often receive substantial precipitation, with the fraction falling as rain or snow often hanging in the balance of small temperature fluctuations – but manifesting with outsized effects on the physical environment (Roe 2005, Shanley et al. 2015, Musselman et al. 2018). Such dynamics not only alter the abundance of snow but its physical structure and stability.

The disproportionate impacts of climatic variability and extreme events in mountain environments carry important implications. Snow avalanches, for example, are driven by changes in the structure and stability of the snowpack and have been shown to exert strong ecological effects on diverse alpine plant and animal communities (Rixen et al. 2007, Bebi et al.

2022, White et al. 2024b). Specialized mountain wildlife populations can be particularly affected, with avalanches comprising a major source of mortality (Jonas et al. 2008a, White et al. 2024b). For example, recent work indicated that annual mortality from avalanches can exceed 20% in some years for mountain goat (*Oreamnos americanus*; Figure 5.1) populations in coastal Alaska (White et al. 2024b). At such rates of mortality, avalanches could produce extreme demographic perturbations and represent an important climate-linked driver of stochastic environmental change – that is, one that largely occurs at random, and likely offering limited opportunity for local adaptation.

Mountain wildlife populations might be particularly vulnerable to stochastic and ecologically extreme events, given that animals in alpine ecosystems often persist in small, isolated populations. Mountain bighorn sheep (*Ovis canadensis*), for instance, experience short-term but intense, and apparently unpredictable, predation events that precipitate acute population declines, resulting in demographic restructuring and long recovery times (Festa-Bianchet et al. 2006, Turgeon et al. 2024). Snow avalanches may have demographically analogous implications. Indeed, avalanches are an important agent of change in mountain systems and are difficult to predict, arising through multiple, complex mechanistic pathways linked to terrain characteristics, synoptic meteorology, local weather chronology, snow pack evolution, and extreme events (Schweizer et al. 2003, McClung and Schaerer 2006). Yet, the impacts of snow avalanches may differ from predation events in important ways. For example, predation is selective and typically removes poorer quality young and old animals from a population (Hoy et al. 2021). Conversely, avalanches largely remove animals at random, including a substantial fraction of reproductively critical, prime-aged females (White et al. 2024b). Thus, the way stochastic extreme events impact population structure can vary, carrying important implications for population dynamics.

How populations might be affected will relate to life history characteristics. The severe environmental conditions in mountain ecosystems have led to specialized adaptations among alpine specialists, such as mountain goats, and typically involve conservative life-history strategies, low growth rates and resilience (Festa-Bianchet and Côté 2008, Festa-Bianchet et al. 2019). Individuals, for example, preferentially allocate energetic resources to survival at the cost of reproduction. This adaptation has led to low reproductive and realized growth rates (1-4%) among mountain goat populations (Hamel et al. 2006, Rice and Gay 2010, White et al. 2021a), relative to other northern ungulates. As a consequence, even small impacts can elicit deleterious changes that might entail prolonged recovery periods – raising pressing questions about the potentially important role stochastic processes and climate-linked extreme events, such as avalanches, might play in population trajectories. To date, such dynamics have not been quantitatively examined, and the specific demographic implications of variability in avalanche-linked mortality on population growth, viability, and recovery time is needed.

To advance our understanding of this important driver of mountain ungulate population dynamics and viability, we developed and implemented a population dynamics modeling approach for simulating the effects of varying levels of avalanche-caused mortality on mountain goat population growth and recovery times. We parameterized a sex-and age-specific population projection model using a spatially and temporally extensive, 44-year known-fates data set collected from mountain goats throughout coastal Alaska (n = 14 study sites, 600 individuals)

(White et al. 2011, 2018, 2021, this study). Using a subset of the data for which avalanche-caused mortality data were systematically recorded (n = 4 study sites, 421 individuals, 17 yrs; White et al. 2024), we estimated the relationship between avalanche-caused mortality and annual mountain goat survival. This sub-model was used to quantify the degree to which avalanche mortality was additive vs. compensatory, and was integrated into our population model to simulate the effects of avalanche mortality on population growth rate (λ). We designed simulations to assess population responses across a range of scenarios encapsulating the variation observed during our long-term avalanche mortality studies (n = 43 study area years) to explicitly examine the impacts of extreme avalanche-caused mortality events. We also assessed the resilience of simulated populations to extreme events by calculating recovery time to baseline, pre-avalanche levels (assuming populations resumed average growth rates following the simulated perturbation). We provide ecological context of our findings by estimating recurrence intervals of events in relation to key population biology criteria (i.e. generation time) of mountain goats. Overall, our modeling framework fills an important knowledge gap by providing realistic insights about avalanche impacts on mountain goat population dynamics to inform management and conservation strategies. More broadly, it provides a deeper understanding about the increasingly important role of climate-linked perturbations and extreme events on population dynamics and resilience.

5.3 Methods

5.3.1 Study System

Mountain goats are a sentinel species of North American alpine ecosystems due to their sensitivity to variation in environmental conditions (White et al. 2024a). We studied mountain goats and avalanche relationships in four separate areas across a broad geographic range in coastal Alaska (5537 km^2; Figure 5.1) from 2005-2021. This area is within the Coast Mountains biogeographic region (Gallant et al. 1995) and is largely characterized by maritime snow climate; though transitional snow climate characteristics occur in the northernmost part of the Klukwan study area (McClung and Schaerer 2006). Mean monthly temperatures range from -2 to 14°C and mean annual precipitation is 1400 mm in Juneau (Fellman et al. 2014), a regionally representative location. Across the region, annual precipitation ranges from 1 to >8 m and winter snowfall ranges from 0.5 to > 3 m of snow water equivalent (Shanley et al. 2015). During the study period, annual snowfall at sea level in Juneau averaged 233 cm with a range of 89-501 cm (Juneau Forecast Office, National Weather Service, Juneau, AK).

The region is varied, rugged and influenced by avalanche activity. It is dominated by coastal temperate rainforest, composed primarily of Sitka spruce-western hemlock (*Picea sitchensis-Tsuga heterophylla*) forests at lower elevations (below 450-750 m). At higher elevations, subalpine and alpine habitats dominated by krummholtz forest, low-growing herbaceous meadows and ericaceous heathlands are widespread and persist to elevations of about 1400 m. The geologic terrain is complex and strongly influenced by terrain accretion and uplift processes (Stowell 2006). The resulting landscape is highly fractured and dominated by steep, rugged topography that is fragmented by active glaciers, icefields, high-volume river systems and marine waters (Stowell 2006). The avalanche paths in this area extend from sea level to 2000 m and include a variety of aspects as a result of the complex topography of the Coast Mountains. Overall, 62% of the area used by mountain goats in this area is comprised of terrain delineated as avalanche hazard (White et al. 2024b).

Mountain goats in this region are widespread and occur at low to moderate densities (0.4 – 1.2/km^2), typical of northern coastal areas inhabited by the species (White et al., 2016; White, unpublished data). Populations exhibit a high degree of local-scale population genetic differentiation, with limited movement among geographically discrete mountain complexes (Shafer et al. 2012, White et al. 2021a). Mountain goats are habitat specialists and extensively utilize steep, rugged terrain in close proximity to cliffs – a behavioral strategy that mitigates the risk of predation but also increases vulnerability to avalanche mortality (Shafer et al. 2012, Sarmento and Berger 2020, White et al. 2024b). Mountain goats are partially migratory and exhibit seasonal variation in altitudinal distribution, with some individuals, depending on study area, residing in alpine and subalpine habitats throughout the year while others migrate to low elevation wintering areas (White and Gregovich 2017, 2018, Shakeri et al. 2021). As such, wintering strategies are variable and influence their exposure to avalanche-risk (White et al. 2024b).

5.3.2 Mountain goat monitoring

Adult male and female mountain goats were captured using standard helicopter darting techniques (White et al. 2021b). During handling, all animals were fitted with mortality-sensing very high frequency (VHF) and/or global positioning system (GPS) radio-collars (Telonics Inc., Mesa, AZ). Age of animals was determined by counting horn annuli and, in some cases, cross validated by examination of tooth eruption patterns (for young animals) (Smith 1988) and/or cementum analysis of incisors (for deceased animals; Matson's Laboratory, Milltown, MT). Following capture, animals were typically monitored at least once per month (often multiple times per month) via aerial telemetry to determine whether animals were alive or dead. Survival status was also determined via examination of GPS radio-collar location, activity and temperature sensor data, an approach that often enabled temporal determination of death to within a 6-hr time window. In cases where animals were determined to have died, an initial fixed-wing aerial reconnaissance of the site was conducted and followed up with a ground-based examination to determine context and causes of death, to the extent possible. Due to safety and logistic considerations, ground-based examinations were typically conducted after initial aerial reconnaissance and determination of death. Due to the delay, it was not always possible to definitively distinguish among non-avalanche related causes of death (i.e. due to scavenging of carcasses). However, avalanche-caused mortality determinations were definitive and associated with carcasses being buried under, or associated with, avalanche debris and located within active avalanche paths. Capture and handling procedures complied with all relevant ethical regulations for animal use and were approved by the Alaska Department of Fish and Game Institutional Animal Care and Use Committee (protocols 05-11, 2016-25, 0078-2018-68, 0039-2017-39) and followed American Society of Mammalogists guidelines (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

5.3.3 Mountain goat population modeling

To examine demographic responses of mountain goat populations to simulated avalanche perturbations, we took several steps (Figure 5.2). First, we updated and expanded a post-breeding, sex- and age-structured (20 age classes) population model previously described by White et al. (2018, 2021b). Briefly, the model is parameterized using sex- and age-specific vital rate estimates statistically derived using a spatially and temporally extensive, 44-year (1977-

2021) known-fates data set collected from mountain goats throughout coastal Alaska (n = 14 study sites, 600 individuals, 1,910 mountain goat yrs; Figure 5.2, D1, D2) (White et al. 2011, 2018, 2021, this study). Age-specific fecundity was estimated based on direct observations of radio-marked females (n = 180 females, 640 female-yrs) during the parturition period in a subset of three study areas during a 16-yr period (2005-2021) (White et al. 2018, 2021, unpub. data). Neonate survival was parameterized following Rice and Gay (2010), as described in White et al. (2018). Although the model was originally designed to simulate population trajectories given user specified climate inputs (White et al. 2018) and human harvest removals (White et al. 2021), we simulated dynamics of non-harvested populations at average climate conditions. Such specifications were also used to calculate the stable stage distribution used for the initial population size input. To account for uncertainty, we sampled from within the error distribution of beta coefficients (i.e. sex- and age-specific survival) accounting for covariance structure among coefficients using the RMark package in R (Laake 2013). We also modeled interannual variation in annual fecundity as a lognormally distributed random variable. The standard deviation of the distribution was parameterized using the observed variance across the range of interannual fecundity estimates (SD = 0.106, n = 16 years, 2006 – 2021; data described above). This approach enabled us to simulate demographic stochasticity using empirical data collected in our study system.

5.3.4 Modeling effects of avalanche mortality on survival

Using the framework described above to calculate annual change in population size over time, we next developed a sub-model to simulate how avalanches remove individuals from a population across a range of different scenarios. The sub-model was parameterized using a subset of the of our data for which cause-specific mortality was systematically collected (n = 4 study areas, 421 individuals, 1218 mountain goat years, 2005-2021). While the complete (44-yr) data set used for developing the population model (see above) enabled derivation of the best possible estimates of sex- and age-specific survival, it did not allow for estimation of avalanche-specific mortality. Thus, we used an two-step approach for simulating the effects of avalanches on population dynamics. First, we used the full data set to parameterize the population model and then, employed the sub-model to simulate avalanche impacts on projected population dynamics.

Avalanche-risk is considered to be an unpredictable phenomenon, and mortality is expected to be largely additive and remove animals from a population at random (White et al. 2024b). To quantify the extent that avalanche mortality is additive and reduces overall survival, we estimated the relationship between the proportion of individuals within each life-stage (following sex- and age-structures defined by White et al. 2011, 2018) that died due to avalanches and total annual survival. Parameterization of this relationship enabled estimation of annual survival per life-stage for any given rate of avalanche-caused mortality. We estimated this relationship using a binomial generalized linear mixed modeling approach (package “lmer”, R version 4.3.1; Bates et al. 2014, R Core Team 2023). This model, parameterized using known-fate data from each individual animal (coded based on whether an animal died due to avalanches, other causes or survived), was used to estimate annual survival for each life-stage (following White et al. 2011) at the average population-level avalanche mortality rate observed during our study (i.e. 7%; White et al. 2024). We also used the model to estimate annual survival, for each life-stage, across the range of observed avalanche mortality values (i.e. 0 - 23%; White et al. 2024). We then calculated the ratio between each of these survival values (i.e. specified at each avalanche mortality rate) and the survival value that occurred at mean avalanche mortality rate. This ratio, we refer to as the 'proportional survival change factor', was derived because estimated survival probabilities (used in the population model, see above) incorporate mortality due to all natural causes, including avalanches. Thus, the proportional survival change factor enabled adjustment of total annual survival in relation to changes in avalanche mortality from the mean. For example, annual survival at the user-defined avalanche mortality is equal to the survival at average avalanche mortality multiplied by the change in survival in relation to varying avalanche mortality:

$$\hat{S}_{avy} = \hat{S}_{avy\_mean} \times \hat{S}_{change} \tag{1}$$

where, $\hat{S}_{avy}$ = annual survival at a specified level of avalanche mortality, $\hat{S}_{avy\_mean}$ = annual survival at the mean level of avalanche mortality, and $\hat{S}_{change}$ = proportional survival change factor, or difference between survival estimated at the mean avalanche mortality value and the specified avalanche mortality value.

Thus, the proportional survival change factor represents the expected annual survival for a particular avalanche mortality rate divided by the survival at the mean avalanche mortality rate. For example, the proportional survival change factor is less than one if avalanche mortality increases above the mean value, and greater than one if it declines toward zero. We computed the proportional survival change factor for every life-stage, except neonates. As mentioned above, we parameterized offspring survival based on mean values reported in the literature (i.e. Rice and Gay, 2010). However, to account for the effects of avalanche mortality on neonates, we used the slope derived from our generalized linear model and computed the intercept by setting annual survival to the reported neonate survival value (as described above) and avalanche mortality set to the mean avalanche mortality rate. This enabled derivation of a linear equation for predicting neonate survival on the logit scale with the same slope used for other life-stages. This latter step involved an assumption that patterns of avalanche mortality among neonates were similar to older-age classes; a reasonable assumption given the tight maternal bond (and spatial co-occurrence) that persists through the first year of life between offspring and mothers, and associated nursery groups (Festa-Bianchet and Côté 2008).

5.3.5 Simulating effects of avalanche mortality

To simulate avalanche impacts on mountain goat population dynamics, we first specified the population-level avalanche mortality rate of interest and applied the appropriate proportional survival change factor for each life-stage. During each year of the simulation, this resulted in a new population state vector at the current time step of the model to account for the change in survival when varying avalanche mortality. We then projected the population to the next time step (i.e. year) using matrix multiplication, which incorporates baseline life-stage specific survival estimates derived using the entire long-term data set (i.e. calculated at the mean avalanche mortality rate), as well as age-specific fecundity estimates (described above).

To understand the implications of avalanches on mountain goat population growth and resilience, we conducted simulations across a range of avalanche mortality scenarios we observed during our long-term studies (White et al. 2024). Specifically, we simulated avalanche mortality across a range of empirically derived percentiles (min = 0%, mean = 7%, max = 23%;

Figure D3). We conducted 1000 simulations for each scenario over a specified time period (yearly increments) and summarized average annual population growth rate (λ). We chose an initial population size of 100, which corresponds with common population sizes among mountain goats in coastal Alaska (test simulations using different initial population sizes resulted in qualitatively similar results). For each set of avalanche mortality scenarios, we conducted simulations across two different temporal extents. First, we conducted simulations over a 2-yr period. This simulation length was designed to emulate a single annual avalanche mortality event (i.e. the proportion of the population killed by avalanches over a single winter season). We also conducted simulations over a longer, 30-yr period (i.e. greater than 3 generations, IUCN 2012). In this case, the specified avalanche mortality rate was applied to each year of the simulation, and was intended to emulate longer-term avalanche mortality driven change in population growth. In practice, differences in estimated effects of avalanche mortality on average annual population growth rate were minimal with respect to the length (yrs) of simulation runs.

5.3.6 Recovery time

In scenarios predicting population decline, we conducted a separate analysis to estimate the amount of time required for a population to re-attain initial population size. For these calculations we assumed average population growth rate (i.e. $\lambda = 1.015$; see below) following the simulated avalanche event (population decline). Specifically, we derived the recovery time for a particular percent decline and population growth rate as follows. After a population decline is x%, the resulting population is $(1 - \mathrm{x})\,N$. For a population growing at rate lambda after time t this population will be $(1 - \mathrm{x})\,N\,\lambda^t$. Setting this equal to the original population size N, we solve for the recovery time, t, to yield:

$$\text{Recovery time (yrs)} = \frac{\log\left(\frac{1}{1-\%\,decline}\right)}{\log(\lambda)} \quad (2)$$

where, % decline represents the decline in the population under a given scenario (x above) and λ corresponds to the realized annual population growth rate under average conditions. To account for variability in our estimates of recovery time, we also derived estimates using the 25th and 75th percentiles of the average annual population growth distribution (i.e. λ, mean = 1.015, λ_{25} = 1.009, λ_{75} = 1.020). Ultimately, we calculated recovery time for three ecologically relevant scenarios anchored to the species demographic characteristics: 1) the maximum perturbation (population decline) observed (i.e. 23% of the population killed by avalanches), 2) the maximum perturbation expected to occur during a typical mountain goat lifetime (generation time = 7.2 yrs), and 3) the perturbation level that would require a generation for recovery. The frequency distribution of population-level avalanche mortality events that occurred during our study (n = 43 study area years) was used to empirically estimate exceedance probability and ultimately recurrence interval (*sensu* Mays, 2011) for each specified avalanche mortality scenario and associated recovery time calculation.

5.4 Results

5.4.1 Effects of avalanche-caused mortality on total annual survival

Generalized linear mixed effects modeling quantified the relationship between avalanche-caused mortality and total annual survival of mountain goats, and was used to parameterize population modeling simulations (Table 5.1, Figure 5.3, D4). This sub-model was specified *a priori* to match the sex- and age-structure used in the population model and earlier survival analyses (*sensu* White et al. 2011, 2018, 2021). Annual survival estimates, under baseline (average) conditions, revealed similar sex- and age-specific patterns, as compared to previous estimates in this study system (White et al. 2011). Relatively low survival was estimated for old males ($\hat{S}$ = 0.61 ± 0.07) and females ($\hat{S}$ = 0.77 ± 0.06) with prime-age males ($\hat{S}$ = 0.82 ± 0.05) and females ($\hat{S}$ = 0.88 ± 0.04), young adults ($\hat{S}$ = 0.90 ± 0.04), subadults ($\hat{S}$ = 0.96 ± 0.04) and yearlings ($\hat{S}$ = 0.86 ± 0.19) exhibiting moderate to high annual survival. We specified the same generalized effect of avalanche mortality on annual survival across all sex- and age-categories (sample size precluded rigorous examination of potential interactions; Table 5.1, Figure 5.3, D4). Overall, this relationship revealed that avalanche-caused mortality consistently tracked total annual survival when avalanche mortality was between mean and maximum levels, but decreased when avalanche-caused mortality dropped below the mean (i.e., 7%; Figure 5.3). Thus, avalanche mortalities appear to be largely additive when occurring at high rates, while at low rates (< 7%) a small proportion of avalanche mortalities are compensatory.

5.4.2 Simulating effects of avalanche mortality

To illustrate how avalanche-caused mortality can influence population growth rates across a range of scenarios, we incorporated sex- and age-specific avalanche mortality relationships into our analytical framework and implemented population modeling simulations. Short-term (2-yr) single winter avalanche simulations indicated that under average conditions (i.e. 7% of a population killed by avalanches) mountain goat populations were expected to exhibit relatively low annual rates of growth (λ = 1.015, 25th percentile P_{25} = 0.999 , 75th percentile P_{75} = 1.033, Figure 5.4a). Under conditions where no animals were killed by avalanches, populations were expected to exhibit 7.0% annual population growth (λ = 1.070, P_{25} = 1.053, P_{75} = 1.089; Figure 5.4a). In contrast, during severe conditions (23% population-level avalanche mortality), populations were estimated to decline 15.5% decline ($\lambda = 0.845$, $P_{25} = 0.831$, $P_{75} = 0.860$; Figure 5.4a). Thus, across the range of conditions observed avalanche mortality is capable of shifting annual population growth by 22.5% (Figure 5.4a).

Longer-term (30-yr) simulations revealed similar patterns of avalanche impacts on average annual population growth across scenarios but showed less variation within simulations (Figure 5.4). Under average avalanche mortality conditions populations exhibited low annual growth rates ($\lambda = 1.016$, $P_{25} = 1.013$, $P_{75} = 1.019$, Figure 5.4b). In contrast, average annual population growth rate was higher ($\lambda = 1.066$, $P_{25} = 1.063$, $P_{75} = 1.070$, Figure 5.4b) when no animals were killed by avalanches, and substantially lower under the most severe conditions ($\lambda = 0.853$, $P_{25} = 0.850$, $P_{75} = 0.855$, Figure 5.4b). Across the range of scenarios examined, average annual population growth varied by 21.3% (Figure 5.4b). Notably, the 30-yr time period simulations enabled determination of the change in average annual avalanche-caused mortality required to cause populations to decline over the long-term. Specifically, if average annual avalanche mortality shifted from the current baseline (7%) to 8.8%, populations were predicted to have an equal likelihood of increasing or decreasing. That is, at this threshold ~50% of simulations predicted population decline over a 30-yr period.

We simulated population dynamics and recovery time associated with several illustrative scenarios that involved population declines. First, we considered the most extreme event (23% population-level avalanche mortality, 15.5% population decline, 43 yr recurrence interval, 2.3% annual chance of occurrence), followed by average annual conditions during the recovery phase. Under such a scenario, we determined that population recovery would not be attained for 11.2

years (P_{25} = 9.4, P_{75} = 12.9 yrs; Figure 5.5). We also calculated recovery time under a scenario of the maximum perturbation expected to occur during a typical mountain goat lifetime (16% population-level avalanche mortality, 7.3% population decline, 7.2 yr recurrence interval, 14% annual chance of occurrence) and determined that 5.1 years (0.7 mountain goat generations) would be required for recovery (Figure 5.5). Finally, we estimated it would take one mountain goat generation (7.2 yrs) for a population to recover following a year when 19% of the population was killed by avalanches (10.1% population decline, 14.3 yr recurrence interval, 7% annual chance of occurrence; Figure 5.5).

5.5 Discussion

Avalanches represent a major climate-linked driver of mountain goat populations and are capable of catalyzing extreme biological responses. Previous analyses revealed that avalanches comprise 36% (and up to 65%, depending on area) of mountain goat mortalities, and that prime-aged, reproductively critical individuals are heavily impacted (61% of all mortalities) (White et al. 2024b). Translated to the population-level, an average of 7% of a given population was estimated to be killed by avalanches annually, with mortality exceeding 22% in severe years (White et al. 2024b). Such high rates of mortality are striking and carry important implications for viability and resilience of slow growing, mountain adapted wildlife populations. Our population modeling approach, parameterized using extensive, long-term data, provided important quantitative insight and revealed that avalanches can elicit major population declines requiring extended periods (multi-generational, in some cases) for recovery to baseline levels. That avalanches are capable of exerting such pronounced and long-lasting impacts on populations has not previously been documented, and represents an important, new advance in our understanding of the effects of climate-linked factors, and associated change, on mountain wildlife populations.

Snow influences population dynamic processes in complex ways, often exerting strong impacts in mountain ecosystems. Ecological pathways though which snow influences demography have been extensively studied and include nutritional limitation (forage burial and nutritional dynamics), energetic costs of locomotion, and predation-risk (Penczykowski et al. 2017, Boelman et al. 2019, Reinking et al. 2022). These processes typically result in selective, often compensatory, removal of young and old individuals that are predisposed to mortality due heightened vulnerability, incomplete physical development or otherwise poor body condition (Gilbert et al. 2020, LaSharr et al. 2023b). Avalanches, on the other hand, represent a direct physical mechanism through which snow kills animals, largely removing individuals from a population at random, including reproductively critical prime-aged individuals that otherwise exhibit high survival (White et al. 2024b). Our modeling work reveals important insights about these dynamics, and involved empirical determination that avalanche mortality is primarily additive, except at low levels. That is, avalanches largely kill animals that would have otherwise survived (thus adding to baseline mortality rates), yet at low levels a small fraction of animals killed by avalanches would have died anyway (i.e. compensatory mortality). Translated into an applied example, our scenario-based simulations illustrated that mountain goat populations experiencing average levels of avalanche mortality are capable of exhibiting relatively modest population growth (i.e. $\lambda = 1.015$, similar to what has been described elsewhere for the species; Hamel et al. 2006, Rice and Gay 2010, White et al. 2021). However, during severe years avalanche mortality is capable of eliciting significant population declines (~15%) that can require extended periods (~11 years, or 1.5 mountain goat generations) before populations recover to baseline levels, provided average conditions persist during the recovery phase.

In the context of the species' biology and life-history characteristics, avalanches can clearly precipitate extreme demographic effects. Impacts may be exacerbated if conditions driving avalanche mortality, and associated demographic impacts, are temporally related with weather patterns that persist across consecutive years, leading to commensurately large cumulative demographic effects. For example, large-scale atmosphere-oceanic oscillations, such as the Oceanic Niño Index and other Pacific Oscillation indices, influence winter weather and avalanche occurrence and risk in mountain ecosystems across western North America (Mantua and Hare 2002, Haegeli et al. 2021), including within our coastal Alaska study area (Peitzsch et al. 2023). Alternating warm and cool phases associated with large-scale atmosphere-oceanic oscillations typically persist for multiple years (Mantua and Hare 2002), and hold potential to impose multi-year cumulative impacts on mountain goat demography via impacts to avalanche frequency. As such, our single year avalanche impact scenarios are likely conservative and negative impacts can be greater than we illustrate when multi-year climate oscillations occur. Alternatively, recovery times may accelerate if multiple persisting 'good' years follow a deleterious impact. These insights can have important practical implications. In an analytical context, for example, explicitly considering such dynamics can improve realism of modeling projections, and may be especially useful in applied settings where empirical field observations are available and allow for custom tuning of modeling simulations and projecting population performance.

The long-term data used to parameterize our modeling approach offers important insights about current and, potentially, projected future population dynamics for mountain goats in coastal mountain systems. For example, our data revealed that over the course of typical generation, a population is expected to experience an avalanche-caused mortality event eliciting a 6.8% decline, requiring 4.8 years for recovery to baseline levels. Thus, over the course of a mountain goat lifetime an individual is likely to experience a significant avalanche-linked population perturbation, with associated transient demographic effects altering population structure, impacting specific cohorts and exerting long-lasting effects (*sensu* Gilbert et al., 2020; Turgeon et al., 2024). Climate-linked impacts of avalanches are therefore meaningfully embedded in the history and trajectory of mountain goat populations on a routine, generationally recurrent basis. The impacts of these events, therefore, cannot be solely regarded as rare or extreme cases in isolation. Extreme events can result in severe (and long-lasting) demographic responses, and are of particular interest in relation to climate-linked phenomena (Ummenhofer and Meehl 2017, Maxwell et al. 2019). Shifting climate baselines and associated distributional extremes suggest historically rare events are likely to be more common (Smith 2011b). While extreme events are often defined using statistical criteria (i.e. 5% of occurrences, or years), from an ecological perspective it can be equally important to situate them in relation to a species' life-history characteristics and capacity to recover from perturbations (Bailey and Van De Pol 2016).

Whereas mountain goat populations have the capacity to recover from snow avalanche impacts, benefits of mild conditions appear to be outweighed by negative impacts of severe events. For example, in the most deleterious avalanche-caused mortality scenario, populations are expected to decline 17.0% ($\lambda = 0.845$) below baseline ($\lambda = 1.015$) levels, whereas during the most extreme positive scenario populations were only expected to increase 5.5% above the baseline (λ = 1.070). Thus, benefits of mild conditions are unable to equivalently compensate for negative effects that occur during winters with severe conditions. Avalanches have particularly strong effects on population dynamics because they act upon the vital rate (survival) that exerts the strongest effect on the species' population growth (Gaillard et al. 2000, Hamel et al. 2006), with negative impacts spanning a broader range of possible outcomes than positive effects. Considered in relation to climate change forecasts – that project distributional shifts in snow and greater climatological variability – favorable conditions (years with low avalanche mortality) would need to occur 2 – 3 times more frequently than extreme negative events to compensate for impacts, all other conditions being equal. Only in the Lynn Canal population did we observe a low occurrence of years (3 of 16 years, 18.7%) in which avalanches were predicted to elicit population declines (Figure D5). In other populations, years with predicted avalanche-driven declines were more common, occurring about 1 of every 3 years on Baranof Island (4 of 11 years, 36.3%) and nearly as common as favorable years in the Klukwan population (5 of 11 years declining, 45.4%; Figure D5).

Whether the rate of avalanche occurrences documented here persist over longer time horizons in the face of projected changes in climate is uncertain. Avalanches already represent a hard to perceive risk for animals (i.e. a 'wicked problem'; Hogarth et al., 2015; Fisher et al., 2022; White et al., 2024) and, according to recent syntheses (Eckert et al. 2024), patterns of avalanche risk are expected to change going into the future. Atmospheric rivers, for instance, and the extraordinary snowfalls they deposit in high elevation areas (Figure 5.1b), are expected to increase in frequency with climate change (Payne et al. 2020) and are disproportionately linked to elevated avalanche occurrence and risk (Hatchett et al. 2017). Such relationships represent an important mechanistic example of how extreme events can affect avalanche processes and, ultimately, demography of alpine wildlife. Upward shifts in snow linked to warmer winter temperatures (Shanley et al. 2015), however, may exert countervailing impacts and illustrate an alternative pathway by which mountain wildlife might increasingly benefit from projected climate-linked changes in snowcover and avalanche dynamics. The future prevalence of 'good' vs 'bad' avalanche years will loom large over the fate of mountain goats, and other similar mountain species.

Climatic variability represents an increasingly important driver of population dynamics and persistence worldwide (Parmesan 2006, Scheffers et al. 2016, Urban 2024). The pressing challenges associated with understanding and mitigating forecasted changes highlight the need to develop and implement analytical frameworks to acquire reliable and actionable knowledge. In this study, we describe and highlight the major role that ecologically extreme events, specifically avalanches, play in influencing the population dynamics and resilience of a culturally and ecologically significant mountain wildlife species. Integration of such knowledge into quantitative modeling approaches, such as those described here, represent a key tool for advancing mechanistic insights about the underlying demographic consequences of avalanches on population dynamics and for examining conservation-relevant scenarios. For example, our modeling approach enables examination of how variation in climate-linked processes explicitly impact population size, composition, growth rate and, ultimately, recovery time. Such knowledge is critical for devising appropriate, time-sensitive conservation decisions and to support longer-term strategic planning. Application of this, and similar, demographic modeling approaches have traditionally been underutilized among studies at the climate – ecology interface (Urban 2024) but offer an important means for assessing the underlying mechanisms and impacts of environmental variation on demography, viability and resilience of climate sensitive species. Such efforts are especially needed in mountain ecosystems that are otherwise relatively understudied yet particularly vulnerable to climate-linked impacts and extirpations (Marris 2007, Schmeller et al. 2022, White et al. 2024a, Urban 2024).

If climate change alters the distribution, frequency and character of avalanches, as has been suggested (Ballesteros-Cánovas et al. 2018, Giacona et al. 2021, Eckert et al. 2024), possible futures may include restructuring of mountain communities. Globally, thirty-two species of mountain ungulates across 70 countries occupy rugged, often avalanche-prone, alpine terrain. Many of these species exhibit similarly low demographic capacity, with several species already considered vulnerable or imperiled (Shackleton 1997). That avalanches comprise a major pathway by which snow can elicit substantial demographic effects on slow-growing, mountain-adapted animal populations has only recently been reported (White et al. 2024). Our work here builds upon initial descriptions, quantifying in detail the pronounced, sometimes multi-generational, impacts that avalanches can impose on mountain goat populations. The implications of such findings can be far-reaching. Mountain goats are an iconic species of North American mountain landscapes and their viability is central to the persistence of cultural and subsistence relationships that have endured for millennia (Rofkar 2014, Jessen et al. 2022, Greening (La’goot) 2024). The species also plays a key role in nutritionally subsidizing mountain carnivore food webs that rely on mountain goats, including those killed in avalanches (Figure D6). Thus, understanding the extent that mountain goat populations fluctuate in response to avalanches offers deeper insight into the functionality and dynamics of mountain ecosystems and communities – relationships that are tightly coupled with future changes in the climate and the cryosphere.

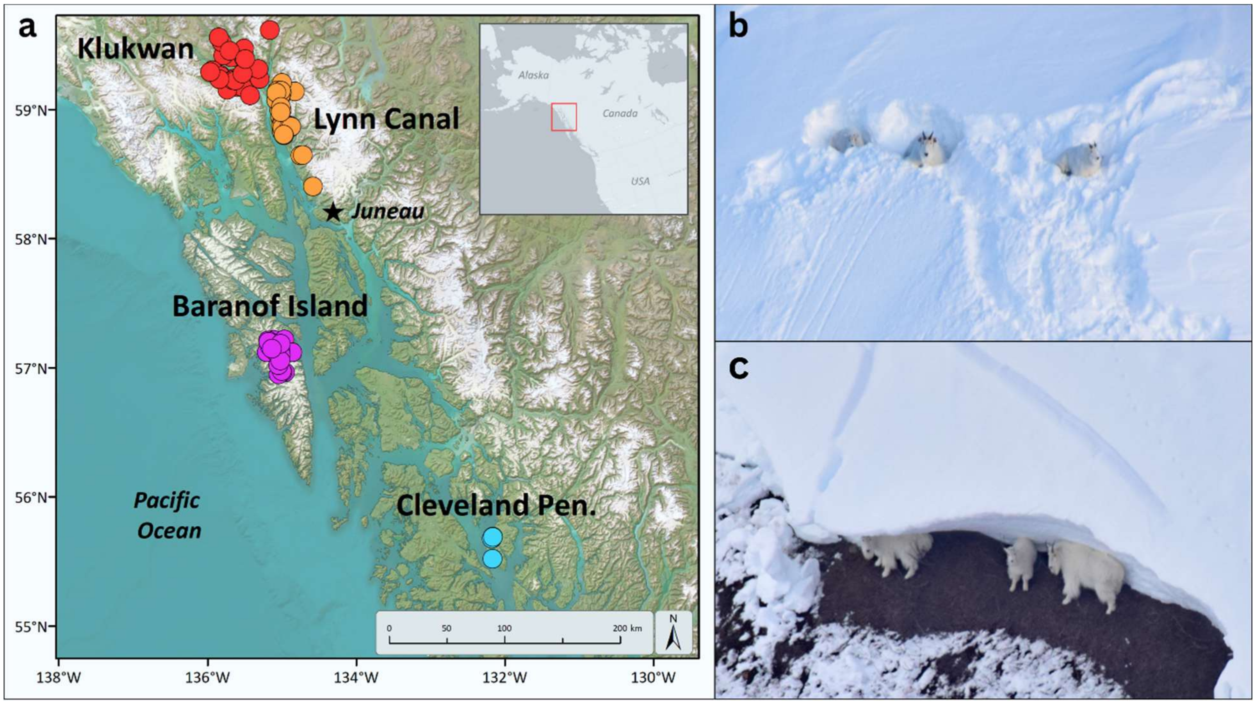

Figure 5.1. The mountain goat and avalanche study system. (a) Map depicting the four study areas and locations where radio-marked mountain goats were studied and died in avalanches during 2005 – 2021 in coastal Alaska. (b) Mountain goats in extensively excavated beds within mapped avalanche terrain following an extreme snowfall event (2.4 m over 6 days) associated with an atmospheric river weather system during December 2020, near Porcupine Mountain, Klukwan, Alaska. (c) Mountain goats sheltering beneath the fracture line of a mid-winter glide avalanche, Summit Creek, Klukwan, Alaska.

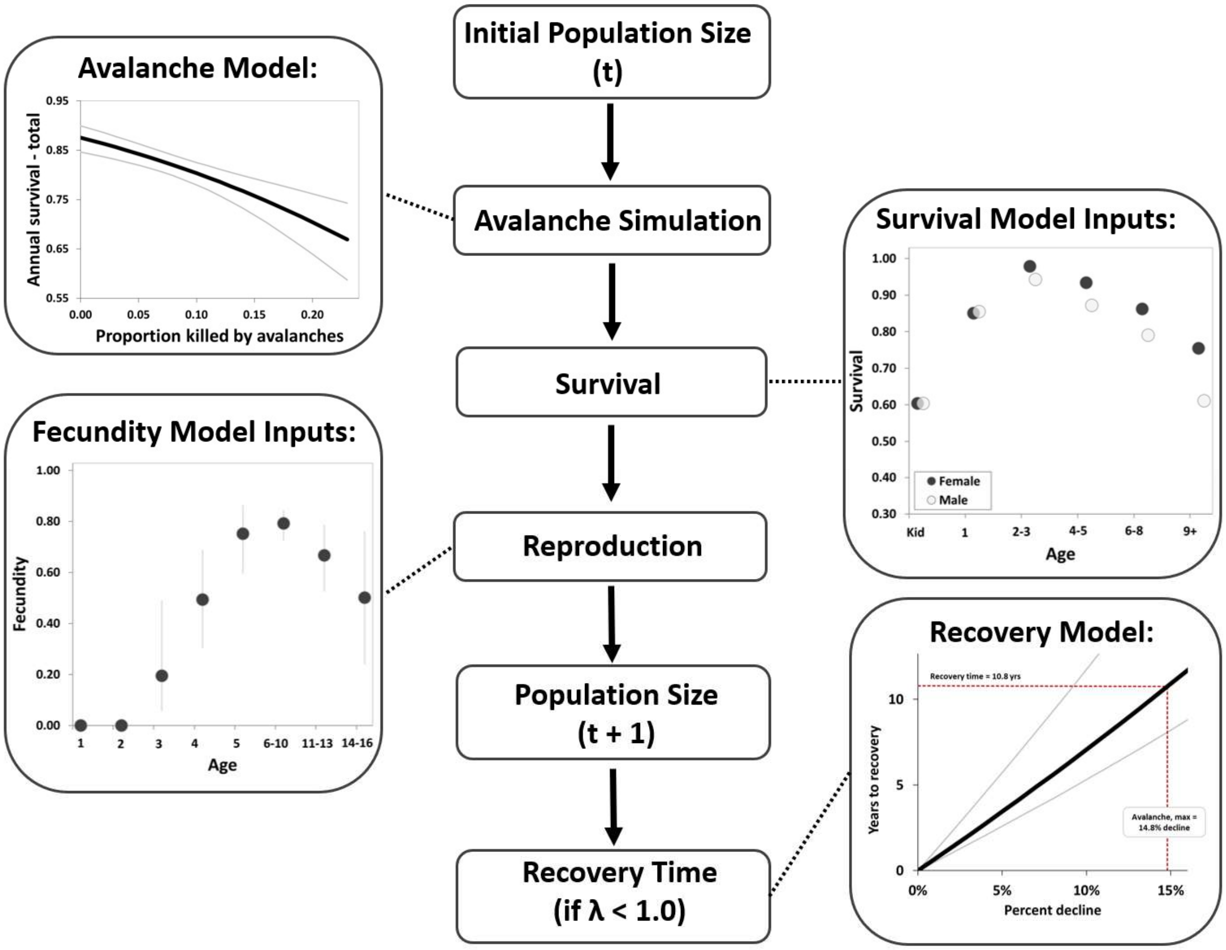

Figure 5.2. Conceptual diagram describing the dual-sex, post-breeding, age-structured population model. The model accounts for variation in sex- and age-specific fecundity and survival based on empirical data collected from radio-marked individuals in coastal Alaska. The avalanche sub-model (top left) modifies population size based on empirical relationships between avalanche mortality and annual survival, enabling scenario-based simulation of avalanche impacts on population trajectories. Recovery time (bottom right) was calculated for scenarios resulting in population decline. Population growth during the recovery phase was modeled to coincide with average annual population growth observed during our study (λ = 1.015).

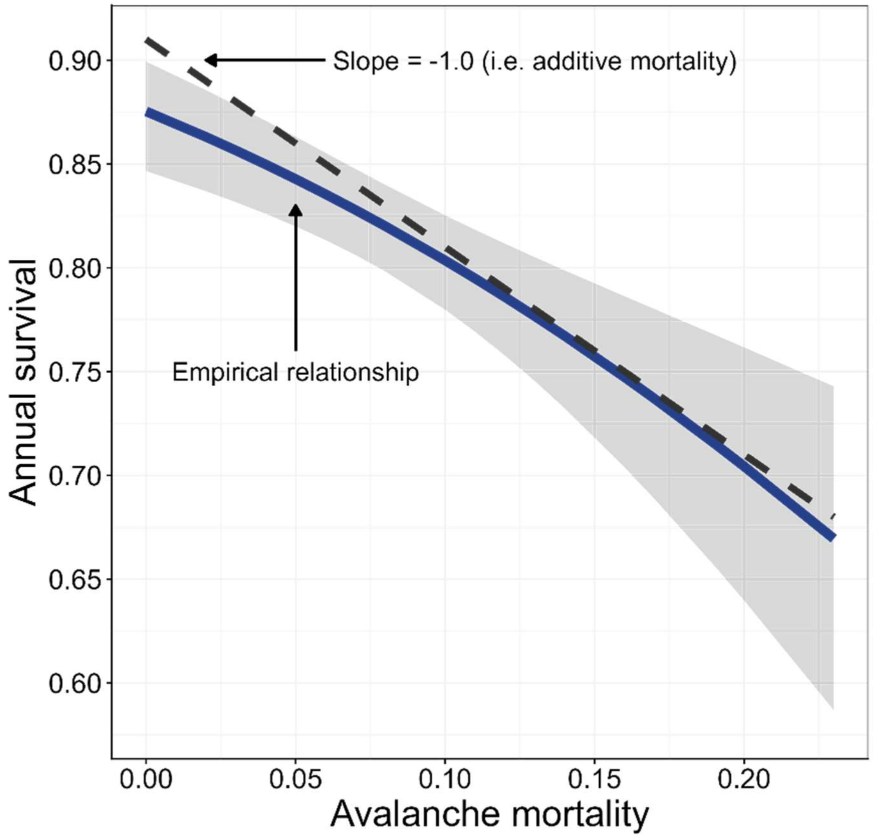

Figure 5.3. Diagram illustrating the relationship between the proportion of a mountain goat population dying in avalanches in a given year and total annual survival. The dashed black line illustrates a scenario where avalanche-caused mortalities are completely additive. The solid dark blue line describes the empirical relationship based on radio-marked mountain goats monitored in coastal Alaska during 2005-2021.

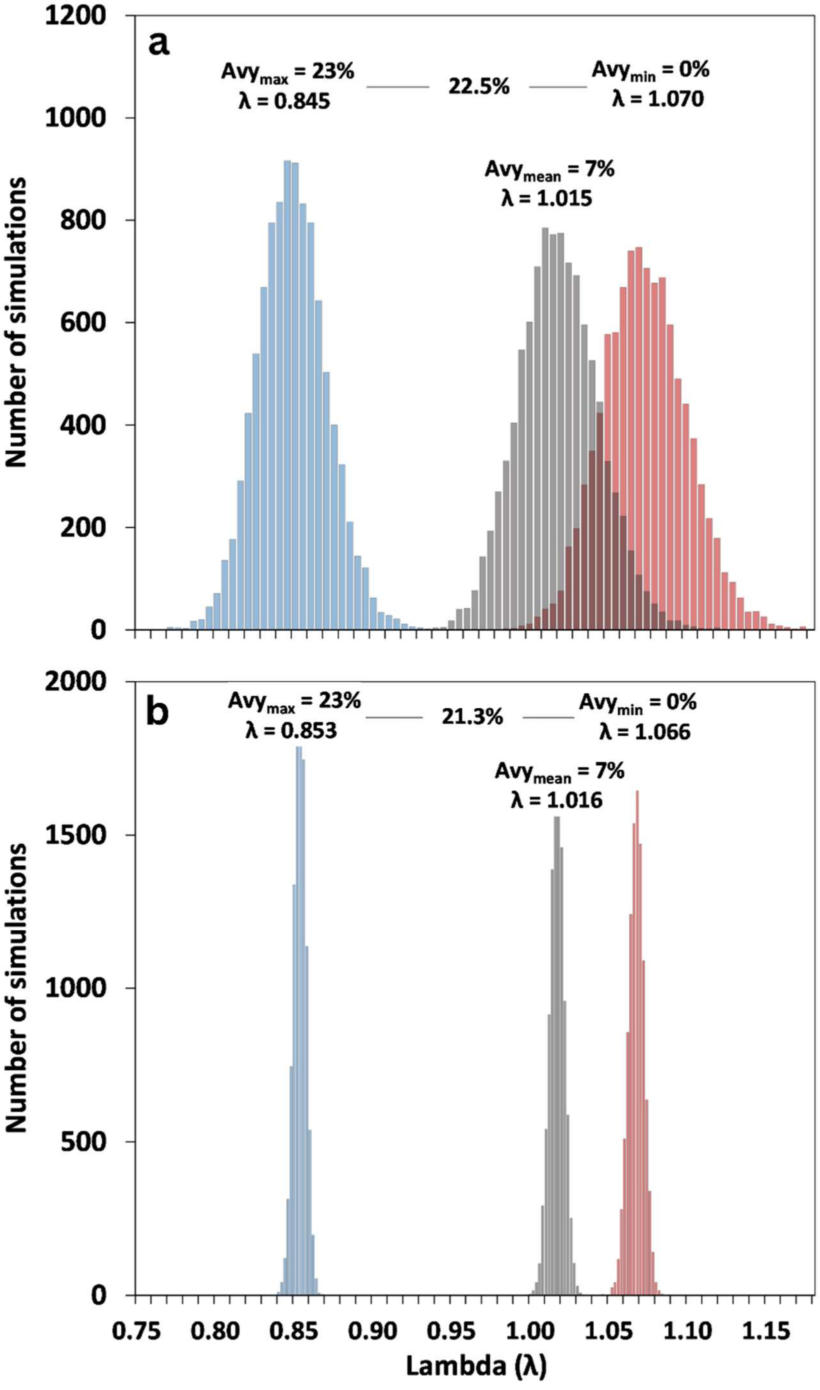

Figure 5.4. Variation in annual population growth (λ) across the range [minimum (Avy$_{min}$), mean (Avy$_{mean}$), and maximum (Avy$_{max}$)] of avalanche-caused mountain goat mortality observed in four areas of coastal Alaska during 2005 – 2021. Population growth estimates represent the average annual λ for each (a) 2-yr and (b) 30-yr model simulation. The difference in annual population growth between the 'best case' (Avy$_{min}$) and 'worst case' (Avy$_{max}$) scenario is annotated atop the panel. Each scenario was simulated 1000 times by randomly drawing input values from each parameter coefficient error distribution.

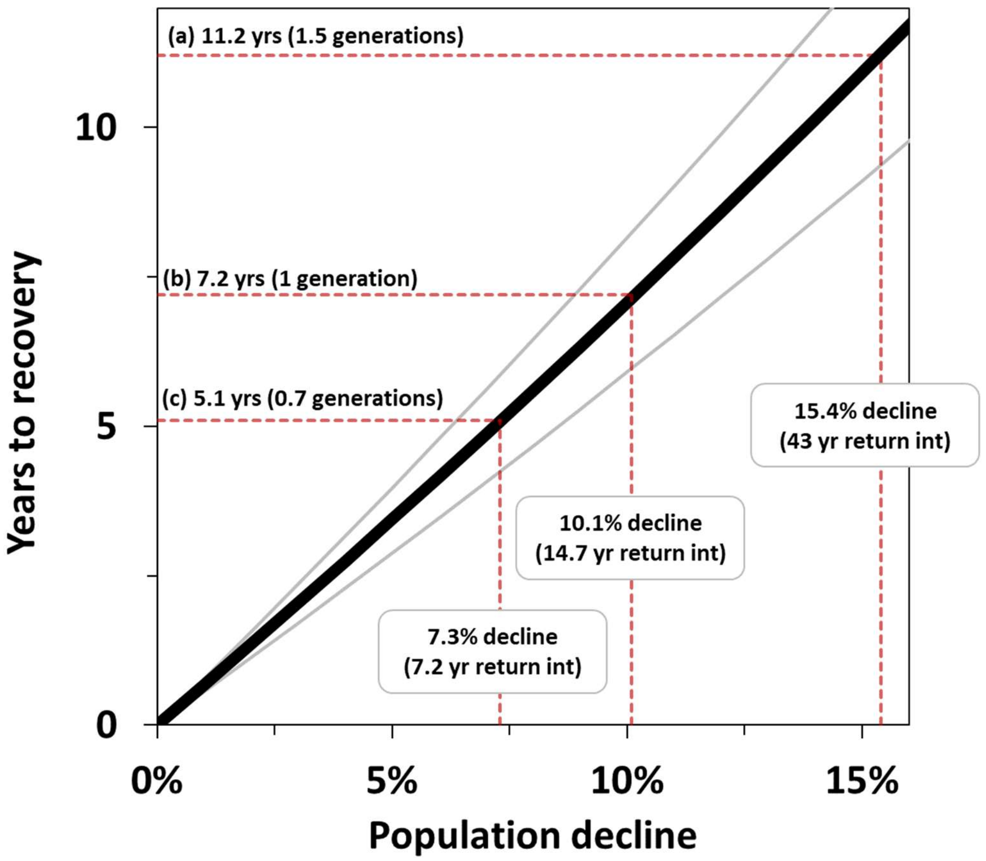

Figure 5.5. Mountain goat population recovery time estimated in relation to population declines associated with ecologically relevant avalanche impact scenarios. (a) worst-case scenario, illustrating the maximum percent of a population observed killed by avalanches (23%), resulting in a 15.4% population decline and requiring 11.2 years (~1.5 mountain goat generations) to recover to original population size (at average population growth rates, λ = 1.015), (b) generational recovery scenario, illustrating a simulated perturbation (10.1% decline) requiring ~one mountain goat generation (7.2 yrs) for recovery, (c) once in a generation scenario, a simulated perturbation (7.3% decline) expected to occur during a typical mountain goat generation (every 7.2 yrs), and requiring 5.1 yrs for recovery.

Chapter 6. Conclusions

Understanding how mountain-adapted wildlife are influenced by climate-linked environmental variability and processes is critical. Such knowledge is necessary for ensuring future viability and conservation of alpine organisms, and the rapidly changing ecosystems they inhabit (Schmeller et al. 2022). Mountains comprise 25% of the Earth's surface area, harbor extraordinary geographic and biological diversity, and contribute major ecological services (Immerzeel et al. 2010, Rahbek et al. 2019). Yet, they are the understudied, relative to other areas. The physical difficulties of scientific investigation in remote, rugged landscapes present objective challenges – but collection of long-term data is necessary to attain reliable knowledge about demographic processes to support science-based conservation and management of these sensitive and important systems. Our research was undertaken with this goal in mind.

Enduring scientific and conservation relevant contributions require implementing a multi-faceted approach. In this research, integration of long-term ecological field data with remote-sensing technology and analytical methodology provided a framework for understanding alpine ecosystem dynamics in a conservation-relevant context. Anchored in population ecology theory, this research synthesized existing knowledge and contributed new insights about animal – environment interactions in mountain systems. To link ecological relationships together and understand population-level implications, we developed modeling frameworks that were well suited for addressing specific research questions and also for use in applied conservation and management contexts. In sum, this work bridged population ecology with environmental science and theory with practice, to advance our understanding and capacity to address current and future challenges.

6.1 Mountain sentinels in a changing world

Mountain goats are sentinels of change in alpine ecosystems. They offer timely insight into the ecological effects and conservation challenges associated with climate change in sensitive and biodiverse alpine environments. Chapter 2 involved facilitating a collaboration among a diverse group of mountain goat ecologists and environmental scientists, and synthesizing existing knowledge about the influence of weather and climate on mountain goat behavior, nutritional ecology, demography, health, and interspecific interactions. Characterizing mechanistic relationships between mountain goats and variation in climate and weather provided a foundation for understanding the species' sensitivity to climate change. Combined with analyses about how climate is expected to change in representative mountain goat ranges throughout their North American distribution, our assessment provided a means for evaluating projected impacts of climate change on mountain goat population ecology. In sum, this research generated recommendations for monitoring, management and conservation planning. It also revealed knowledge gaps and guidance for prioritizing future monitoring and research activities. Given the identified vulnerability of mountain goats to future changes in climate, this work highlights the necessity of increased collaboration among diverse networks (government agencies, indigenous communities, non-governmental organizations, academia and more) for ensuring the resiliency and persistence of mountain goats and the alpine environments they inhabit. Already, this work made tangible contributions having been endorsed by the professional organization of North American mountain ungulate biologists (Northern Wild Sheep and Goat Council) and integrated into conservation planning efforts among indigenous communities (Tlákw Aan – Klukwan), government agencies (Tongass National Forest) and non-governmental organizations (Rocky Mountain Goat Alliance).

6.2 Life-history trade-offs and environmental variation shape reproductive demography

Advancing knowledge of how demographic processes are influenced by variation in weather and climate, and relate to life-history trade-offs, is an important information need. This is especially the case for mountain goats, one of the least studied large mammal species in North America. Using long-term monitoring data from individually marked female mountain goats, Chapter 3 examined how reproduction is influenced by life-history trade-offs and variation in winter snowfall and summer temperature. Findings from these analyses illustrated the complexity with which intrinsic and extrinsic forces influence successful reproduction. For example, we found that mountain goats incur significant age-specific costs of reproduction that require animals to balance the expense of current vs future reproduction, along with the probability of survival. These findings revealed that females employ a conservative reproductive strategy that prioritizes survival over reproduction. Situated at the 'slow' end of the pace of life continuum (*sensu* Bielby et al. 2007), this life-history strategy is suited for persistence in highly variable, seasonal environments. Within this context, our analyses indicated that mountain goat reproductive performance is sensitive to seasonal weather conditions. Late-winter snow depth, for example, exerted strong negative effects on probability of parturition. We also detected evidence (albeit weaker) that summer temperature negatively influenced parturition. Overall, integrating these relationships into follow-up population modeling analyses (Chapter 3) indicated that these environmental drivers, especially winter snow, are capable of shaping reproductive demography and exerting biologically meaningful effects on population growth.

This work provided an important contribution to our broader understanding of mountain goat reproductive ecology, as previous work using long-term data had been conducted in interior systems (Hamel et al. 2010, Festa-Bianchet et al. 2019). Earlier identification of ‘coastal’ and ‘interior’ ecotypes among the species (Herbert and Turnbull 1977, Michaud et al. 2024) raised questions about whether ecotypes differ in productivity and, by extension, capacity to support harvest (Rice et al. 2022). Our research filled an important knowledge gap about reproductive ecology among coastal mountain goats, and revealed little evidence that reproductive performance differed among ecotypes. This finding carries important conservation implications. That is, in contrast to recent suggestions based on indirect evidence (Rice et al. 2022), our analyses does not support allowing higher harvest rates among coastal vs interior populations on the basis of reproductive performance. This knowledge is critical for a species that has a ‘slow’ life-history strategy, occurs in small, isolated populations and exhibits low realized population growth rates (i.e. 1 – 4%) – demographic characteristics that require careful and conservative harvest management to ensure population sustainability (Hamel et al. 2006, Rice and Gay 2010, White et al. 2021a).

6.3 Snow avalanches and the costs of living dangerously

Snow can exert substantial impacts on animal populations through a variety of mechanistic pathways. Previous study has principally focused on ecologically oriented snow – wildlife interactions (Williams et al. 2015, Boelman et al. 2019, Reinking et al. 2022). In Chapter 4, we examined an important and largely unexamined physical process through which snow can impose major impacts on mountain wildlife populations – avalanches. Mountain goats, and other alpine ungulates, utilize steep, rugged terrain to minimize the risk of predation but, during winter, such behavior exposes them to the risk of avalanches (which most often occur on similarly steep terrain). That snow avalanches have the capacity to kill mountain wildlife had not previously been extensively studied, and largely described via anecdotal reports. Our long-term mountain goat data provided an opportunity to examine the spatiotemporal dimensions and demographic impacts of avalanche mortality, along with the underlying behavioral ecology of vulnerability.

Avalanche terrain is widespread in mountain environments (comprising 62% of our study area footprint, on average), with occurrence being linked to climate and weather conditions through multiple, complex pathways (Glazovskaya 1998, McClung and Schaerer 2006). In chapter 4, our analyses indicated that avalanches are a major source of mortality among mountain goats, comprising 23 – 65% of all mortalities, depending on area. Avalanche mortalities mostly occurred during early- and late-winter, periods when snow packs are typically least stable. We further assessed relationships between individual exposure to avalanche hazard and mortality by spatially integrating GPS location data collected from instrumented mountain goats with avalanche simulation modeling spatial data (that delineate potential release areas and paths). These results indicated that avalanche-caused mortality was related to vulnerability, as measured through the amount of time individuals spent in avalanche terrain – revealing an explicit cost of living dangerously. Translated into demographic terms, avalanches kill 7% of mountain goats per year, on average, with greater than 22% under the most severe circumstances. For a species with a conservative life-history strategy and low realized population growth rates such impacts are likely consequential. This may especially be the case given that avalanches largely kill animals at random (i.e. a 'wicked problem'), removing a substantial fraction of reproductively critical prime-aged individuals that are otherwise relatively invulnerable to most sources of natural mortality. Such impacts foreshadow the potentially major demographic implications of avalanche mortality.

The rates of avalanche-caused mortality among our mountain goat study populations are striking, and identified a clear need to understand how population viability is affected under such extraordinary conditions. In Chapter 5, we developed and implemented a population modeling approach to simulate the impacts of avalanche mortality on mountain goat population growth and resilience. We first developed a sub-model to examine the relationship between avalanche mortality and total annual survival. This analysis revealed that avalanche mortality is largely additive, except low rates when a small fraction of animals killed by avalanches would have otherwise died (i.e. compensatory mortality). This sub-model was subsequently integrated into a broader modeling framework, comprised of an extensively parameterized (n = 14 study sites, 600 individuals, 44 yrs) post-breeding, sex- and age-structured population model, to simulate impacts of avalanche mortality on population growth rate across an array of empirically-based scenarios. These analyses revealed that under the worst case scenario (23% avalanche-caused mortality), avalanche impacts were expected to elicit a >15% population decline. In contrast, populations were predicted to grow by 1.5% annually under average conditions. To provide deeper demographic context, we calculated recovery times (assuming average population growth rate) and determined that a population suffering a severe impact would require 11 years (1.5 mountain goat generations) to recover to the original abundance. Further analyses showed that during the course of a typical mountain goat lifetime significant avalanche-linked perturbations can be expected to occur, suggesting that demographic signatures of avalanche impacts are generationally recurrent and routinely imbedded in population histories. Taken together, these findings reveal the extent that avalanches can comprise biologically meaningful, climate-linked extreme events – an insight that deserves special attention given projected future increases in extreme weather events due to climate change (Hock et al. 2019). Severe storms, for example, are a principal driver of major avalanche cycles (Strapazzon et al. 2021) and, even if rare, extreme events can impose long-lasting impacts on mountain goat populations. Yet, the overall impacts of climate change on avalanche dynamics are complex and not yet fully resolved (Eckert et al. 2024), requiring further study to fully understand whether such impacts might be counterbalanced by other climate change – avalanche dynamics (i.e. upslope shifting of snow distribution, reduction in average snowfall).

This research made new, and likely far-reaching, contributions about how snow, particularly avalanches, influence population dynamic processes and carry important implications. Thirty-two species of alpine ungulate across 70 countries inhabit mountain environments with avalanche hazard (Shackleton 1997, Glazovskaya 1998). Characterizing the extent these, and other, mountain species are subject of avalanche mortality comprise important considerations when developing population assessments and conservation strategies necessary to ensuring population viability. The IUCN Caprinae Specialist Group, for example, indicates that most mountain ungulate species worldwide are vulnerable due to a variety of threats, including environmental change and prevalence of stochastic events (among others; Shackleton 1997). Our emerging knowledge about the role of avalanches driving ecological, behavioral and demographic processes provides new depth to our understanding of how climate-linked processes may influence population resilience and viability. Such insights are timely given the increasing importance of climate change in altering ecosystems.

6.4 Applied Conservation Science

Effective conservation can be attained through generation of reliable knowledge and development of applied frameworks for translating knowledge into action. An important aspect of this process is developing and scaling down generalized theory to systems, species and spatial domains upon which conservation and management strategies are needed. This research has made contributions across multiple dimensions that bolster our capability to employ science-based conservation. Whether synthesizing existing knowledge to guide policy and priorities (Chapter 2), rigorously describing and bringing recognition to an underappreciated animal – environment interactions subfield (Chapter 4 and 5), or developing mechanistic modeling frameworks to reveal key ecological relationships through approaches well suited to also address real-time and future conservation and management needs (Chapters 3 – 5), this body of work is situated to aid conservation in diverse and tangible ways.

Yet, more work remains to be done. Avalanche – wildlife relationships likely involve complex trade-offs. Our research has principally focused on deleterious impacts but potential benefits have been largely unexplored. The extent that avalanche-linked landscape disturbance and redistribution of snow beneficially alters plant phenology, succession and forage resource availability (and balance costs of utilizing avalanche terrain) comprise important areas of future study. Alternatively, an improved understanding is needed about whether avalanche terrain may instead represent ecological traps – wicked learning environments for which individuals are unable to perceive risk due to limited opportunities for trial and error learning (Hale and Swearer 2016b, Fisher et al. 2022). Research is also needed to more precisely link avalanche-related mortality to weather patterns and snow conditions to enable forecasting and insight about future trends. Finally, ongoing efforts are required to communicate existing research findings, guide implementation of analytic tools and ensure knowledge is effectively transferred to inform decision-making and implementation of strategic planning. Contributing to our capacity to understand and conserve mountain ecosystems is an extraordinary opportunity, and embracing the challenges through collaboration, science and communication promises a key pathway to ensuring timely, effective and enduring conservation strategies can be implemented.

References

Acevedo-Whitehouse, K., and A. L. J. Duffus. 2009. Effects of environmental change on wildlife health. Philosophical Transactions of the Royal Society B: Biological Sciences 364:3429–3438.

Aikens, E. O., K. L. Monteith, J. A. Merkle, S. P. H. Dwinnell, G. L. Fralick, and M. J. Kauffman. 2020. Drought reshuffles plant phenology and reduces the foraging benefit of green-wave surfing for a migratory ungulate. Global Change Biology 26:4215–4225.

Alba, R., L. Oddi, D. Rosselli, and D. Chamberlain. 2023. Avalanches create unique habitats for birds in the European Alps. Journal of Ornithology 164:377–388.

Alerstam, T., A. Hedenström, and S. Åkesson. 2003. Long-distance migration: evolution and determinants. Oikos 103:247–260.

Aleuy, O. A., and S. Kutz. 2020. Adaptations, life-history traits and ecological mechanisms of parasites to survive extremes and environmental unpredictability in the face of climate change. International Journal for Parasitology: Parasites and Wildlife 12:308–317.

Aleuy, O. A., K. Ruckstuhl, E. P. Hoberg, A. Veitch, N. Simmons, and S. J. Kutz. 2018. Diversity of gastrointestinal helminths in Dall's sheep and the negative association of the abomasal nematode, Marshallagia marshalli, with fitness indicators. PLOS ONE 13:e0192825.

Antão, L. H., B. Weigel, G. Strona, M. Hällfors, E. Kaarlejärvi, T. Dallas, Ø. H. Opedal, J. Heliölä, H. Henttonen, O. Huitu, E. Korpimäki, M. Kuussaari, A. Lehikoinen, R. Leinonen, A. Lindén, P. Merilä, H. Pietiäinen, J. Pöyry, M. Salemaa, T. Tonteri, K. Vuorio, O. Ovaskainen, M. Saastamoinen, J. Vanhatalo, T. Roslin, and A.-L. Laine. 2022. Climate change reshuffles northern species within their niches. Nature Climate Change 12:587–592.

Arnold, T. W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Arthur, S. M., and L. R. Prugh. 2010. Predator-Mediated Indirect Effects of Snowshoe Hares on Dall's Sheep in Alaska. The Journal of Wildlife Management 74:1709–1721.

Bailey, J. A. 1991. Reproductive success in female mountain goats. Canadian Journal of Zoology 69:2956–2961.

Bailey, L. D., and M. Van De Pol. 2016. Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. Journal of Animal Ecology 85:85–96.

Ballesteros-Cánovas, J. A., D. Trappmann, J. Madrigal-González, N. Eckert, and M. Stoffel. 2018. Climate warming enhances snow avalanche risk in the Western Himalayas. Proceedings of the National Academy of Sciences 115:3410–3415.

Barboza, P. S., and K. L. Parker. 2008. Allocating Protein to Reproduction in Arctic Reindeer and Caribou. Physiological and Biochemical Zoology 81:835–855.

Bårdsen, B.-J., P. Fauchald, T. Tveraa, K. Langeland, N. G. Yoccoz, and R. A. Ims. 2008a. Experimental evidence of a risk-sensitive reproductive allocation in a long-lived mammal. Ecology 89:829–837.

Bårdsen, B.-J., P. Fauchald, T. Tveraa, K. Langeland, N. G. Yoccoz, and R. A. Ims. 2008b. Experimental evidence of a risk-sensitive reproductive allocation in a long-lived mammal. Ecology 89:829–837.

Barry, R. G., and C. C. Van Wie. 1974. Topo- and microclimatology in alpine areas. Pages 73–83 Arctic and Alpine Environments. Methuen, London, United Kingdom.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting Linear Mixed-Effects Models using lme4. arXiv.

Bebi, P., P. Bartelt, and C. Rixen. 2022. Avalanches and Other Snow Movements. Pages 195–210 *in* T. Wohlgemuth, A. Jentsch, and R. Seidl, editors. Disturbance Ecology. Springer International Publishing, Cham.

Bebi, P., D. Kulakowski, and C. Rixen. 2009. Snow avalanche disturbances in forest ecosystems—State of research and implications for management. Forest Ecology and Management 257:1883–1892.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15:365–377.

Beniston, M., and M. Stoffel. 2016. Rain-on-snow events, floods and climate change in the Alps: Events may increase with warming up to 4 °C and decrease thereafter. Science of The Total Environment 571:228–236.

Berg, J. E., M. Hebblewhite, C. C. St. Clair, and E. H. Merrill. 2019. Prevalence and mechanisms of partial migration in ungulates. Frontiers in Ecology and Evolution 7:325.

Berger, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. Conservation Biology 4:91–98.

Berger, J. 2018. Extreme conservation: life at the edges of the world. The University of Chicago Press, Chicago London.

Berger, J., C. Hartway, A. Gruzdev, and M. Johnson. 2018. Climate degradation and extreme icing events constrain life in cold-adapted mammals. Scientific Reports 8:1156.

Berman, E. E., T. A. Graves, N. L. Mikle, J. A. Merkle, A. N. Johnston, and G. W. Chong. 2020. Comparative quality and trend of remotely sensed phenology and productivity metrics across the western United States. Remote Sensing 12:2538.

Bielby, J., G. M. Mace, O. R. P. Bininda-Emonds, M. Cardillo, J. L. Gittleman, K. E. Jones, C. D. L. Orme, and A. Purvis. 2007. The Fast-Slow Continuum in Mammalian Life History: An Empirical Reevaluation. The American Naturalist 169:748–757.

Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. Van Moorter, and A. Mysterud. 2012. A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? The American Naturalist 180:407–424.

Blanchong, J. A., C. A. Anderson, N. J. Clark, R. W. Klaver, P. J. Plummer, M. Cox, C. McAdoo, and P. L. Wolff. 2018. Respiratory disease, behavior, and survival of mountain goat kids. The Journal of Wildlife Management 82:1243–1251.

Bø, S., and O. Hjeljord. 1991. Do continental moose ranges improve during cloudy summers? Canadian Journal of Zoology 69:1875–1879.

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

Boertje, R. D., G. G. Frye, and D. D. Young. 2019. Lifetime, known-age moose reproduction in a nutritionally stressed population. The Journal of Wildlife Management 83:610–626.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135.

Bowen, L., K. Longshore, P. Wolff, R. Klinger, M. Cox, S. Bullock, S. Waters, and A. K. Miles. 2020. Gene Transcript Profiling in Desert Bighorn Sheep. Wildlife Society Bulletin 44:323–332.

Bowen, L., K. Manlove, A. Roug, S. Waters, N. LaHue, and P. Wolff. 2022. Using transcriptomics to predict and visualize disease status in bighorn sheep (*Ovis canadensis*). Conservation Physiology 10:coac046.

Brambilla, A., A. Von Hardenberg, B. Bassano, L. Ranghetti, L. Keller, and M. Festa-Bianchet. 2024. Climate drives body mass changes in a mountain ungulate: shorter winters lead to heavier Alpine ibex. Oikos:e10643.

Brandborg, S. M. 1955. Life history and management of the mountain goat in idaho. Idaho Wildlife Bulletin:1–142.

Broadbent, A. A. D., L. K. Newbold, W. J. Pritchard, A. Michas, T. Goodall, I. Cordero, A. Giunta, H. S. K. Snell, V. V. L. H. Pepper, H. K. Grant, D. X. Soto, R. Kaufmann, M. Schloter, R. I. Griffiths, M. Bahn, and R. D. Bardgett. 2024. Climate change disrupts the seasonal coupling of plant and soil microbial nutrient cycling in an alpine ecosystem. Global Change Biology 30:e17245.

Bühler, Y., P. Bebi, M. Christen, S. Margreth, L. Stoffel, A. Stoffel, C. Marty, G. Schmucki, A. Caviezel, R. Kühne, S. Wohlwend, and P. Bartelt. 2022. Automated avalanche hazard indication mapping on a statewide scale. Natural Hazards and Earth System Sciences 22:1825–1843.

Bühler, Y., D. von Rickenbach, M. Christen, S. Margreth, L. Stoffel, A. Stoffel, and R. Kühne. 2018a. Linking modelled potential release areas with avalanche dynamic simulations: An automated approach for efficient avalanche hazard indication mapping. Proceedings of the International Snow Science Workshop:810–814.

Bühler, Y., D. von Rickenbach, A. Stoffel, S. Margreth, L. Stoffel, and M. Christen. 2018b. Automated snow avalanche release area delineation – validation of existing algorithms and proposition of a new object-based approach for large-scale hazard indication mapping. Natural Hazards and Earth System Sciences 18:3235–3251.

Büntgen, U., L. Greuter, K. Bollmann, H. Jenny, A. Liebhold, J. D. Galván, N. C. Stenseth, C. Andrew, and A. Mysterud. 2017. Elevational range shifts in four mountain ungulate species from the Swiss Alps. Ecosphere 8.

Burles, D. W., and M. Hoefs. 1984. Winter mortality of Dall sheep, Ovis dalli dalli, in Kluane National Park, Yukon. Canadian Field-Naturalist 98:479–484.

Burnham, K. P., and D. R. Anderson. 2010. Model selection and multimodel inference: a practical information-theoretic approach. 2. ed., [4. printing]. Springer, New York, NY.

Cady, S. M., D. W. Londe, S. D. Fuhlendorf, C. A. Davis, A. J. Kanz, K. L. Kauffman, J. K. Knutson, A. G. Barnes, N. A. McMillan, and L. K. Neumann. 2023. Climate change literature across ecological disciplines: A review of the scope and level of specificity in management recommendations. Global Ecology and Conservation 46:e02544.

Carlsson, A. M., R. Justin Irvine, K. Wilson, S. B. Piertney, O. Halvorsen, S. J. Coulson, A. Stien, and S. D. Albon. 2012. Disease transmission in an extreme environment: Nematode parasites infect reindeer during the Arctic winter. International Journal for Parasitology 42:789–795.

Chadwick, D. H. 1983. A beast the color of winter: the mountain goat observed. Sierra Club Books, San Francisco.

Christen, M., J. Kowalski, and P. Bartelt. 2010. RAMMS: Numerical simulation of dense snow avalanches in three-dimensional terrain. Cold Regions Science and Technology 63:1–14.

Clark, P. U., A. S. Dyke, J. D. Shakun, A. E. Carlson, J. Clark, B. Wohlfarth, J. X. Mitrovica, S. W. Hostetler, and A. M. McCabe. 2009. The Last Glacial Maximum. Science 325:710–714.

Clutton-Brock, T. H. 1984. Reproductive Effort and Terminal Investment in Iteroparous Animals. The American Naturalist 123:212–229.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1983. The costs of reproduction to red deer hinds. The Journal of Animal Ecology 52:367.

Clutton-Brock, T., and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology & Evolution 25:562–573.

Cohen, J. M., E. L. Sauer, O. Santiago, S. Spencer, and J. R. Rohr. 2020. Divergent impacts of warming weather on wildlife disease risk across climates. Science 370:eabb1702.

Collins, C., and R. Kays. 2011. Causes of mortality in North American populations of large and medium-sized mammals: Causes of mortality in mammals. Animal Conservation 14:474–483.

Conner, M. M., T. R. Stephenson, D. W. German, K. L. Monteith, A. P. Few, and E. H. Bair. 2018. Survival analysis: Informing recovery of Sierra Nevada bighorn sheep. The Journal of Wildlife Management 82:1442–1458.

Côté, S. D., and M. Festa-Bianchet. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia 127:230–238.

Côté, S. D., and M. Festa-Bianchet. 2003. Mountain goat. Page *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. 2nd ed. Johns Hopkins University Press, Baltimore, Md.

Côté, S. D., S. Hamel, A. St-Louis, and J. Mainguy. 2013. Do mountain goats habituate to helicopter disturbance?: Mountain Goat Responses to Helicopter Disturbance. The Journal of Wildlife Management 77:1244–1244.

Dailey, T. V., and N. T. Hobbs. 1989. Travel in alpine terrain: energy expenditures for locomotion by mountain goats and bighorn sheep. Canadian Journal of Zoology 67:2368–2375.

DeCesare, N., and B. Smith. 2018. Contrasting native and introduced mountain goat populations in Montana. Proceedings of the Northern Wild Sheep and Goat Council 21:80–104.

DeMars, C. A., C. J. Johnson, M. Dickie, T. J. Habib, M. Cody, A. Saxena, S. Boutin, and R. Serrouya. 2023. Incorporating mechanism into conservation actions in an age of multiple and emerging threats: The case of boreal caribou. Ecosphere 14:e4627.

D'Eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening: Effects of radio-collar position. Journal of Applied Ecology 42:383–388.

D'Eon, R. G., R. Serrouya, G. Smith, and C. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin . 30:430–439.

Déry, F., S. Hamel, and S. D. Côté. 2019. Getting ready for the winter: Timing and determinants of molt in an alpine ungulate. Ecology and Evolution 9:2920–2932.

Desforges, J., G. M. Marques, L. T. Beumer, M. Chimienti, L. H. Hansen, S. H. Pedersen, N. M. Schmidt, and F. M. Van Beest. 2021. Environment and physiology shape Arctic ungulate population dynamics. Global Change Biology 27:1755–1771.

Dial, R. J., T. Scott Smeltz, P. F. Sullivan, C. L. Rinas, K. Timm, J. E. Geck, S. Carl Tobin, T. S. Golden, and E. C. Berg. 2016. Shrubline but not treeline advance matches climate velocity in montane ecosystems of south-central Alaska. Global Change Biology 22:1841–1856.

Diaz, H. F., M. Grosjean, and L. Graumlich. 2003. Climate Variability and Change in High Elevation Regions: Past, Present and Future. Climatic Change 59:1–4.

Douhard, M., S. Guillemette, M. Festa-Bianchet, and F. Pelletier. 2018. Drivers and demographic consequences of seasonal mass changes in an alpine ungulate. Ecology 99:724–734.

Dulude-de Broin, F., S. Hamel, G. F. Mastromonaco, and S. D. Côté. 2020. Predation risk and mountain goat reproduction: Evidence for stress-induced breeding suppression in a wild ungulate. Functional Ecology 34:1003–1014.

Eckert, N., C. Corona, F. Giacona, J. Gaume, S. Mayer, A. Van Herwijnen, P. Hagenmuller, and M. Stoffel. 2024. Climate change impacts on snow avalanche activity and related risks. Nature Reviews Earth & Environment 5:369–389.

Elsen, P. R., and M. W. Tingley. 2015. Global mountain topography and the fate of montane species under climate change. Nature Climate Change 5:772–776.

Endler, J. A. 1986. Natural Selection in the Wild. Princeton University Press, Princeton, N.J.

Ericsson, G., K. Wallin, J. P. Ball, and M. Broberg. 2001. Age-related reproductive effort and senescence in free-ranging moose (Alces alces). Ecology 82:1613–1620.

Ernst, R. 2002. Caribou herd reduction accomplished natural. Refuge Notebook 4:63–64.

Feder, C., J. G. A. Martin, M. Festa-Bianchet, C. Bérubé, and J. Jorgenson. 2008. Never too late? Consequences of late birthdate for mass and survival of bighorn lambs. Oecologia 156:773–781.

Fellman, J. B., S. Nagorski, S. Pyare, A. W. Vermilyea, D. Scott, and E. Hood. 2014. Stream temperature response to variable glacier coverage in coastal watersheds of Southeast Alaska. Hydrological Processes 28:2062–2073.

Festa-Bianchet, M., and S. D. Côté. 2008. Mountain goats: ecology, behavior, and conservation of an alpine ungulate. Island Press, Washington, DC.

Festa-Bianchet, M., S. D. Côté, S. Hamel, and F. Pelletier. 2019. Long-term studies of bighorn sheep and mountain goats reveal fitness costs of reproduction. Journal of Animal Ecology 88:1118–1133.

Festa-Bianchet, M., T. Coulson, J.-M. Gaillard, J. T. Hogg, and F. Pelletier. 2006. Stochastic predation events and population persistence in bighorn sheep. Proceedings of the Royal Society B: Biological Sciences 273:1537–1543.

Festa-Bianchet, M., M. Douhard, J.-M. Gaillard, and F. Pelletier. 2017a. Successes and challenges of long-term field studies of marked ungulates. Journal of Mammalogy 98:612–620.

Festa-Bianchet, M., M. Douhard, J.-M. Gaillard, and F. Pelletier. 2017b. Successes and challenges of long-term field studies of marked ungulates. Journal of Mammalogy 98:612–620.

Festa-Bianchet, M., J. Gaillard, and J. T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. The American Naturalist 152:367–379.

Fieberg, J. 2022. Statistics for Ecologists: A Frequentist and Bayesian Treatment of Modern Regression Models. An open-source online textbook., https://fw8051statistics4ecologists.netlify.app/.

Fisher, K. C., P. Haegeli, and P. Mair. 2022. Exploring the avalanche bulletin as an avenue for continuing education by including learning interventions. Journal of Outdoor Recreation and Tourism 37:100472.

Fisk, E. A., E. F. Cassirer, K. S. Huggler, A. P. Pessier, L. A. White, J. D. Ramsay, E. W. Goldsmith, H. R. Drankhan, R. M. Wolking, K. R. Manlove, T. Nordeen, J. T. Hogg, and K. R. Taylor. 2023. Abortion and neonatal mortality due to Toxoplasma gondii in bighorn sheep (Ovis canadensis). Journal of Wildlife Diseases 59.

Flesch, E. P., R. A. Garrott, P. J. White, D. Brimeyer, A. B. Courtemanch, J. A. Cunningham, S. R. Dewey, G. L. Fralick, K. Loveless, D. E. McWhirter, H. Miyasaki, A. Pils, M. A. Sawaya, and S. T. Stewart. 2016. Range expansion and population growth of non-native mountain goats in the Greater Yellowstone Area: Challenges for management. Wildlife Society Bulletin 40:241–250.

Foord, V. 2016. Climate patterns, trends, and projections for the Omineca, Skeena, and Northeast Natural Resource Regions, British Columbia. Page 17. Technical Report, Ministry of Forests, Lands and Natural Resource Operations, Victoria, BC.

Foster, B. R., and E. Y. Rahs. 1985. A study of canyon-dwelling mountain goats in relation to proposed hydroelectric development in northwestern British Columbia, Canada. Biological Conservation 33:209–228.

Fox, J. 1983. Constraints on winter habitat selection by the mountain goat in Alaska. PhD Thesis, University of Washington.

Fox, J. L. 1978. Weather as a determinant factor in summer mountain goat activity and habitat use. MS Thesis, University of Alaska Fairbanks, Fairbanks, AK.

Fox, J. L. 1991. Forage Quality of Carex macrochaeta Emerging from Alaskan Alpine Snowbanks through the Summer. American Midland Naturalist 126:287.

Frederick, J. H. 2015. Alpine thermal dynamics and associated thermal constraints on the behavior of mountain goats. MS Thesis, University of Alaska Fairbanks, Fairbanks, AK.

Frid, A., and L. Dill. 2002. Human-caused Disturbance Stimuli as a Form of Predation Risk. Conservation Ecology 6.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal Variation in Fitness Components and Population Dynamics of Large Herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gallant, A. L., J. M. Binnian, J. M. Omernik, and M. B. Shasby. 1995. Ecoregions of Alaska. U.S. Government Printing Office, Washington D. C.

Gamon, J. A., K. F. Huemmrich, R. S. Stone, and C. E. Tweedie. 2013. Spatial and temporal variation in primary productivity (NDVI) of coastal Alaskan tundra: Decreased vegetation growth following earlier snowmelt. Remote Sensing of Environment 129:144–153.

Garcia-Gonzalez, R., and P. Cuartas. 1996. Trophic utilization of a montane/subalpine forest by chamois (Rupicapra pyrenaica) in the Central Pyrenees. Forest Ecology and Management 88:15–23.

Giacona, F., N. Eckert, C. Corona, R. Mainieri, S. Morin, M. Stoffel, B. Martin, and M. Naaim. 2021. Upslope migration of snow avalanches in a warming climate. Proceedings of the National Academy of Sciences 118:e2107306118.

Gilbert, S. L., K. J. Hundertmark, M. S. Lindberg, D. K. Person, and M. S. Boyce. 2020. The Importance of Environmental Variability and Transient Population Dynamics for a Northern Ungulate. Frontiers in Ecology and Evolution 8:531027.

Glazovskaya, T. G. 1998. Global distribution of snow avalanches and changing activity in the Northern Hemisphere due to climate change. Annals of Glaciology 26:337–342.

Grayson, D. K. 2011. The Great Basin: A Natural Prehistory. First edition. University of California Press.

Greening (La'goot), S. 2024. Gugwilx'ya'ansk and goats: Indigenous perspectives on governance, stewardship and relationality in mountain goat (mati) hunting in Gitga'at territory. People and Nature:pan3.10688.

Greenwood, S., and A. S. Jump. 2014. Consequences of Treeline Shifts for the Diversity and Function of High Altitude Ecosystems. Arctic, Antarctic, and Alpine Research 46:829–840.

Gude, J. A., N. J. DeCesare, K. M. Proffitt, S. N. Sells, R. A. Garrott, I. Rangwala, M. Biel, J. Coltrane, J. Cunningham, T. Fletcher, K. Loveless, R. Mowry, M. O'Reilly, R. Rauscher, and M. Thompson. 2022. Demographic uncertainty and disease risk influence climate-informed management of an alpine species. The Journal of Wildlife Management 86:e22300.

Gultepe, I. 2015. Mountain Weather: Observation and Modeling. Pages 229–312 Advances in Geophysics. Elsevier.

Haegeli, P., B. Shandro, and P. Mair. 2021. Using avalanche problems to examine the effect of large-scale atmosphere–ocean oscillations on avalanche hazard in western Canada. The Cryosphere 15:1567–1586.

Hagedorn, F., K. Gavazov, and J. M. Alexander. 2019. Above- and belowground linkages shape responses of mountain vegetation to climate change. Science 365:1119–1123.

Hägeli, P., and D. M. McClung. 2003. Avalanche characteristics of a transitional snow climate—Columbia Mountains, British Columbia, Canada. Cold Regions Science and Technology 37:255–276.

Hale, R., and S. E. Swearer. 2016a. Ecological traps: current evidence and future directions. Proceedings of the Royal Society B: Biological Sciences 283:20152647.

Hale, R., and S. E. Swearer. 2016b. Ecological traps: current evidence and future directions. Proceedings of the Royal Society B: Biological Sciences 283:20152647.

Hamel, S., S. D. Côté, and M. Festa-Bianchet. 2010. Maternal characteristics and environment affect the costs of reproduction in female mountain goats. Ecology 91:2034–2043.

Hamel, S., S. D. Côté, K. G. Smith, and M. Festa-Bianchet. 2006. Population dynamics and harvest potential of mountain goat herds in Alberta. Journal of Wildlife Management 70:1044–1053.

Hamel, S., J.-M. Gaillard, M. Festa-Bianchet, and S. D. Côté. 2009a. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. Ecology 90:1981–1995.

Hamel, S., M. Garel, M. Festa-Bianchet, J. Gaillard, and S. D. Côté. 2009b. Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. Journal of Applied Ecology 46:582–589.

Happe, P. J., K. Mansfield, J. Powers, W. Moore, S. Piper, B. Murphie, and R. Harris. 2020. Removing non-native mountain goats from the Olympic Peninsula. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 22:77–93.

Hardie, D. C., and J. A. Hutchings. 2010. Evolutionary ecology at the extremes of species' ranges. Environmental Reviews 18:1–20.

Harris, R. B., P. J. Happe, W. R. Moore, C. G. Rice, J. M. Sevigny, D. J. Vales, K. S. White, and E. C. Wirtz. 2024. Survival of adult mountain goats in Washington: effects of season, translocation, snow, and precipitation. The Journal of Wildlife Management 88:e22495.

Harris, R. B., F. Hayes, C. G. Rice, and D. J. Vales. 2022. Landscape factors inhibiting mountain goat movements: a contribution to delineating demographic units. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council:12–26.

Harris, R. B., C. G. Rice, R. Milner, and P. J. Happe. 2020. Reintroducing and augmenting mountain goat populations in the north Cascades: Translocations from the Olympic Peninsula, 2018-2020. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 22:58–78.

Harris, R. B., and B. Steele. 2014. Factors predicting success of mountain goat reintroductions. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 15:17–35.

Harris, R. M. B., L. J. Beaumont, T. R. Vance, C. R. Tozer, T. A. Remenyi, S. E. Perkins-Kirkpatrick, P. J. Mitchell, A. B. Nicotra, S. McGregor, N. R. Andrew, M. Letnic, M. R. Kearney, T. Wernberg, L. B. Hutley, L. E. Chambers, M.-S. Fletcher, M. R. Keatley, C. A. Woodward, G. Williamson, N. C. Duke, and D. M. J. S. Bowman. 2018. Biological responses to the press and pulse of climate trends and extreme events. Nature Climate Change 8:579–587.

Hatchett, B. J., S. Burak, J. J. Rutz, N. S. Oakley, E. H. Bair, and M. L. Kaplan. 2017. Avalanche Fatalities during Atmospheric River Events in the Western United States. Journal of Hydrometeorology 18:1359–1374.

Haunschild, R., L. Bornmann, and W. Marx. 2016. Climate Change Research in View of Bibliometrics. PLOS ONE 11:e0160393.

Hayes, F. P. 2023. Ecological consequences of warming climaes for cold-adapted species - evidence frommountain goats. PhD Thesis, Colorado State University, Fort Collins, CO.

Hayes, F. P., and J. Berger. 2023. Snow patch refugia benefits for species of periglacial zones—Evidence from a high-elevation obligate. PNAS Nexus 2:pgad339.

Hayes, F. P., and J. Berger. 2024. Inadvertent climate refugia. Conservation Letters:e13063.

Hazen, E. L., B. Abrahms, S. Brodie, G. Carroll, M. G. Jacox, M. S. Savoca, K. L. Scales, W. J. Sydeman, and S. J. Bograd. 2019. Marine top predators as climate and ecosystem sentinels. Frontiers in Ecology and the Environment 17:565–574.

Healy, K., T. H. G. Ezard, O. R. Jones, R. Salguero-Gómez, and Y. M. Buckley. 2019. Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. Nature Ecology & Evolution 3:1217–1224.

Hellmann, J. J., J. E. Byers, B. G. Bierwagen, and J. S. Dukes. 2008. Five Potential Consequences of Climate Change for Invasive Species. Conservation Biology 22:534–543.

Herbert, D. M., and W. G. Turnbull. 1977. A description of southern interior and coastal mountain goat ecotypes in British Columbia. Proceedings of the First International Mountain Goat Symposium 1:126–146.

Hill, J. E., T. L. DeVault, and J. L. Belant. 2019. Cause-specific mortality of the world's terrestrial vertebrates. Global Ecology and Biogeography 28:680–689.

Hing, S., E. J. Narayan, R. C. A. Thompson, and S. S. Godfrey. 2016. The relationship between physiological stress and wildlife disease: consequences for health and conservation. Wildlife Research 43:51.

Hock, R., G. Rasul, C. Adler, B. Caceres, S. Gruber, Y. Hirabayashi, M. Jackson, A. Kääb, S. Kang, S. Kutuzov, A. Milner, U. Molau, S. Morin, B. Orlove, and H. Steltzer. 2019. High mountain areas. Page IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. First edition. Cambridge University Press.

Hogarth, R. M., T. Lejarraga, and E. Soyer. 2015. The two settings of kind and wicked learning environments. Current Directions in Psychological Science 24:379–385.

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

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. 2nd ed. Wiley, New York.

Houston, D. B., E. B. Schreiner, and B. Morehead. 1994. Mountain Goats in Olympic National Park: Biology and Management of an Introduced Species. Scientific Monograph, National Park Service, Washington D.C.

Hoy, S. R., D. R. MacNulty, M. C. Metz, D. W. Smith, D. R. Stahler, R. O. Peterson, and J. A. Vucetich. 2021. Negative frequency-dependent prey selection by wolves and its implications on predator–prey dynamics. Animal Behaviour 179:247–265.

Humphries, M. M., D. W. Thomas, and D. L. Kramer. 2003. The Role of Energy Availability in Mammalian Hibernation: A Cost-Benefit Approach. Physiological and Biochemical Zoology 76:165–179.

Hurley, K., and C. Clark. 2006. GIS mapping of North American wild sheep and mountain goat translocations in North America, exclusive of desert bighorn sheep ranges. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 15:33.

Hurley, M. A., M. Hebblewhite, J.-M. Gaillard, S. Dray, K. A. Taylor, W. K. Smith, P. Zager, and C. Bonenfant. 2014. Functional analysis of Normalized Difference Vegetation Index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. Philosophical Transactions of the Royal Society B: Biological Sciences 369:20130196.

Hutchings, J. A. 2021. A primer of life histories: ecology, evolution, and application. First edition. Oxford University Press, Oxford.

Immerzeel, W. W., L. P. H. van Beek, and M. F. P. Bierkens. 2010. Climate Change Will Affect the Asian Water Towers. Science 328:1382–1385.

Ion, P. G., and G. P. Kershaw. 1989. The selection of snowpatches as relief habitat by woodland caribou (Rangifer tarandus), Macmillan Pass, Selwyn/Mackenzie Mountains, N.W.T., Canada. Arctic and Alpine Research 21:203–211.

IUCN. 2012. IUCN Red List Categories and Criteria: Version 3.1. IUCN, Gland, Switzerland.

Jacobson, A. R., A. Provenzale, A. Von Hardenberg, B. Bassano, and M. Festa-Bianchet. 2004a. Climate forcing and density dependence in a mountain ungulate population. Ecology 85:1598–1610.

Jacobson, A. R., A. Provenzale, A. Von Hardenberg, B. Bassano, and M. Festa-Bianchet. 2004b. Climate forcing and density dependence in a mountain ungulate population. Ecology 85:1598–1610.

Jędrzejewski, W., B. Jędrzejewska, H. Okarma, and A. L. Ruprecht. 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Bialowieża National Park, Poland. Oecologia 90:27–36.

Jenkins, K. J., P. J. Happe, K. F. Beirne, R. A. Hoffman, P. C. Griffin, W. T. Baccus, and J. Fieberg. 2012. Recent Population Trends of Mountain Goats in the Olympic Mountains, Washington. Northwest Science 86:264–275.

Jessen, T. D., C. N. Service, K. G. Poole, A. C. Burton, A. W. Bateman, P. C. Paquet, and C. T. Darimont. 2022. Indigenous peoples as sentinels of change in human-wildlife relationships: Conservation status of mountain goats in Kitasoo Xai'xais territory and beyond. Conservation Science and Practice 4.

John, C., T. Avgar, K. Rittger, J. A. Smith, L. W. Stephenson, T. R. Stephenson, and E. Post. 2024. Pursuit and escape drive fine-scale movement variation during migration in a temperate alpine ungulate. Scientific Reports 14:15068.

John, C., J. T. Kerby, T. R. Stephenson, and E. Post. 2023. Fine-scale landscape phenology revealed through time-lapse imagery: implications for conservation and management of an endangered migratory herbivore. Remote Sensing in Ecology and Conservation 9:628–640.

John, C., and E. Post. 2022. Projected bioclimatic distributions in Nearctic *Bovidae* signal the potential for reduced overlap with protected areas. Ecology and Evolution 12:e9189.

Johnson, H. E., M. Hebblewhite, T. R. Stephenson, D. W. German, B. M. Pierce, and V. C. Bleich. 2013. Evaluating apparent competition in limiting the recovery of an endangered ungulate. Oecologia 171:295–307.

Johnson, H. E., L. Scott Mills, J. D. Wehausen, and T. R. Stephenson. 2010. Combining ground count, telemetry, and mark–resight data to infer population dynamics in an endangered species. Journal of Applied Ecology 47:1083–1093.

Johnson, R. F. 1983. Mountain goats and mountain sheep of Washington. Washington Department of Game Biological Bulletin, Washington Department of Fish and Wildlife, Olympia, WA., Olympia, WA.

Jonas, T., F. Geiger, and H. Jenny. 2008a. Mortality pattern of the alpine chamois: the influence of snow–meteorological factors. Annals of Glaciology 49:56–62.

Jonas, T., F. Geiger, and H. Jenny. 2008b. Mortality pattern of the Alpine chamois: the influence of snow–meteorological factors. Annals of Glaciology 49:56–62.

Knopff, K. H., N. F. Webb, and M. S. Boyce. 2014. Cougar population status and range expansion in Alberta during 1991–2010. Wildlife Society Bulletin 38:116–121.

Kock, R. A., M. H. Woodford, and P. B. Rossiter. 2010. Disease risks associated with the translocation of wildlife. Revue Scientifique et Technique 29:329–350.

Kuramoto, R. T., and L. C. Bliss. 1970. Ecology of subalpine meadows in the Olympic Mountains, Washington. Ecological Monographs 40:317–347.

Kutz, S. J., S. Checkley, G. G. Verocai, M. Dumond, E. P. Hoberg, R. Peacock, J. P. Wu, K. Orsel, K. Seegers, A. L. Warren, and A. Abrams. 2013. Invasion, establishment, and range expansion of two parasitic nematodes in the Canadian Arctic. Global Change Biology 19:3254–3262.

Kutz, S. J., E. P. Hoberg, L. Polley, and E. J. Jenkins. 2005. Global warming is changing the dynamics of Arctic host–parasite systems. Proceedings of the Royal Society B: Biological Sciences 272:2571–2576.

Kutz, S., J. Rowell, J. Adamczewski, A. Gunn, C. Cuyler, O. A. Aleuy, M. Austin, J. Berger, J. Blake, K. Bondo, C. Dalton, A. Dobson, J. Di Francesco, C. Gerlach, P. Kafle, F. Mavrot, J. Mosbacher, M. Murray, A. Nascou, K. Orsel, F. Rossouw, N.-M. Schmidt, M. Suitor, M. Tomaselli, and B. Ytrehus. 2017. Muskox Health Ecology Symposium 2016: Gathering to Share Knowledge on Umingmak in a Time of Rapid Change. Arctic 70:225.

Laake, J. L. 2013. RMark: An R Interface for analysis of capture-recapture data with MARK. Page 25 pp. AFSC Processed Report, Alaska Fisheries Science Center, NOAA, Seattle, WA.

Lader, R., A. Bidlack, J. E. Walsh, U. S. Bhatt, and P. A. Bieniek. 2020. Dynamical downscaling for Southeast Alaska: historical climate and future projections. Journal of Applied Meteorology and Climatology 59:1607–1623.

Langman, V. A., S. L. Langman, and N. Ellifrit. 2015. Seasonal acclimatization determined by non-invasive measurements of coat insulation. Zoo Biology 34:368–373.

LaSharr, T. N., S. P. H. Dwinnell, R. P. Jakopak, J. Randall, R. C. Kaiser, M. Thonhoff, B. Scurlock, T. Fieseler, N. Hymas, A. Hymas, N. Roberts, J. Hobbs, M. Zornes, D. G. Brimeyer, G. Fralick, and K. L. Monteith. 2023a. Behavior, nutrition, and environment drive survival of a large herbivore in the face of extreme winter conditions. Ecosphere 14:e4601.

LaSharr, T. N., S. P. H. Dwinnell, R. P. Jakopak, J. Randall, R. C. Kaiser, M. Thonhoff, B. Scurlock, T. Fieseler, N. Hymas, A. Hymas, N. Roberts, J. Hobbs, M. Zornes, D. G. Brimeyer, G. Fralick, and K. L. Monteith. 2023b. Behavior, nutrition, and environment drive survival of a large herbivore in the face of extreme winter conditions. Ecosphere 14:e4601.

Lemaître, J., and J. Gaillard. 2017. Reproductive senescence: new perspectives in the wild. Biological Reviews 92:2182–2199.

Lenart, E. A., R. T. Bowyer, J. V. Hoef, and R. W. Ruess. 2002. Climate change and caribou: effects of summer weather on forage. Canadian Journal of Zoology 80:664–678.

Lewinson, R. T., and D. J. Stefanyshyn. 2016. A descriptive analysis of the climbing mechanics of a mountain goat (Oreamnos americanus). Zoology 119:541–546.

Lomolino, M. V., B. R. Riddle, and R. J. Whittaker. 2017. Biogeography: biological diversity across space and time. Fifth edition. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts, U.S.A.

Lovari, S., F. Ferretti, M. Corazza, I. Minder, N. Troiani, C. Ferrari, and A. Saddi. 2014. Unexpected consequences of reintroductions: competition between reintroduced red deer and Apennine chamois: Interactions between red deer and Apennine chamois. Animal Conservation 17:359–370.

Lovari, S., S. Franceschi, G. Chiatante, L. Fattorini, N. Fattorini, and F. Ferretti. 2020. Climatic changes and the fate of mountain herbivores. Climatic Change 162:2319–2337.

Lowrey, B., C. J. Butler, W. H. Edwards, M. E. Wood, S. R. Dewey, G. L. Fralick, J. Jennings-Gaines, H. Killion, D. E. McWhirter, H. M. Miyasaki, S. T. Stewart, K. S. White, P. J. White, and R. A. Garrott. 2018. A Survey of Bacterial Respiratory Pathogens in Native and Introduced Mountain Goats (*Oreamnos americanus*). Journal of Wildlife Diseases 54:852–858.

Lowrey, B., D. E. McWhirter, K. M. Proffitt, K. L. Monteith, A. B. Courtemanch, P. J. White, J. T. Paterson, S. R. Dewey, and R. A. Garrott. 2020. Individual variation creates diverse migratory portfolios in native populations of a mountain ungulate. Ecological Applications 30.

Lynas, M., B. Z. Houlton, and S. Perry. 2021. Greater than 99% consensus on human caused climate change in the peer-reviewed scientific literature. Environmental Research Letters 16:114005.

MacDonald, S. O., and J. A. Cook. 1996. The land mammal fauna of Southeast Alaska. Canadian Field-Naturalist 4:571–598.

Mahoney, P. J., K. Joly, B. L. Borg, M. S. Sorum, T. A. Rinaldi, D. Saalfeld, H. Golden, A. D. M. Latham, A. P. Kelly, B. Mangipane, C. L. Koizumi, L. Neufeld, M. Hebblewhite, N. T. Boelman, and L. R. Prugh. 2020. Denning phenology and reproductive success of wolves in response to climate signals. Environmental Research Letters 15:125001.

Mainguy, J., S. D. Côté, M. Festa-Bianchet, and D. W. Coltman. 2009. Father–offspring phenotypic correlations suggest intralocus sexual conflict for a fitness-linked trait in a wild sexually dimorphic mammal. Proceedings of the Royal Society B: Biological Sciences 276:4067–4075.

Mantua, N. J., and S. R. Hare. 2002. The Pacific Decadal Oscillation. Journal of Oceanography 58:35–44.

Marris, E. 2007. The escalator effect. Nature Climate Change 1:94–96.

Martin, K. M. 2000. Wildlife in alpine and subalpine habitats. Pages 239–260 Wildlife-habitat relationships in Oregaon and Washington. Oregon State University Press, Corvallis, OR.

Martin, L. B. 2009. Stress and immunity in wild vertebrates: Timing is everything. General and Comparative Endocrinology 163:70–76.

Mason, T. H. E., F. Brivio, P. A. Stephens, M. Apollonio, and S. Grignolio. 2017. The behavioral trade-off between thermoregulation and foraging in a heat-sensitive species. Behavioral Ecology 28:908–918.

Maxwell, S. L., N. Butt, M. Maron, C. A. McAlpine, S. Chapman, A. Ullmann, D. B. Segan, and J. E. M. Watson. 2019. Conservation implications of ecological responses to extreme weather and climate events. Diversity and Distributions 25:613–625.

Mays, L. W. 2011. Water resources engineering. 2nd ed. John Wiley, Hoboken, NJ.

McArt, S. H., D. E. Spalinger, W. B. Collins, E. R. Schoen, T. Stevenson, and M. Bucho. 2009. Summer dietary nitrogen availability as a potential bottom-up constraint on moose in south-central Alaska. Ecology 90:1400–1411.

McClung, D., and P. A. Schaerer. 2006. The Avalanche Handbook. 3rd ed. Mountaineers Books, Seattle, WA.

McDonough, T. J., and J. S. Selinger. 2008. Mountain goat management on the Kenai Peninsula, Alaska: a new direction. Proceedings of the Northern Wild Sheep and Goat Council:50–67.

Mead, J. I., L. D. Agenbroad, A. M. Phillips, and L. T. Middleton. 1987. Extinct Mountain Goat (*Oreamnos harringtoni*) in Southeastern Utah. Quaternary Research 27:323–331.

Mead, J. I., P. S. Martin, R. C. Euler, A. Long, A. J. T. Jull, L. J. Toolin, D. J. Donahue, and T. W. Linick. 1986. Extinction of Harrington's mountain goat. Proceedings of the National Academy of Sciences 83:836–839.

Michaud, A., K. S. White, S. Hamel, J. H. Richard, and S. D. Côté. 2024. Of goats and heat, the differential impact of summer temperature on habitat selection and activity patterns in mountain goats of different ecotypes. Oecologia 206:359–379.

Mills, L. S. 2013. Conservation of wildlife populations: demography, genetics, and management. 2nd ed. Wiley-Blackwell, Hoboken, NJ.

Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: Effects of nutrition in a variable environment. Wildlife Monographs 186:1–62.

Monteith, K. L., T. R. Stephenson, V. C. Bleich, M. M. Conner, B. M. Pierce, and R. T. Bowyer. 2013. Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. Journal of Animal Ecology 82:377–388.

Morin, A., M. Rughetti, S. Rioux-Paquette, and M. Festa-Bianchet. 2016. Older conservatives: reproduction in female Alpine chamois (Rupicapra rupicapra) is increasingly risk-averse with age. Canadian Journal of Zoology 94:311–321.

Moritz, C., and R. Agudo. 2013. The Future of Species Under Climate Change: Resilience or Decline? Science 341:504–508.

Mountain Research Initiative EDW Working Group. 2015. Elevation-dependent warming in mountain regions of the world. Nature Climate Change 5:424–430.

Muller, K., and P. Straub. 2016. A review of avalanche ecology: forest habitat structure and wildlife biodiversity. Proceedings of the International Snow Science Workshop:1389–1391.

Murray, D. L. 2006. On Improving Telemetry-Based Survival Estimation. Journal of Wildlife Management 70:1530–1543.

Musselman, K. N., F. Lehner, K. Ikeda, M. P. Clark, A. F. Prein, C. Liu, M. Barlage, and R. Rasmussen. 2018. Projected increases and shifts in rain-on-snow flood risk over western North America. Nature Climate Change 8:808–812.

Myatt, N., P. Matthews, B. Ratliff, and R. Torland. 2010. Rocky mountain goat trap and transplant program and survival of transplanted kids in Oregon. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council:80.

Nandi, S., U. K. De, and S. Chowdhury. 2011. Current status of contagious ecthyma or orf disease in goat and sheep—A global perspective. Small Ruminant Research 96:73–82.

Natori, Y., and W. P. Porter. 2007. Model of Japanese serow (Capricornis crispus) energetics predicts distribution on Honshu, Japan. Ecological Applications 17:1441–1459.

Nietvelt, C. G., S. Rochetta, and S. Gordon. 2018. The impacts of wildfire on mountain goats and their winter range habitats in a coastal ecosystem. Biennial Proceedings of the Northern Wild Sheep and Goat Council 21:19–31.

Northern Wild Sheep and Goat Council. 2020. Commercial and recreational disturbance of mountain goats: recommendations for management. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 22:1–15.

Northern Wild Sheep and Goat Council. 2022. Impacts of climate change on mountain goats and their habitats: considerations for conservation, management and mitigation. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 23:vii–xxxvi.

Nowak, K., J. Berger, A. Panikowski, D. G. Reid, A. L. Jacob, G. Newman, N. E. Young, J. P. Beckmann, and S. A. Richards. 2020. Using community photography to investigate phenology: A case study of coat molt in the mountain goat (Oreamnos americanus) with missing data. Ecology and Evolution 10:13488–13499.

O’Grady, J. J., D. H. Reed, B. W. Brook, and R. Frankham. 2004. What are the best correlates of predicted extinction risk? Biological Conservation 118:513–520.

O’Leary, D., D. Inouye, R. Dubayah, C. Huang, and G. Hurtt. 2020. Snowmelt velocity predicts vegetation green-wave velocity in mountainous ecological systems of North America. International Journal of Applied Earth Observation and Geoinformation 89:102110.

Ortega, A. C., J. A. Merkle, H. Sawyer, K. L. Monteith, P. Lionberger, M. Valdez, and M. J. Kauffman. 2024. A test of the frost wave hypothesis in a temperate ungulate. Ecology 105:e4238.

Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. Coupled dynamics of body mass and population growth in response to environmental change. Nature 466:482–485.

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

Parks, L. C., D. O. Wallin, S. A. Cushman, and B. H. McRae. 2015. Landscape-level analysis of mountain goat population connectivity in Washington and southern British Columbia. Conservation Genetics 16:1195–1207.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Paul, T. 2009. Game transplants in Alaska. Technical Bulletin, Alaska Department of Fish and Game, Juneau, AK.

Payne, A. E., M.-E. Demory, L. R. Leung, A. M. Ramos, C. A. Shields, J. J. Rutz, N. Siler, G. Villarini, A. Hall, and F. M. Ralph. 2020. Responses and impacts of atmospheric rivers to climate change. Nature Reviews Earth & Environment 1:143–157.

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

Peeters, B., Å. Ø. Pedersen, L. E. Loe, K. Isaksen, V. Veiberg, A. Stien, J. Kohler, J.-C. Gallet, R. Aanes, and B. B. Hansen. 2019. Spatiotemporal patterns of rain-on-snow and basal ice in high Arctic Svalbard: detection of a climate-cryosphere regime shift. Environmental Research Letters 14:015002.

Peitzsch, E. H., E. Hood, J. R. Harley, D. K. Stahle, N. E. Kichas, and G. J. Wolken. 2023. Tree-ring derived avalanche frequency and climate associations in a high-latitude, maritime climate. Journal of Geophysical Research: Earth Surface 128:e2023JF007154.

Peitzsch, E., G. T. Pederson, K. W. Birkeland, J. Hendrikx, and D. B. Fagre. 2021. Climate drivers of large magnitude snow avalanche years in the U.S. northern Rocky Mountains. Scientific Reports 11:10032.

Pelletier, F., J. Mainguy, and S. D. Côté. 2009. Rut-Induced Hypophagia in Male Bighorn Sheep and Mountain Goats: Foraging Under Time Budget Constraints. Ethology 115:141–151.

Penczykowski, R. M., B. M. Connolly, and B. T. Barton. 2017. Winter is changing: Trophic interactions under altered snow regimes. Food Webs 13:80–91.

Pepin, N. C., E. Arnone, A. Gobiet, K. Haslinger, S. Kotlarski, C. Notarnicola, E. Palazzi, P. Seibert, S. Serafin, W. Schöner, S. Terzago, J. M. Thornton, M. Vuille, and C. Adler. 2022. Climate changes and their elevational patterns in the mountains of the world. Reviews of Geophysics 60.

Pettorelli, N., F. Pelletier, A. von Hardenberg, M. Festa-Bianchet, and S. D. Côté. 2007. Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology 88:381–390.

Pianka, E. R., and W. S. Parker. 1975. Age-Specific Reproductive Tactics. The American Naturalist 109:453–464.

Pigeon, K. E., G. Stenhouse, and S. D. Côté. 2016. Drivers of hibernation: linking food and weather to denning behaviour of grizzly bears. Behavioral Ecology and Sociobiology 70:1745–1754.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. The Journal of Wildlife Management 53:7–15.

Poole, K. G., K. D. Bachmann, and I. E. Teske. 2010. Mineral lick use by GPS radio-collared mountain goats in southeastern British Columbia. Western North American Naturalist 70:208–217.

Poole, K. G., K. Stuart-Smith, and I. E. Teske. 2009. Wintering strategies by mountain goats in interior mountains. Canadian Journal of Zoology 87:273–283.

Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B: Biological Sciences 363:2367–2373.

Post, E., C. Pedersen, C. C. Wilmers, and M. C. Forchhammer. 2008. Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. Proceedings of the Royal Society B: Biological Sciences 275:2005–2013.

Prichard, A. K., K. Joly, and J. Dau. 2012. Quantifying telemetry collar bias when age is unknown: A simulation study with a long-lived ungulate. The Journal of Wildlife Management 76:1441–1449.

Prugh, L. R., and K. J. Sivy. 2020. Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. Ecology Letters 23:902–918.

Quante, L., S. N. Willner, R. Middelanis, and A. Levermann. 2021. Regions of intensification of extreme snowfall under future warming. Scientific Reports 11:16621.

R Core Team. 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rahbek, C., M. K. Borregaard, R. K. Colwell, B. Dalsgaard, B. G. Holt, N. Morueta-Holme, D. Nogues-Bravo, R. J. Whittaker, and J. Fjeldså. 2019. Humboldt's enigma: What causes global patterns of mountain biodiversity? Science 365:1108–1113.

Ray, C., E. Beever, and S. Loarie. 2013. Retreat of the American Pika: Up the Mountain or into the Void? Pages 245–270 *in* J. F. Brodie, E. Post, and D. F. Doak, editors. Wildlife conservation in a changing climate. The University of Chicago Press, Chicago, Ill. and London.

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

Renecker, L. A., and W. M. Samuel. 1991. Growth and seasonal weight changes as they relate to spring and autumn set points in mule deer. Canadian Journal of Zoology 69:744–747.

Requena, E., R. Alba, D. Rosselli, and D. Chamberlain. 2022. Avalanche Tracks are Key Habitats for the Rock Bunting Emberiza cia in the Alps. Ardeola 69.

Rice, C. G., and D. Gay. 2010. Effects of mountain goat harvest on historic and contemporary populations. Northwestern Naturalist 91:40–57.

Rice, C., B. Larue, and M. Festa-Bianchet. 2022. Variation in age of primiparity in mountain goats (Oreamnos americanus) estimated from horn growth increments. Canadian Journal of Zoology 100:176–183.

Richard, J. H., J. Wilmshurst, and S. D. Côté. 2014. The effect of snow on space use of an alpine ungulate: recently fallen snow tells more than cumulative snow depth. Canadian Journal of Zoology 92:1067–1074.

Rivieccio, E., C. Troiano, S. Petrelli, V. Maselli, G. De Filippo, D. Fulgione, and M. Buglione. 2022. Population development and landscape preference of reintroduced wild ungulates: successful rewilding in Southern Italy. PeerJ 10:e14492.

Rixen, C., S. Haag, D. Kulakowski, and P. Bebi. 2007. Natural avalanche disturbance shapes plant diversity and species composition in subalpine forest belt. Journal of Vegetation Science 18:735–742.

Roe, G. H. 2005. Orographic precipitation. Annual Review of Earth and Planetary Sciences 33:645–671.

Rofkar, T. 2014. Managing and harvesting mountain goats for traditional purposes by indigenous user groups. Proceedings of the Northern Wild Sheep and Goat Council 19:37–41.

Rughetti, M., C. Toïgo, A. Von Hardenberg, E. Rocchia, and M. Festa-Bianchet. 2011. Effects of an exceptionally snowy winter on chamois survival. Acta Theriologica 56:329.

Samuel, W. M., G. A. Chalmers, J. G. Stelfox, A. Loewen, and J. J. Thomsen. 1975. Contagious ecthyma in bighorn sheep and mountain goat in western Canada. Journal of Wildlife Diseases 11:26–31.

Sandercock, B. K., K. Martin, and S. J. Hannon. 2005. Demographic consequences of age-structure in extreme environments: population models for arctic and alpine ptarmigan. Oecologia 146:13–24.

Sanderfoot, O. V., S. B. Bassing, J. L. Brusa, R. L. Emmet, S. J. Gillman, K. Swift, and B. Gardner. 2021. A review of the effects of wildfire smoke on the health and behavior of wildlife. Environmental Research Letters 16:123003.

Sarmento, W., and J. Berger. 2020. Conservation implications of using an imitation carnivore to assess rarely used refuges as critical habitat features in an alpine ungulate. PeerJ 8:e9296.

Sarmento, W., M. Biel, and J. Berger. 2019. Seeking snow and breathing hard – Behavioral tactics in high elevation mammals to combat warming temperatures. PLOS ONE 14:e0225456.

Schaller, G. B. 1977. Mountain monarchs: wild sheep and goats of the Himalaya. University of Chicago Press, Chicago.

Scheffers, B. R., L. De Meester, T. C. L. Bridge, A. A. Hoffmann, J. M. Pandolfi, R. T. Corlett, S. H. M. Butchart, P. Pearce-Kelly, K. M. Kovacs, D. Dudgeon, M. Pacifici, C. Rondinini, W. B. Foden, T. G. Martin, C. Mora, D. Bickford, and J. E. M. Watson. 2016. The broad footprint of climate change from genes to biomes to people. Science 354:aaf7671.

Schmeller, D. S., D. Urbach, K. Bates, J. Catalan, D. Cogălniceanu, M. C. Fisher, J. Friesen, L. Füreder, V. Gaube, M. Haver, D. Jacobsen, G. Le Roux, Y.-P. Lin, A. Loyau, O. Machate, A. Mayer, I. Palomo, C. Plutzar, H. Sentenac, R. Sommaruga, R. Tiberti, and W. J. Ripple. 2022. Scientists' warning of threats to mountains. Science of The Total Environment 853:158611.

Schmidt, N. M., J. Reneerkens, J. H. Christensen, M. Olesen, and T. Roslin. 2019. An ecosystem-wide reproductive failure with more snow in the Arctic. PLOS Biology 17:e3000392.

Schweizer, J., J. Bruce Jamieson, and M. Schneebeli. 2003. Snow avalanche formation. Reviews of Geophysics 41:1016.

Sergio, F., J. Blas, and F. Hiraldo. 2018. Animal responses to natural disturbance and climate extremes: a review. Global and Planetary Change 161:28–40.

Serrouya, R., M. Dickie, C. Lamb, H. Van Oort, A. P. Kelly, C. DeMars, P. D. McLoughlin, N. C. Larter, D. Hervieux, A. T. Ford, and S. Boutin. 2021. Trophic consequences of terrestrial eutrophication for a threatened ungulate. Proceedings of the Royal Society B: Biological Sciences 288:20202811.

Serrouya, R., B. N. Mclellan, G. D. Pavan, and C. D. Apps. 2011. Grizzly bear selection of avalanche chutes: Testing the effectiveness of forest buffer retention. The Journal of Wildlife Management 75:1597–1608.

Shackleton, D. M., editor. 1997. Wild sheep and goats and their relatives: status survey and conservation action plan for caprinae. IUCN, Gland, Switzerland.

Shafer, A. B. A., S. D. Côté, and D. W. Coltman. 2011. Hot spots of genetic diversity descended from multiple Pleistocene refugia in an alpine ungulate. Evolution 65:125–138.

Shafer, A. B. A., J. M. Northrup, K. S. White, M. S. Boyce, S. D. Côté, and D. W. Coltman. 2012. Habitat selection predicts genetic relatedness in an alpine ungulate. Ecology 93:1317–1329.

Shakeri, Y. N., K. S. White, and J. N. Waite. 2021. Staying close to home: Ecological constraints on space use and range fidelity in a mountain ungulate. Ecology and Evolution 11:11051–11064.

Shanley, C. S., S. Pyare, M. I. Goldstein, P. B. Alaback, D. M. Albert, C. M. Beier, T. J. Brinkman, R. T. Edwards, E. Hood, A. MacKinnon, M. V. McPhee, T. M. Patterson, L. H. Suring, D. A. Tallmon, and M. S. Wipfli. 2015. Climate change implications in the northern coastal temperate rainforest of North America. Climatic Change 130:155–170.

Shenk, T. M., and A. B. Franklin, editors. 2001. Modeling in natural resource management: development, interpretation, and application. Island Press, Washington, DC.

Sikes, R. S. and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education: Journal of Mammalogy 97:663–688.

Skladanowski, M. J., E. C. Weidner, J. L. Bowles, and M. Hebblewhite. 2021. Nineteen rocky mountain elk (Cervus canadensis nelsoni) killed in an avalanche in the Three Sisters Wilderness. Northwestern Naturalist 102:265–268.

Smith, B. L. 1988. Criteria for determining age and sex of American mountain goats in the field. Journal of Mammalogy 69:395–402.

Smith, C. A., and K. J. Raedeke. 1982. Group size and movements of a dispersed, low density goat population with comments on inbreeding and human impact. Proceedings of the Northern Wild Sheep and Goat Council 3:54–67.

Smith, M. D. 2011a. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. Journal of Ecology 99:656–663.

Smith, M. D. 2011b. The ecological role of climate extremes: current understanding and future prospects. Journal of Ecology 99:651–655.

Spitz, D. B., M. Hebblewhite, T. R. Stephenson, and D. W. German. 2018. How plastic is migratory behavior? Quantifying elevational movement in a partially migratory alpine ungulate, the Sierra Nevada bighorn sheep (Ovis canadensis sierrae). Canadian Journal of Zoology 96:1385–1394.

Stearns, S. C. 1989. Trade-Offs in Life-History Evolution. Functional Ecology 3:259.

Stearns, S. C. 1998. The Evolution Of Life Histories. Oxford University PressOxford.

Stephen, C., editor. 2022. Wildlife population health. Springer, Cham, Switzerland.

Stephenson, T. R., D. W. German, E. F. Cassirer, D. P. Walsh, M. E. Blum, M. Cox, K. M. Stewart, and K. L. Monteith. 2020a. Linking population performance to nutritional condition in an alpine ungulate. Journal of Mammalogy 101:1244–1256.

Stephenson, T. R., D. W. German, E. F. Cassirer, D. P. Walsh, M. E. Blum, M. Cox, K. M. Stewart, and K. L. Monteith. 2020b. Linking population performance to nutritional condition in an alpine ungulate. Journal of Mammalogy 101:1244–1256.

Stevens, V. 1983. The dynamics of dispersal in an introduced mountain goat population. PhD Thesis, University of Washington, Seattle, WA.

Stowell, H. H. 2006. Geology of Southeast Alaska : Rock and Ice in Motion. University of Alaska Press.

Strapazzon, G., J. Schweizer, I. Chiambretti, M. Brodmann Maeder, H. Brugger, and K. Zafren. 2021. Effects of climate change on avalanche accidents and survival. Frontiers in Physiology 12:639433.

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.

Sutherland, C., D. Hare, P. J. Johnson, D. W. Linden, R. A. Montgomery, and E. Droge. 2023. Practical advice on variable selection and reporting using Akaike information criterion. Proceedings of the Royal Society B: Biological Sciences 290:20231261.

Tabari, H. 2021. Extreme value analysis dilemma for climate change impact assessment on global flood and extreme precipitation. Journal of Hydrology 593:125932.

Tepper, L. H., J. George, and W. Joseph. 2017. Salish blankets: robes of protection and transformation, symbols of wealth. University of Nebraska Press, Lincoln, NB.

Testa, J. W., and G. P. Adams. 1998. Body Condition and Adjustments to Reproductive Effort in Female Moose (Alces alces). Journal of Mammalogy 79:1345–1354.

Théoret-Gosselin, R., S. Hamel, and S. D. Côté. 2015. The role of maternal behavior and offspring development in the survival of mountain goat kids. Oecologia 178:175–186.

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

Thuiller, W., S. Lavorel, and M. B. Araújo. 2005. Niche properties and geographical extent as predictors of species sensitivity to climate change. Global Ecology and Biogeography 14:347–357.

Tryland, M., K. B. Beckmen, K. A. Burek-Huntington, E. M. Breines, and J. Klein. 2018. Orf virus infection in Alaskan mountain goats, Dall's sheep, muskoxen, caribou and Sitka black-tailed deer. Acta Veterinaria Scandinavica 60:12.

Turgeon, R., F. Pelletier, S. D. Côté, M. Festa-Bianchet, and S. Hamel. 2024. Sporadic events have a greater influence on the dynamics of small, isolated populations than density dependence and environmental conditions. The American Naturalist 204:574–588.

Ummenhofer, C. C., and G. A. Meehl. 2017. Extreme weather and climate events with ecological relevance: a review. Philosophical Transactions of the Royal Society B: Biological Sciences 372:20160135.

Urban, M. C. 2024. Climate change extinctions. Science 386:1123–1128.

Van Eck, N. J., and L. Waltman. 2010. Software survey: VOSviewer, a computer program for bibliometric mapping. Scientometrics 84:523–538.

Van Eck, N. J., and L. Waltman. 2019. Manual for VOSviewer Version 1.6. 10. Univeristeit Leiden, The Netherlands.

Visscher, D. R., E. H. Merrill, D. Fortin, and J. L. Frair. 2006. Estimating woody browse availability for ungulates at increasing snow depths. Forest Ecology and Management 222:348–354.

Wagler, B. L., R. A. Smiley, A. B. Courtemanch, G. Anderson, D. Lutz, D. McWhirter, D. Brimeyer, P. Hnilicka, C. P. Massing, D. W. German, T. R. Stephenson, and K. L. Monteith. 2022. Effects of helicopter net-gunning on survival of bighorn sheep. The Journal of Wildlife Management 86.

Walsh, J. E., T. J. Ballinger, E. S. Euskirchen, E. Hanna, J. Mård, J. E. Overland, H. Tangen, and T. Vihma. 2020. Extreme weather and climate events in northern areas: A review. Earth-Science Reviews 209:103324.

Waltman, L., N. J. Van Eck, and E. C. M. Noyons. 2010. A unified approach to mapping and clustering of bibliometric networks. Journal of Informetrics 4:629–635.

Wang, T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America. PLOS ONE 11:e0156720.

Weladji, R. B., D. R. Klein, Ø. Holand, and A. Mysterud. 2002. Comparative response of Rangifer tarandus and other northern ungulates to climatic variability. Rangifer 22:33.

White, K. S., B. Cadsand, S. D. Côté, T. Graves, S. Hamel, R. B. Harris, F. P. Hayes, E. Hood, K. Hurley, T. Jessen, B. Jex, E. Peitzsch, W. Sarmento, H. Schwantje, and J. Berger. 2024a. Mountain sentinels in a changing world: Review and conservation implications of weather and climate effects on mountain goats (Oreamnos americanus). Global Ecology and Conservation:e03364.

White, K. S., and D. P. Gregovich. 2017. Mountain goat resource selection in relation to mining-related disturbance. Wildlife Biology 2017:1–12.

White, K. S., and D. P. Gregovich. 2018. Mountain goat resource selection in the Haines-Skagway area: Implications for helicopter skiing management. Wildlife Research Report, Alaska Department of Fish and Game, Division of Wildlife Conservation, Juneau, AK.

White, K. S., D. P. Gregovich, and T. Levi. 2018. Projecting the future of an alpine ungulate under climate change scenarios. Global Change Biology 24:1136–1149.

White, K. S., D. P. Gregovich, G. W. Pendleton, N. L. Barten, A. P. Crupi, R. Scott, and D. N. Larsen. 2012. Modeling resource selection of mountain goats in southeastern Alaska: applications for population management and highway development planning. Proceedings of the Northern Wild Sheep and Goat Council. 18:32–42.

White, K. S., E. Hood, G. J. Wolken, E. H. Peitzsch, Y. Bühler, K. Wikstrom Jones, and C. T. Darimont. 2024b. Snow avalanches are a primary climate-linked driver of mountain ungulate populations. Communications Biology 7:423.

White, K. S., T. Levi, J. Breen, M. Britt, J. Meröndun, D. Martchenko, Y. N. Shakeri, B. Porter, and A. B. A. Shafer. 2021a. Integrating genetic data and demographic modeling to facilitate conservation of small, isolated mountain goat populations. The Journal of Wildlife Management 85:271–282.

White, K. S., G. W. Pendleton, D. Crowley, H. J. Griese, K. J. Hundertmark, T. McDonough, L. Nichols, M. Robus, C. A. Smith, and J. W. Schoen. 2011. Mountain goat survival in coastal Alaska: Effects of age, sex, and climate. The Journal of Wildlife Management 75:1731–1744.

White, K. S., G. W. Pendleton, and E. Hood. 2009. Effects of Snow on Sitka Black-Tailed Deer Browse Availability and Nutritional Carrying Capacity in Southeastern Alaska. Journal of Wildlife Management 73:481–487.

White, K. S., G. W. Pendleton, and J. N. Waite. 2016. Development of an aerial survey population estimation technique for mountain goats in Alaska. Final Wildlife Research Report, Alaska Department of Fish and Game, Division of Wildlife Conservation, Juneau, AK.

White, K. S., D. E. Watts, and K. B. Beckmen. 2021b. Helicopter-based chemical immobilization of mountain goats in coastal Alaska. Wildlife Society Bulletin 45:670–681.

White, R. G. 1983. Foraging Patterns and Their Multiplier Effects on Productivity of Northern Ungulates. Oikos 40:377.

Williams, C. M., H. A. L. Henry, and B. J. Sinclair. 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change: Organismal responses to winter climate change. Biological Reviews 90:214–235.

Williams, G. C. 1966. Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. The American Naturalist 100:687–690.

Wilson, E. E., and E. M. Wolkovich. 2011. Scavenging: how carnivores and carrion structure communities. Trends in Ecology & Evolution 26:129–135.

Wolff, P. L., T. Besser, D. Nelson, J. Ridpath, K. McMullen, J. Munoz-Guiterrez, M. Cox, C. Morris, and C. McAdoo. 2014. Mountain goats at the livestock-wildlife interface: a susceptible species. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 19:13.

Wolff, P. L., J. A. Blanchong, D. D. Nelson, P. J. Plummer, C. McAdoo, M. Cox, T. E. Besser, J. Muñoz-Gutiérrez, and C. A. Anderson. 2019. Detection of Mycoplasma ovipneumoniae in Pneumonic Mountain Goat (Oreamnos americanus) Kids. Journal of Wildlife Diseases 55:206.

Wolff, P. L., M. Cox, C. McAdoo, and C. Anderson. 2016. Disease transmission between sympatric mountain goats and bighorn sheep. Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council 20:79.

Young, K. B., T. M. Lewis, K. S. White, and A. B. A. Shafer. 2022. Quantifying the effects of recent glacial history and future climate change on a unique population of mountain goats. Biological Conservation 272:109631.

Yravedra, J., and L. Cobo-Sánchez. 2015. Neanderthal exploitation of ibex and chamois in southwestern Europe. Journal of Human Evolution 78:12–32.

Appendix A – Supplementary Information for Chapter 2

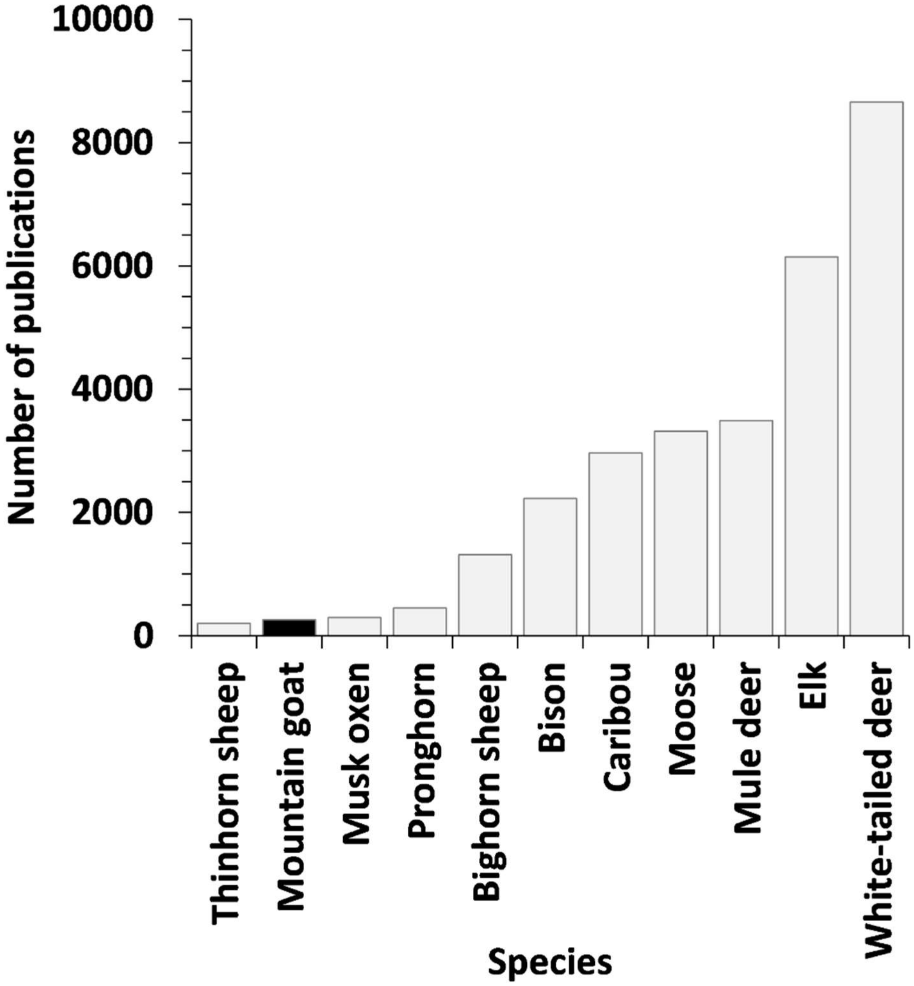

Figure A1. Number of peer-reviewed scientific publications summarized by native North American ungulate species. Publications were compiled using the Web of Science literature database using search terms for the common and scientific name of each species (on 6/27/2023).

Appendix A1: Supporting text

Projected climate change in mountain regions inhabited by mountain goats
Mountain goat distribution encompasses an expansive geographic range and diversity of climatic zones. Within this region, changes in climate are expected to vary spatially. We conducted simulation analyses focused on characterizing projected changes in climate within representative mountain regions inhabited by the species. Our analyses were focused on using a standardized approach to describe broad-scale patterns to attain a general understanding of how climate change dynamics vary in select mountain regions across the species range. Our approach is limited in scope and application, and not intended to comprise a detailed, comprehensive assessment.

We used the spatial climate modeling software Climate WNA 7.31 (Wang et al. 2016) to summarize baseline historical conditions (1990-2020) and derive estimates of climate conditions in the future (2070-2100). The model enables derivation of scale free point estimates of climate values using bilinear interpolation and elevational adjustments, and based on spatially explicit PRISM climate models (4 km^2 resolution; Wang et al. 2016). To describe future climate conditions, we used an ensemble of 13 General Circulation Models (GCMs) and an intermediate emissions scenario (SSP-370), previously determined to be most suitable for western North America (Wang et al. 2016, 2022).

We derived point estimates of climate conditions within a suite of 11 representative mountain regions inhabited by mountain goats (Table S2, Figure S2). Mountain regions were systematically selected based on their geographic position with the intent of characterizing conditions across ecotonal (coastal-interior) and latitudinal gradients, prioritizing populations for which baseline population biology data has been published. Point locations used for deriving climate simulations were selected based on known presence of mountain goats and exclusively occurred in alpine habitats, to standardize geographic comparisons. As such, conditions may not be strictly representative of mountain goat winter distribution in populations that conduct seasonal migrations to low elevation habitats (i.e. populations in coastal and transitional climates). Overall, we synthesized climate simulation data for a subset of climate variables previously determined to influence mountain goat population responses (see Section 3.3 and 3.4), specifically including average summer temperature (ºC; Jun-Aug), total summer precipitation (mm; Jun-Aug), average winter temperature (ºC; Dec-Feb), maximum winter temperature (ºC; Dec-Feb), and total annual precipitation as snow (mm; Jul-Jun). Precipitation as snow was converted to a standardized estimate of total annual snowfall (m) based on White et al. (2018).

Results from the climate simulation modeling (Table S3) showed that, overall, average temperature is expected to increase in all areas in both winter (mean = 3.2 ºC, range: 1.8 – 5.0 ºC, n = 11; Table S3a) and summer (mean = 4.7 ºC, range: 3.7 – 5.4 ºC, n = 11; Table S3b). The smallest projected changes in summer temperature occurred in coastal and northern interior areas, whereas the greatest were predicted for transitional and southern interior regions. Average winter temperature conditions varied substantially across mountain regions inhabited by mountain goats, ranging from -18 ºC (Logan Mountains) to -3.5 ºC (Kitasoo Mountains).

Maximum and average winter temperatures were projected to increase at comparable rates. However, in four coastal and transitional alpine ranges (Coast Range, Kitasoo Mountains, N Cascade Range, Kenai Mountains) maximum temperatures were expected to increase above the freezing point (0º C), on average, in the future. Likewise, such areas also were projected to experience the greatest reduction in winter snowfall (-2.7 to -5.3 m). However, in the colder and drier interior ranges, snowfall was projected to experience limited change (Caw Ridge, Glacier, Pahsimeroi Mountains), or even increase (Logan Mountains, Kluane Range), due to the increased water holding capacity of warmer air. Thus, in the coldest areas, the substantial changes in winter temperature had relatively negligible effects on snowfall, whereas in coastal areas similar shifts had disproportionate effects on snowfall amounts (39-49% decrease). Summer precipitation was generally projected to increase in the future in most areas (up to 37%), but areas influenced by southern coastal weather systems (Kitasoo Mountains, N Cascade Range, Glacier) were projected to experience reduced summer precipitation (15-21% decline).

Table A2. Description of sites used to reference climate change projections in mountain regions inhabited by mountain goats across their distribution in North America.

Ecotype	ID	Range	Region	Locality	Lat	Long	Elev
Coastal	1	Coast Mtns, AK	Grandchild Pks	Windfall Ridge	58.488	-134.669	1020
Coastal	2	Kitasoo Mtns, BC	Kitasoo		52.832	-127.893	1390
Coastal	3	N Cascade Range, WA	Glacier Peak	Image Lk	48.249	-120.995	1720
Trans.	4	Kenai Mtns, AK	Kenai Mtns	Indian Ck	60.083	-150.324	1153
Trans.	5	Chilkat Mtns, AK/BC	Kelsall	Ashmun Mtn	59.629	-136.197	1260
Trans.	6	Skeena Mtns, BC	Babine Mtns	McKendrick Mtn	54.827	-126.747	1590
Interior	7	Logan Mtns, NWT	Nahanni	Fairy Mdw	62.099	-127.656	1480
Interior	8	Kluane Range, YT	Donjek	Hoge Pass	61.294	-139.566	1310
Interior	9	Canadian Rockies, AB	Caw Ridge	Caw Ridge	54.080	-119.414	1952
Interior	10	Rocky Mtns, MT	Glacier NP	Avalanche Lk	48.644	-113.770	1870
Interior	11	Bitterroot Mtns, ID	Pahsimeroi	Saddle Mtn	43.931	-112.961	3000

Table A3a. Projected change in climate in 11 representative mountain regions (spanning ecotonal and latitudinal gradients) inhabited by mountain goats throughout their North American distribution. Baseline historical climate conditions (1990-2020) and estimated future conditions (2070-2100) are summarized for winter climate variables previously determined to influence mountain goat ecology including: average winter temperature, maximum winter temperature, and annual snowfall. Simulations are based on an ensemble of 13 General Circulation Models (GCMs) and an intermediate emissions scenario (SSP-370), previously determined to be most suitable for western North America (Wang et al. 2016, 2022).

	Avg. temperature (ºC) winter			Max. temperature (ºC) winter			Snowfall (m) - annual		
Mountain Range	2020	2100	Δ	2020	2100	Δ	2020	2100	Δ
Coastal:									
Coast Mtns, AK	-6.30	-3.10	3.20	-2.90	1.40	4.30	9.73	5.95	-3.78
Kitasoo Mtns, BC	-3.50	-1.00	2.50	0.30	3.20	2.90	11.84	6.57	-5.27
N Cascade Range, WA	-3.60	-0.70	2.90	-0.30	3.30	3.60	5.52	2.80	-2.72
Transitional:									
Kenai Mtns, AK	-7.30	-2.30	5.00	-3.60	2.60	6.20	5.97	3.50	-2.47
Chilkat Mtns, AK/BC	-9.30	-5.40	3.90	-5.10	-0.10	5.00	4.59	3.49	-1.10
Skeena Mtns, BC	-8.00	-4.70	3.30	-5.00	-0.60	4.40	3.42	2.73	-0.69
Interior:									
Logan Mtns., NWT	-18.30	-14.20	4.10	-13.20	-9.70	3.50	2.22	2.43	0.20
Kluane Range, YT	-15.30	-11.60	3.70	-11.00	-6.40	4.60	1.60	1.84	0.23
Canadian Rockies, AB	-8.10	-5.80	2.30	-2.80	-1.20	1.60	2.02	1.87	-0.15
Rocky Mtns, MT	-6.50	-4.70	1.80	-2.80	-1.30	1.50	5.23	4.67	-0.56
Bitterroot Mtns, ID	-8.10	-5.70	2.40	-4.70	-2.00	2.70	2.41	1.92	-0.50

Table A3b. Projected change in climate in 11 representative mountain regions (spanning ecotonal and latitudinal gradients) inhabited by mountain goats throughout their North American distribution. Baseline historical climate conditions (1990-2020) and estimated future conditions (2070-2100) are summarized for summer climate variables previously determined to influence mountain goat ecology including: average summer temperature, and total summer precipitation. Simulations are based on an ensemble of 13 General Circulation Models (GCMs) and an intermediate emissions scenario (SSP-370), previously determined to be most suitable for western North America (Wang et al. 2016, 2022).

	Avg. temperature (ºC) - summer			Precipitation (mm) - summer		
Mountain Range	2020	2100	Δ	2020	2100	Δ
Coastal:						
Coast Mtns, AK	8.40	12.70	4.30	819	890	71
Kitasoo Mtns, BC	9.90	14.00	4.10	593	507	-86
N Cascade Range, WA	11.20	16.50	5.30	154	122	-32
Transitional:						
Kenai Mtns, AK	11.30	16.20	4.90	324	371	47
Chilkat Mtns, AK/BC	9.90	15.10	5.20	230	284	54
Skeena Mtns, BC	9.10	13.80	4.70	204	206	2
Interior:						
Logan Mtns., NWT	9.20	12.90	3.70	245	287	42
Kluane Range, YT	7.70	12.30	4.60	185	246	61
Canadian Rockies, AB	9.40	14.30	4.90	280	306	26
Rocky Mtns, MT	11.90	17.30	5.40	251	214	-37
Bitterroot Mtns, ID	10.80	15.80	5.00	131	179	48

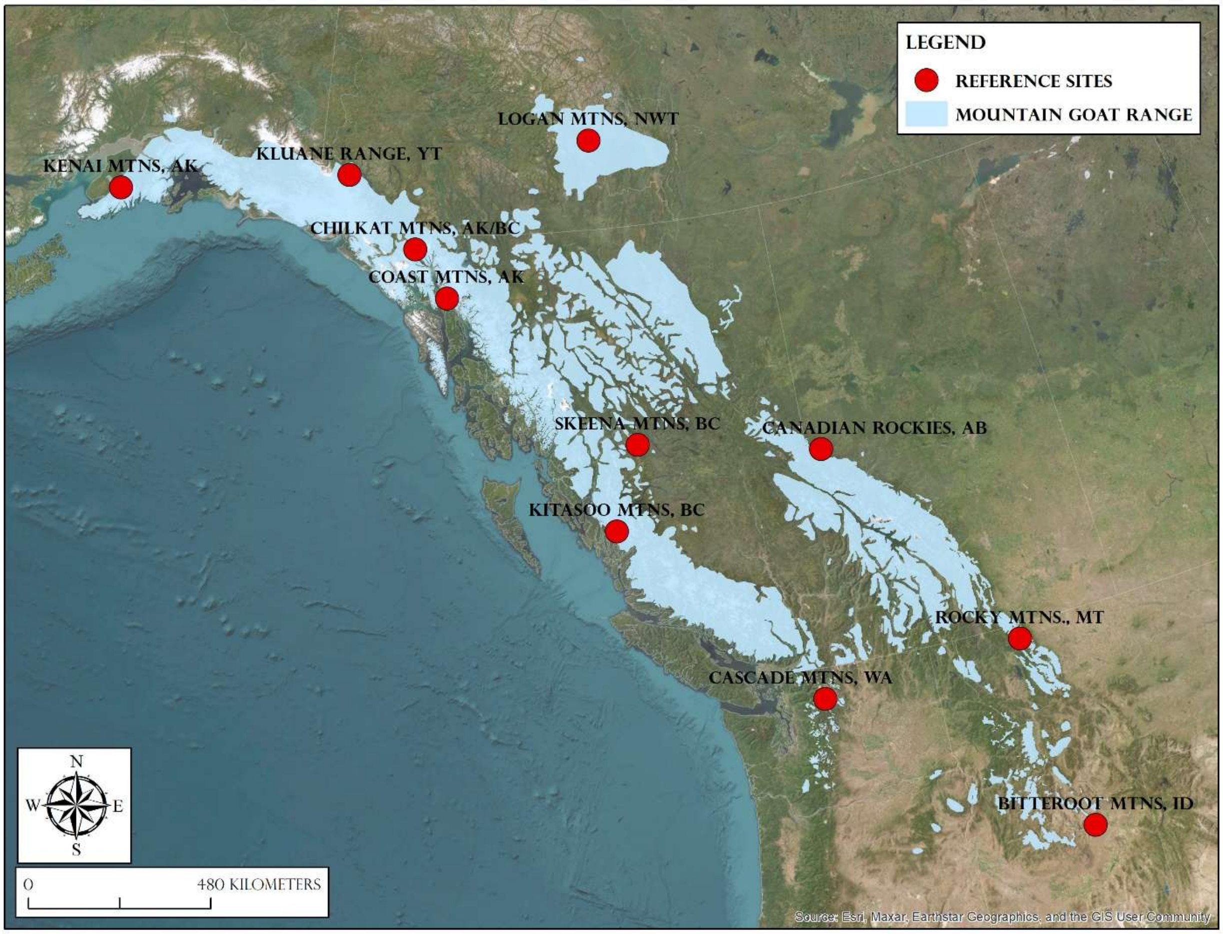

Figure A2. Map illustrating the location of sites used to reference climate change projections in mountain regions inhabited by mountain goats across their native distribution in North America.

References:

Wang, T., A. Hamann, D. L. Spittlehouse, and C. Carroll. 2016. Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America. PLoS ONE 11(6)

Wang, T., C. Mahony, D. L. Spittlehouse and A. Hamann. 2022. ClimateNA v7.30: A program to generate climate normal, annual, seasonal and monthly data for historical and future periods in North America. Users Manual, University of British Columbia, Vancouver, BC.

Appendix B– Supplementary Information for Chapter 3

Table B1. Model selection results, based on Akaike's Information Criterion with small sample size corrections (AICc), for analyses examining mountain goat parturition in relation to age, winter snow depth, summer temperature and reproductive status during the previous year in coastal Alaska, 2005–2021.

Model	df	AICc	Δ AIC$_c$	weight
Age + repro$_{t-1}$ + snow + repro$_{t-1}$ × age(6-10)	10	525.147	0.000	0.283
Age + repro$_{t-1}$ + snow + temp + repro$_{t-1}$ × age(6-10)	11	525.236	0.088	0.271
Age + repro$_{t-1}$ + snow + repro$_{t-1}$ × age(6-10) + repro$_{t-1}$ × snow	11	526.522	1.375	0.142
Age + repro$_{t-1}$ + snow + repro$_{t-1}$ × age(6-10) + repro$_{t-1}$ × age(11-16)	11	527.097	1.949	0.107
Age + repro$_{t-1}$ + snow + temp + repro$_{t-1}$ ×age(6-10) + repro$_{t-1}$×temp	12	527.340	2.193	0.094
Age + repro$_{t-1}$ + snow	9	528.221	3.074	0.061
Age + snow + temp	9	530.063	4.916	0.024
Age + snow	8	530.789	5.642	0.017
Age + repro$_{t-1}$	8	537.598	12.450	0.001
Age + repro$_{t-1}$ + temp + repro$_{t-1}$×age(6-10)	10	537.764	12.616	0.001
Age	7	539.543	14.396	0.000
Age + repro$_{t-1}$ + temp	9	539.677	14.530	0.000
Age + temp	8	541.592	16.445	0.000

Table B2. Model selection results, based on Akaike's Information Criterion with small sample size corrections (AICc), for analyses examining mountain goat adult female annual survival in relation to age, winter snow depth, summer temperature and reproductive status during the previous year in coastal Alaska, 2005–2021.

Model	df	AICc	Δ AIC$_c$	weight
Age(6-10) + Age(11-16) + Snow	5	331.008	0.000	0.171
Age(6-10) + Age(11-16) + Snow + Repro	6	332.026	1.018	0.103
Age(6-10) + Age(11-16) + Snow + Repro + Age(6-10) x Repro	7	332.070	1.063	0.101
Age(6-10) + Age(11-16) + Snow + Age(3-5) x Snow	6	332.325	1.317	0.089
Age(6-10) + Age(11-16) + Snow + Age(6-10) x Snow	6	332.362	1.354	0.087
Age(6-10) + Age(11-16) + Snow + Repro + Age(11-16) x Repro	7	332.853	1.845	0.068
Age(6-10) + Age(11-16) + Snow + Age(11-16) x Snow	6	332.885	1.878	0.067
Age(6-10) + Age(11-16) + Snow + Repro + Age(3-5) x Snow	7	333.263	2.256	0.055
Age(6-10) + Age(11-16)	4	333.570	2.562	0.048
Age(6-10) + Age(11-16) + Snow + Repro + Age(3-5) x Repro	7	333.799	2.792	0.042
Age(6-10) + Age(11-16) + Snow + Temp + Repro	7	334.037	3.029	0.038
Age(6-10) + Age(11-16) + Snow + Age(6-10) x Snow + Age(11-16) x Snow	7	334.070	3.062	0.037
Age(6-10) + Age(11-16) + Snow + Repro + Age(6-10) x Repro + Age(11-16) x Repro	8	334.157	3.149	0.035
Age(6-10) + Age(11-16) + Repro	5	334.697	3.689	0.027
Age(6-10) + Age(11-16) + Temp	5	335.331	4.323	0.020
Age(6-10) + Age(11-16) + Temp + Repro	6	336.392	5.384	0.012

Table B3. Model selection results, based on Akaike's Information Criterion with small sample size corrections (AICc), for analyses examining mountain goat offspring summer survival in relation to maternal age, winter snow depth, summer temperature and reproductive status during the previous year in coastal Alaska, 2005–2021.

Model	df	AICc	Δ AIC_c	weight
Age(11-16)	4	225.297	0.000	0.232
Age(11-16) + Snow	5	226.035	0.738	0.160
Age(11-16) + $Repro_{t-1}$	5	227.012	1.716	0.098
Age(6-10) + Age(11-16)	5	227.215	1.918	0.089
Age(11-16) + Temp	5	227.217	1.920	0.089
Age(11-16) + Snow + $Repro_{t-1}$	6	227.750	2.453	0.068
$Repro_{t-1}$	4	227.778	2.482	0.067
Age(11-16) + Snow + Temp + $Repro_{t-1}$	7	228.603	3.306	0.044
Age(4) + Age(5) + Age(6-10) + Age (11-13) + Age(14-16)	8	228.747	3.450	0.041
Age(11-16) + Temp + $Repro_{t-1}$	6	228.971	3.674	0.037
Age(11-16) + $Repro_{t-1}$ + Age(11-16) x $Repro_{t-1}$	6	229.036	3.740	0.036
Age(11-16) + Snow + $Repro_{t-1}$ + Snow x $Repro_{t-1}$	7	229.776	4.479	0.025
Age(11-16) + Temp + $Repro_{t-1}$ + Temp x $Repro_{t-1}$	7	230.768	5.471	0.015

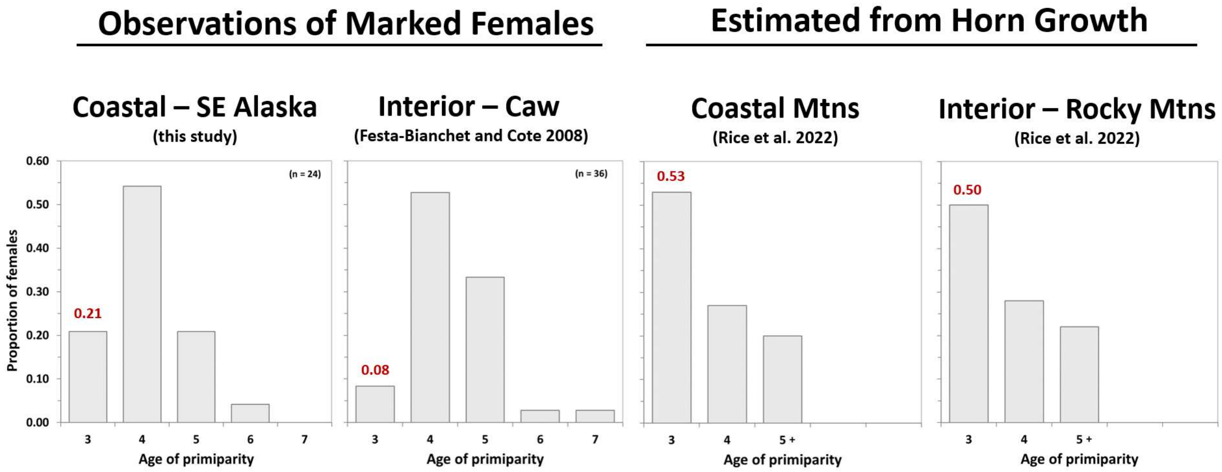

Figure B1. Age of primiparity estimates for mountain goats based on long-term studies of marked females in coastal southeastern Alaska (2005-2021; this study) and interior Canadian Rocky Mountains (Caw Ridge; 1988-1999; Festa-Bianchet and Cote 2008). Estimates of age at primiparity based on horn growth (from Rice et al. 2022) for the Coastal Mountains and Canadian Rocky Mountains are presented for comparison. Horn growth estimates were derived for the median year of each long-term study period by area (coastal, median year = 2013; interior, median year = 1993) to allow for equivalent comparisons between methods. The estimated proportion of 3-yr olds giving is highlighted in red, and indicates that estimates from direct observations are lower than indirect horn growth-based estimates with, overall, minimal differences detected between coastal and interior populations.

Appendix C– Supplementary Information for Chapter 4

Figure C1. Mountain goats and avalanches. (A) Adult male mountain goat in late-winter illustrating specialized adaptations for mountain environments including thick, woolen coat, muscular shoulders, narrow body width and hooves with hard keratinous sheaths and soft, adhesive interior pads (not seen). (B) Mountain goats in extensively excavated beds within mapped avalanche terrain following a major snowfall event (2.4 m over 6 days) during December 2020, Porcupine Mountain, Klukwan, Alaska. (C) Mountain goats sheltering beneath the fracture line of a mid-winter glide avalanche, Summit Creek, Klukwan, Alaska. (D) Adult female mountain goat navigating a 40° slope, Lions Head Mountain, Lynn Canal, Alaska. Resource selection function modeling indicates mountain goats optimally select for slope angles (36-58°) that coincide with those at which avalanches are most likely to release in maritime snow climates (30-45°).

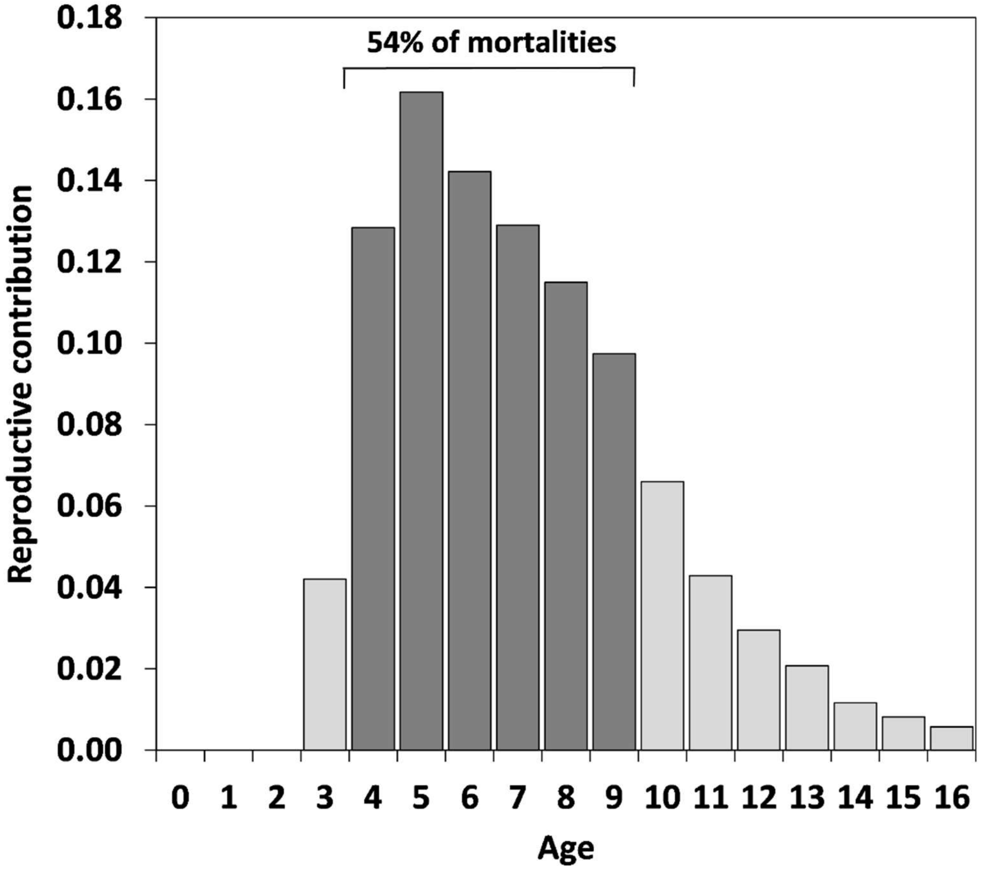

Figure C2. Avalanche impacts on prime-aged females. Avalanches exert strong effects on prime, reproductive-aged females, as illustrated by the relationship between age-specific female mountain goat reproductive contribution in relation avalanche-caused mortality. Among female mountain goats that died in avalanches, most occur among individuals in prime-aged classes (54%). Adult females in prime-aged classes contribute 77% of new recruits into a population annually. Prime aged (4-9 yrs) is defined as the population component with the highest age-specific fecundity and survival (White et al. 2011, 2018). Population age structure was calculated based on average population conditions for mountain goats in southeastern Alaska (White et al. 2021). Age-specific reproductive contribution was calculated by multiplying by age-specific fecundity by the female stable age distribution (White et al. 2018, 2021).

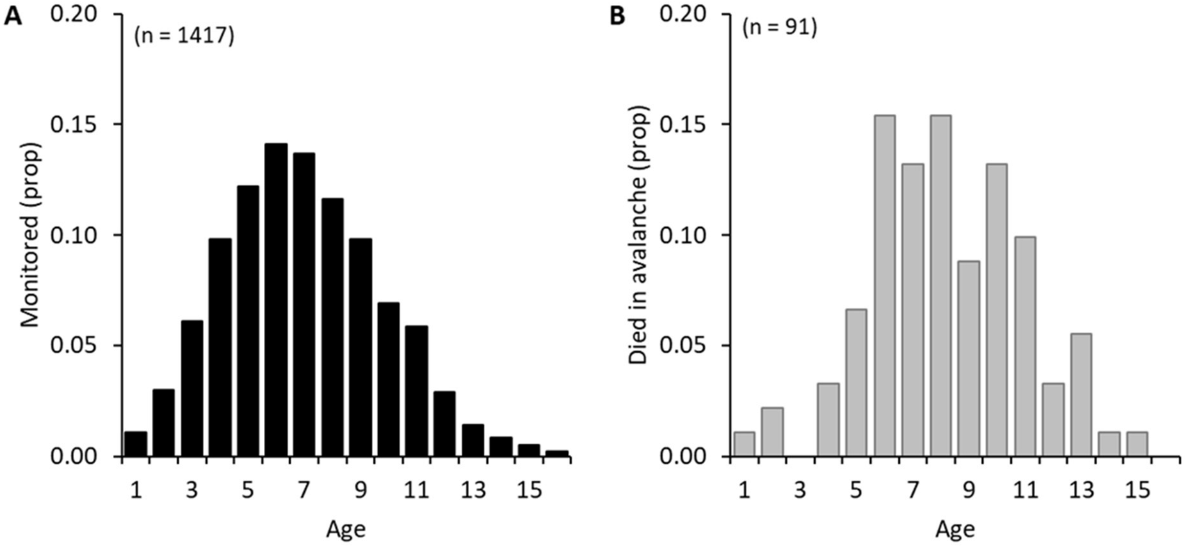

Figure C3. Age distribution of radio-marked mountain goats. (A) The proportion of radio-marked mountain goats monitored in each age class. (B) The proportion of radio-marked mountain goats that died in avalanches in each age class. Radio-marked mountain goats were monitored in four separate populations in coastal Alaska during 2005-2022. It was not possible to precisely ascertain age in two instances.

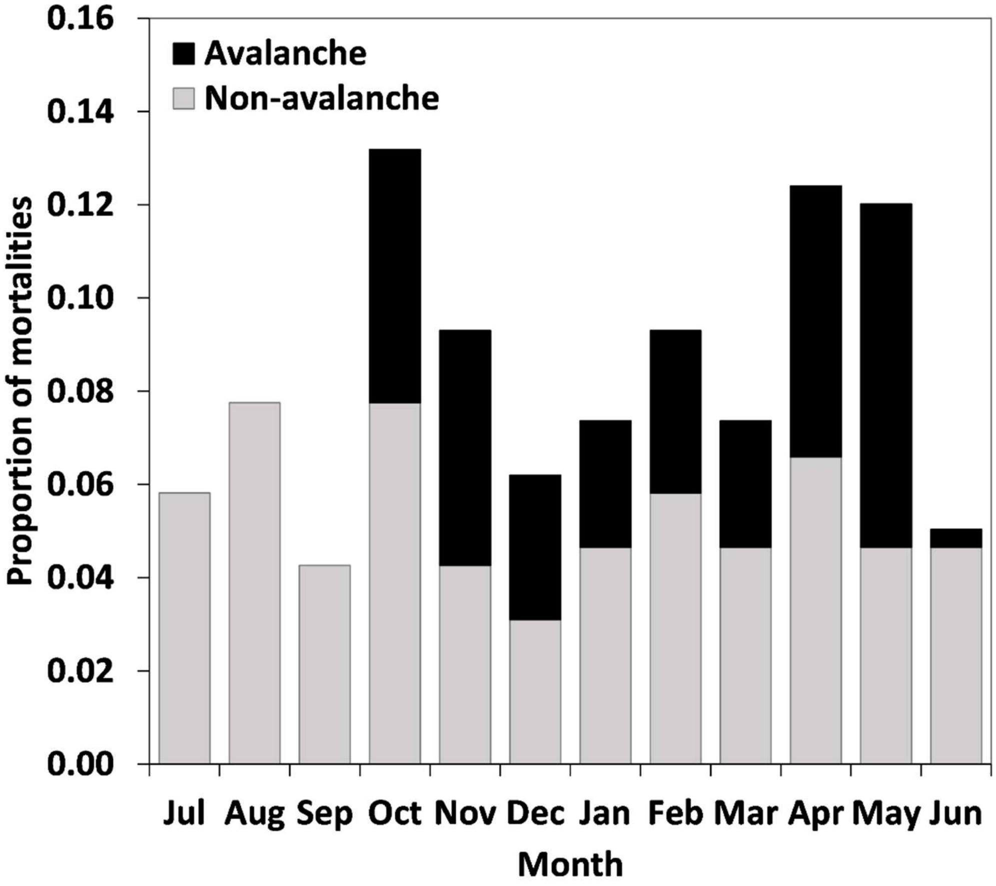

Figure C4. Temporal patterns of mountain goat mortality. Avalanche-caused mortalities of radio-marked mountain goats (n = 93) occurred during nine months, and peaked in early-autumn and late-spring in coastal Alaska (2005-2022). Non-avalanche related mortalities (n = 165) occurred consistently throughout the year.

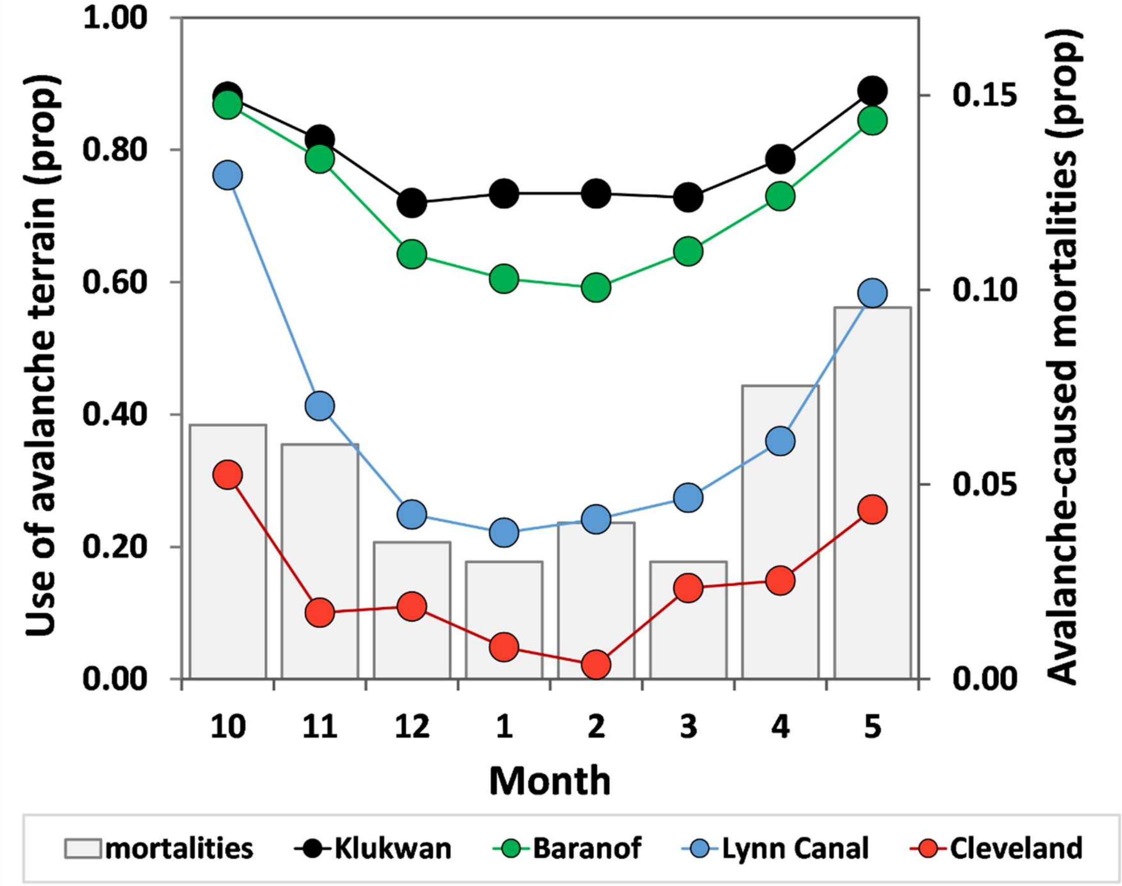

Figure C5. Mountain goat use of avalanche terrain. Spatial and temporal variation in the use of avalanche terrain by mountain goats in four study areas (color coded, left y-axis) in southeastern Alaska during 2005 – 2022. Proportion of mortalities caused by avalanches is summarized by month for the period with snow (grey bars, secondary y-axis) and includes all GPS plus VHF radio-monitored animals (total avalanche mortalities, n = 93). Avalanche terrain includes non-forested predicted avalanche release areas and avalanche paths derived using the RAMMS avalanche simulation model.

Figure C6. Mountain goat carcass subsidy of scavenger food webs. Mountain goat carrion represents an important, and contested, food resource among mountain scavengers that commonly occur in avalanche terrain, and also other habitat types. (A) Coyote (*Canis latrans*) defending a mountain goat carcass from a bald eagle (*Haliaeetus leucocephalus*), with a raven (*Corvus corax*) in association, Klukwan, Alaska. (B) Wolverine (*Gulo gulo*) scavenging on a mountain goat in low elevation forested habitat during late-winter, Lynn Canal, Alaska. (C) Wolverine scavenging on a mountain goat carcass in high elevation alpine habitat during autumn, Lynn Canal, Alaska. (D) Brown bear (*Ursus arctos*) excavating a mountain goat carcass from an avalanche chute, while a black bear (*Ursus americanus*) observes from distance, Klukwan, Alaska.

Table C1. Avalanche footprint in Alaska Coast Range mountains. Area and percentage of avalanche terrain (including release areas and avalanche paths) within each of the four coastal Alaska mountain goat study areas, Alaska.

	Area (km^2)			
Study Area	Non-avalanche	Avalanche	Total	Avalanche (prop.)
Klukwan	1064	2148	3212	0.67
Baranof	369	572	941	0.61
Lynn Canal	534	697	1231	0.57
Cleveland Pen.	142	12	153	0.08
Total	2108	3429	5537	0.62

Table C2. Mountain goat use of avalanche terrain and survival. GPS radio-collared mountain goat use of avalanche terrain during winter months in relation to whether death occurred by avalanche. Data were collected in four study areas in southeastern Alaska during 2005-2022. Avalanche terrain includes non-forested predicted avalanche release areas and avalanche paths derived using the RAMMS avalanche simulation model. Mountain goat GPS radio-collar location data were collected from a subset (87%) of the total individuals monitored (n = 421).

	Avalanche mortality: Yes			Avalanche mortality: No				
Month	mean	SE	n	mean	SE	n	t-value	P-value
Oct	0.85	0.02	85	0.80	0.01	282	1.847	0.03
Nov	0.70	0.03	85	0.58	0.02	274	3.528	<0.01
Dec	0.56	0.04	81	0.44	0.02	272	2.813	<0.01
Jan	0.56	0.04	81	0.41	0.02	268	3.570	<0.01
Feb	0.55	0.04	79	0.42	0.02	265	3.181	<0.01
Mar	0.59	0.04	75	0.44	0.02	261	3.244	<0.01
Apr	0.65	0.04	71	0.53	0.02	252	2.713	<0.01
May	0.78	0.03	62	0.70	0.02	237	1.782	0.04
All Months	0.67	0.03	85	0.54	0.02	282	3.643	<0.01

Table C3. Causes of mountain goat mortality. Summary of fates among radio-marked mountain goats that died (n = 258) in four study areas in southeastern Alaska during 2005 – 2022. Causes of mortality were discerned during aerial reconnaissance and follow-up field investigations. Accidental causes were clearly definitive in all instances. Cases of malnutrition involved definitive proximate evidence of nutritional deprivation. Unknown causes of mortality occurred when evidence of large carnivores, that both kill and scavenge mountain goats, was present but not definitively linked to predation; such cases were considered to represent instances of either malnutrition or predation-related mortality. It is not possible to determine the faction of unknown mortalities caused by predation vs malnutrition based on identified proportions of non-accident causes of mortality.

Cause	Cases	Proportion
Accident		
Avalanche	93	36%
Fall	6	2%
Subtotal	99	38%
Non-accident		
Malnutrition	19	7%
Predation (Wolf)	19	7%
Predation (Bear - Brown or Black)	16	6%
Predation (Unknown Type)	5	2%
Unknown (Non-accident)	100	39%
Subtotal	159	62%
Total	258	100%

Appendix D– Supplementary Information for Chapter 5

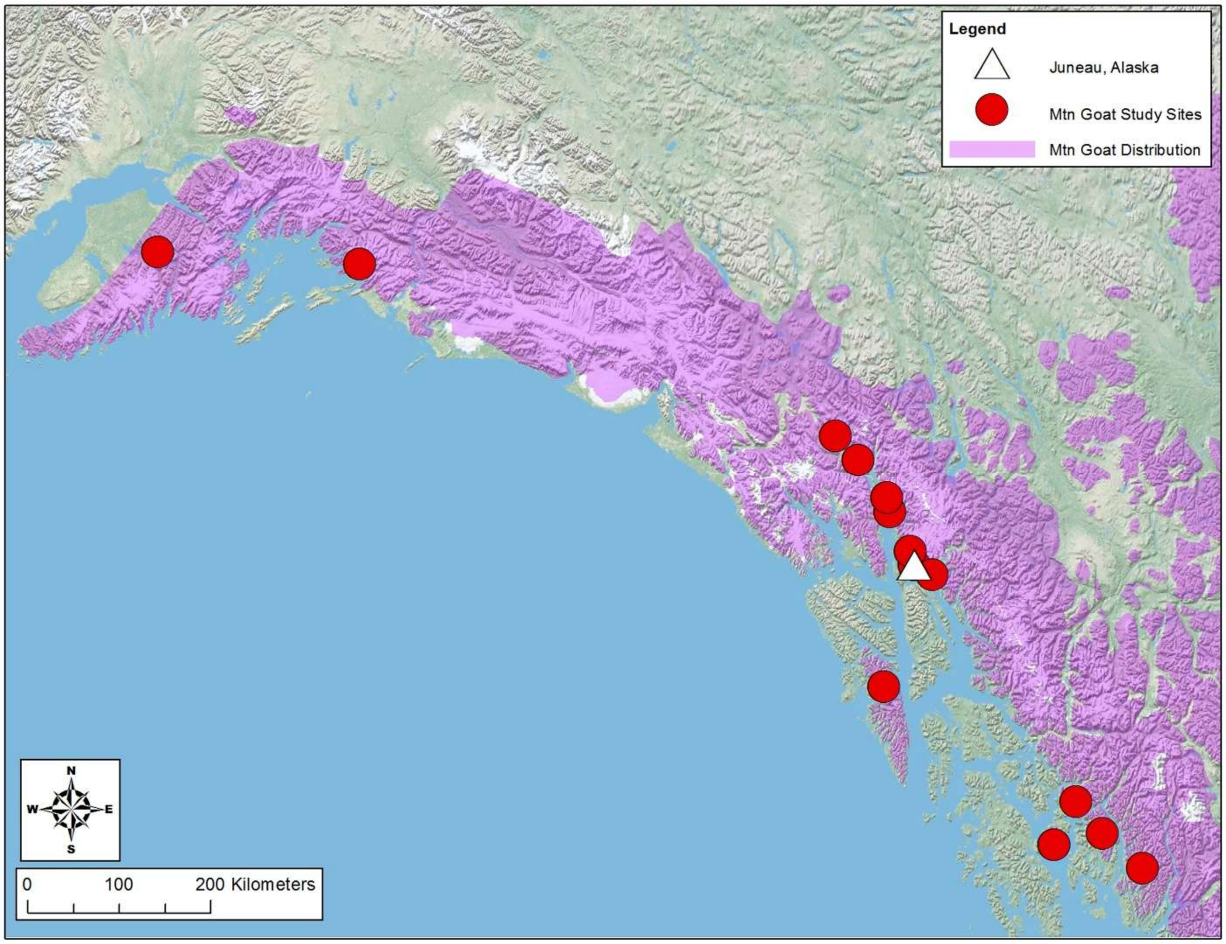

Figure D1. Map depicting mountain goat distribution in Alaska, USA and northwestern Canada. Study sites (red circles) where field data were collected to parameterize mountain goat survival models for input into the dual-sex, post-breeding, age-structured population model (n = 14 study sites, 600 individuals, 1,910 mountain goat yrs, 1977 – 2022; White et al., 2011, 2018, this study). Juneau, Alaska is depicted by the white triangle for reference. Adapted from White et al. 2018.

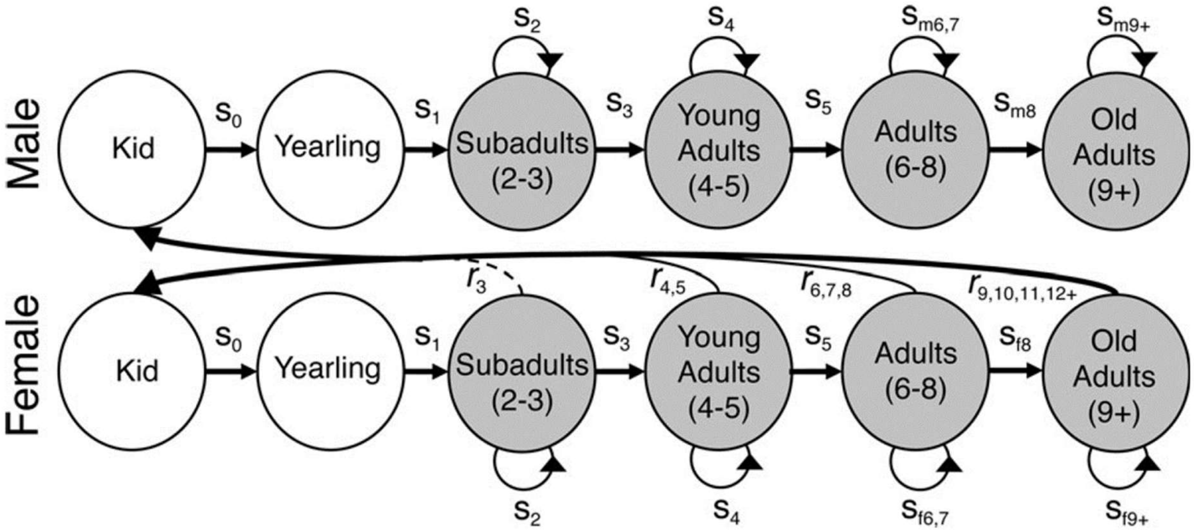

Figure D2. Mountain goat life cycle graph describing the dual-sex, post-breeding, age-structured population model (adapted from White et al. 2018). The model is implemented with 20 age classes (kids to 19+) for each sex but is simplified as a stage-structured model in the life cycle diagram for display purposes. Model description: S_0 = kid survival (no sex effect; based on values from Rice & Gay, 2010), S_1 = yearling survival (White et al., 2011, 2018, this study), $S_{2,3}$ = 2- and 3-year-old survival (White et al., 2011, 2018, this study); $S_{4,5}$ = 4- and 5-year-old survival (White et al., 2011, 2018, this study), $Sm_{6,7,8}/Sf_{6,7,8}$ = 6-, 7-, and 8-year-old survival (White et al., 2011, 2018, this study); Sm_{9+}/Sf_{9+} = 9+-year-old survival (White et al., 2011, 2018, this study); $r_{3–12+}$ = age-specific fecundity (White et al. 2018, unpublished data).

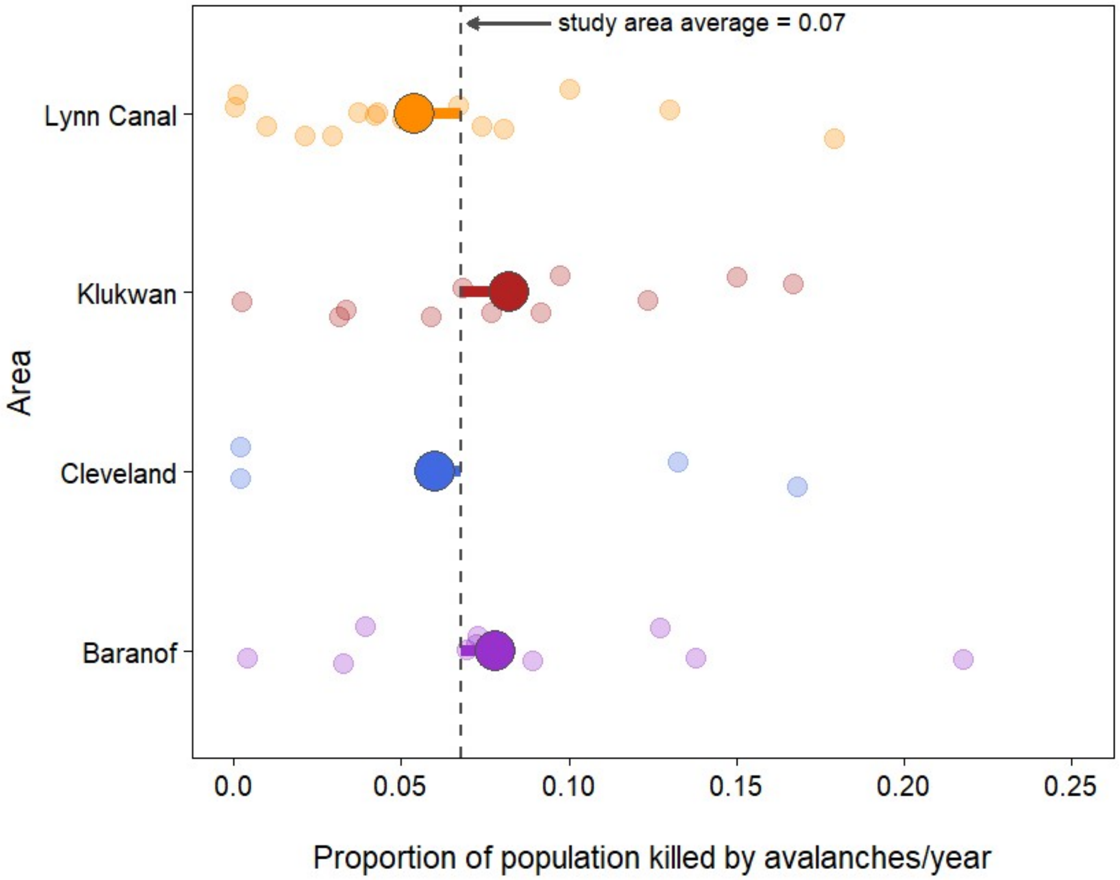

Figure D3. Spatiotemporal variation among populations in avalanche-caused mortality. Proportion of radio-marked mountain goats (n = 421) that died due to avalanches in a given year for each southeastern Alaska study area during 2005 - 2022. Average estimates are depicted by the large colored circles, and small circles represent annual study area estimates. The black vertical line delineates the average across all four study areas and years (adapted from White et al. 2024).

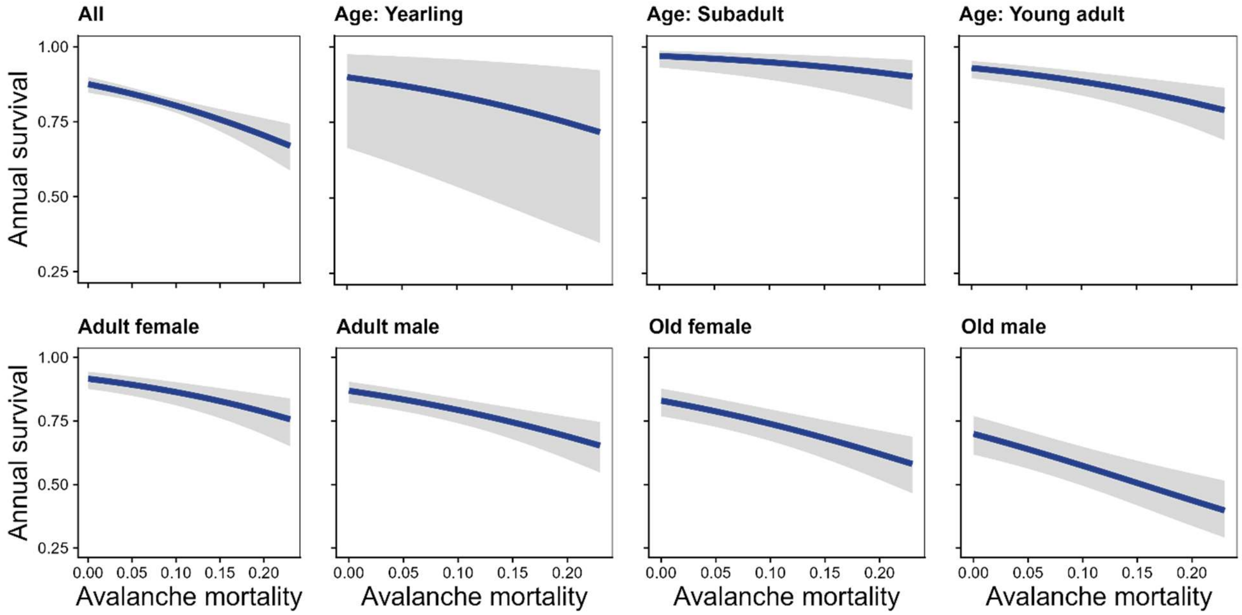

Figure D4. The relationship between the proportion of a sampled mountain goat population dying in avalanches in a given year and total annual survival. Empirical relationships are estimated for each sex-and age category (*sensu* White et al. 2011) and based on radio-marked mountain goats monitored in coastal Alaska during 2005-2021.

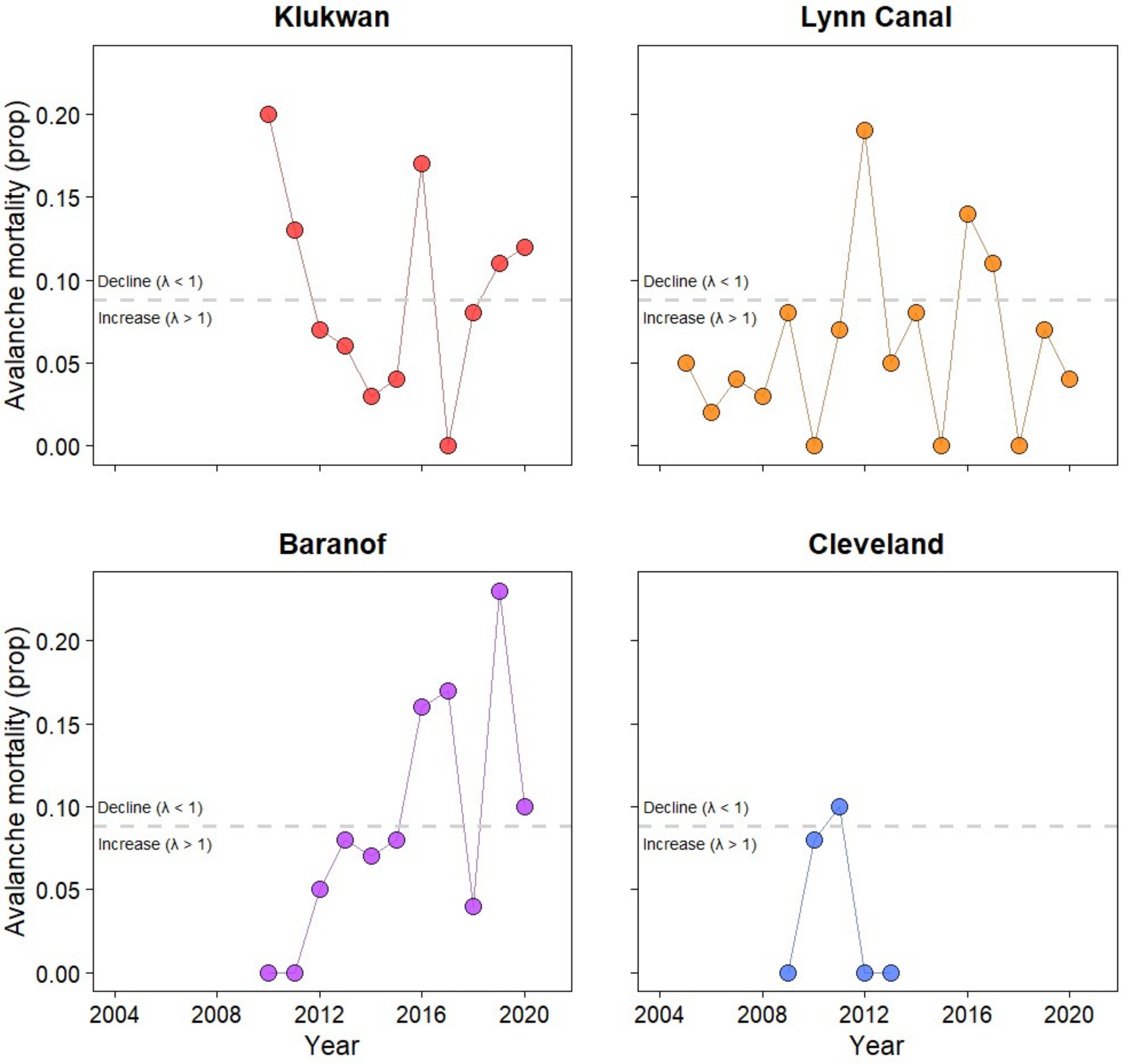

Figure D5. The relationship between proportion of a mountain goat population killed by avalanches across time for four study areas in coastal Alaska during 2005 – 2021. The grey dashed line delineates the threshold level of avalanche mortality (0.088) above which populations are modeled to decline (λ < 1.0 for 50% of simulations or more); below the threshold populations are expected to increase (λ > 1.0).

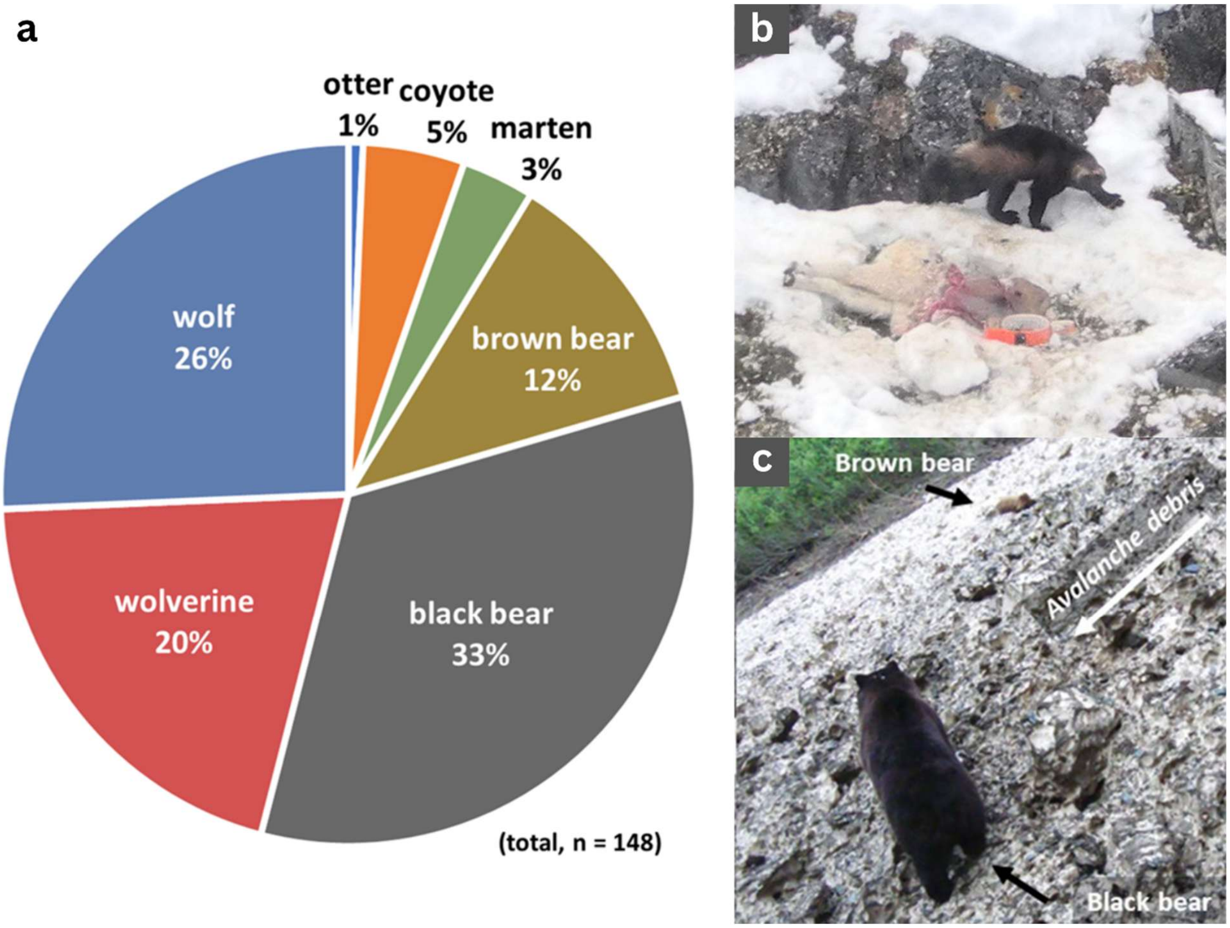

Figure D6. Carnivore scavenging of mountain goat carcasses. (a) Summary of carnivore scavenging activity observed during investigation of radio-collared mountain goat mortalities during 2005 – 2022 in coastal Alaska (n = 148). All species of large- and meso-carnivores that occur in the study area were documented scavenging on mountain goat carcasses. Other large mammalian prey available include: moose (Klukwan, Lynn Canal), Sitka black-tailed deer (Baranof, Cleveland Peninsula). (b) Wolverine scavenging on a mountain goat carcass in high elevation alpine habitat, Lynn Canal, Alaska. (c) Brown bear (*Ursus arctos*) excavating a mountain goat carcass from an avalanche chute, while a black bear (*Ursus americanus*) observes from distance, Klukwan, Alaska.