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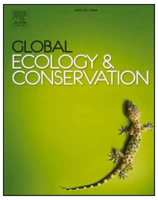

Review Article

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

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ABSTRACT

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

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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.

1. 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

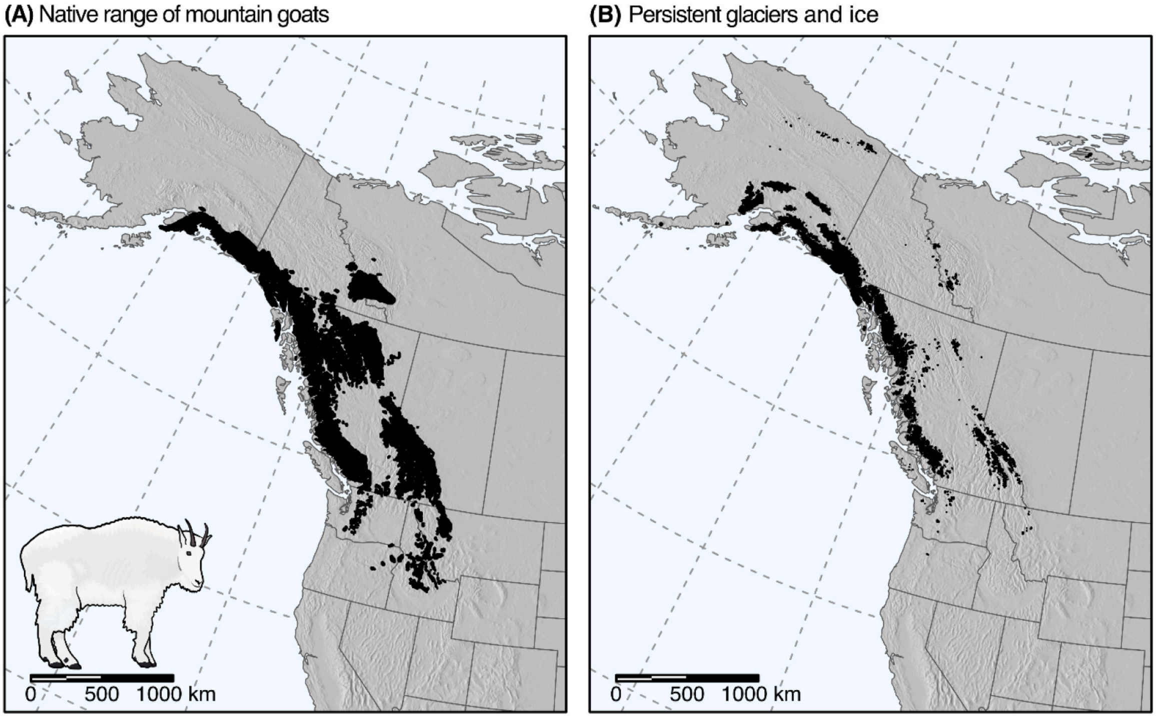

Fig. 1. (A) The native distribution of mountain goats (*Oreamnos americanus*)(Mountain Goat Management Team 2010) and (B) persistent glaciers and ice in western North America (B) (adapted with permission from Hayes, 2023).

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 (Fig. 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., 2021). Indeed, the specialization required to persist in extreme mountain environments (Fig. 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 (Festa-Bianchet et al., 2019). 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 (Fig. 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. Methods

2.1. 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).

2.2. 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 (Fig. 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 (Fig. 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.

Fig. 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.

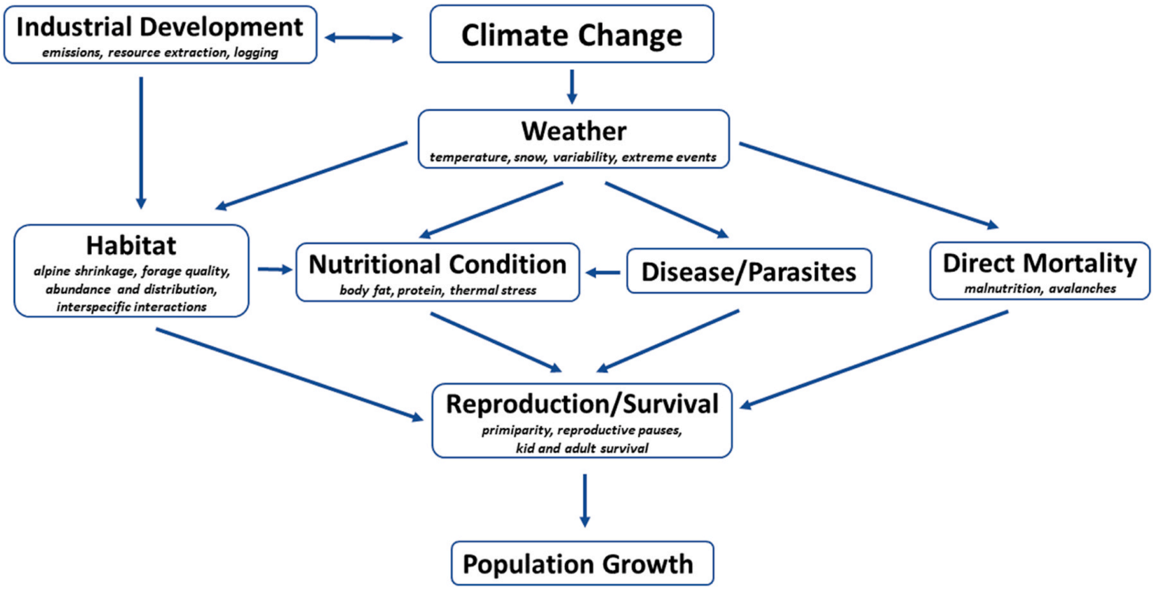

Fig. 3. Schematic of relationships between climate change and other factors influencing mountain goat population ecology.

3. Synthetic review

3.1. 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 Fig. 5, Appendix B). 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 (Fig. 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 (Fig. 5, Appendix B) (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 (Fig. 5, Appendix B). However, sub-freezing winter warming may increase atmospheric water-holding capacity, leading to increased snowfall in such areas (Fig. 5, Appendix B) (Quante et al., 2021).

3.2. 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

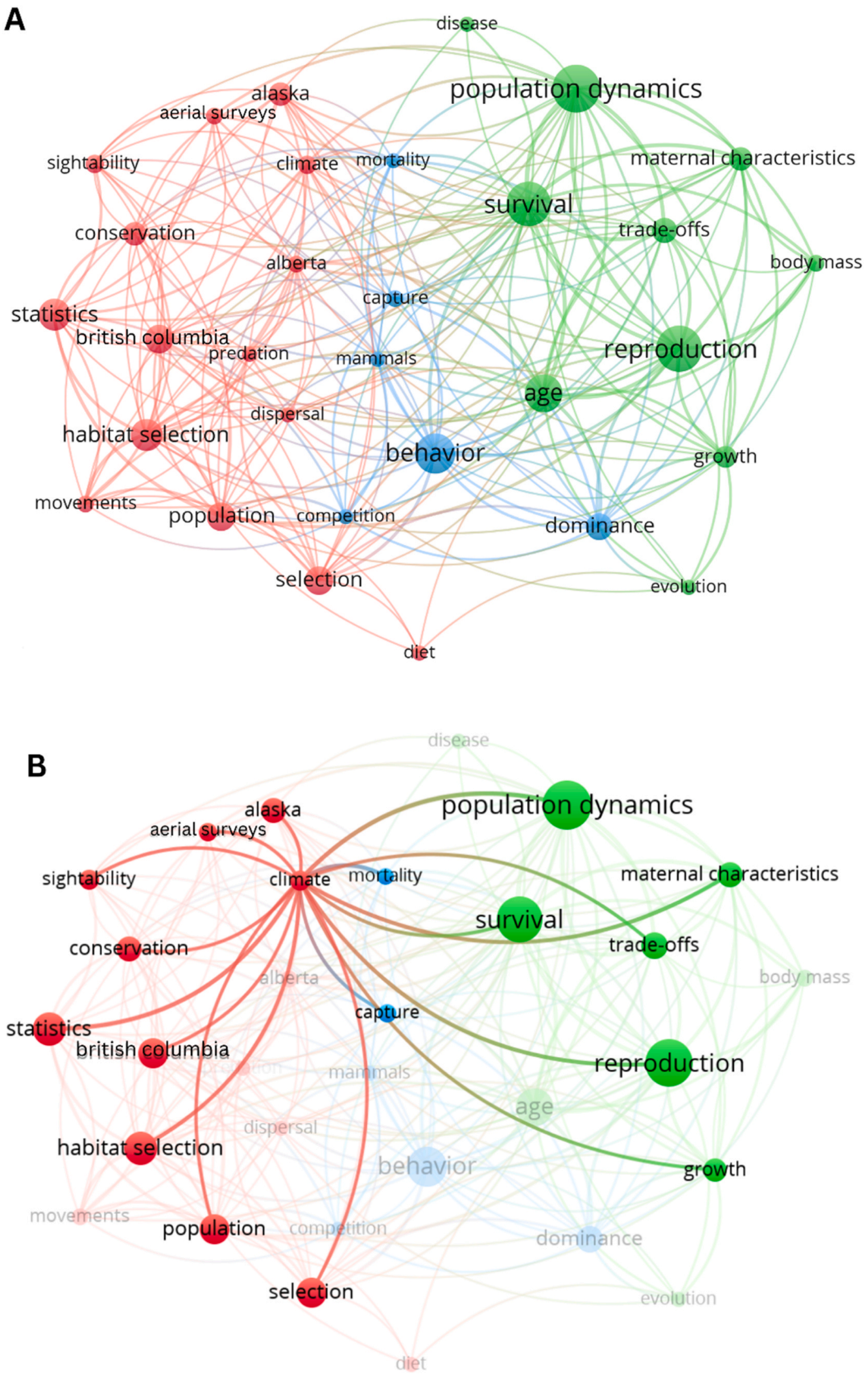

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Fig. 4. Network diagram describing (A) relative proportion and connections between published mountain goat research studies during 1904 – 2023 (n = 258), and (B) relationship linkages between climate and other topic areas. Publications were compiled using a Web of Science literature query using the terms "mountain goat" and "*Oreamnos americanus*" (27 June 2023).

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 (Fig. 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., 2021; 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

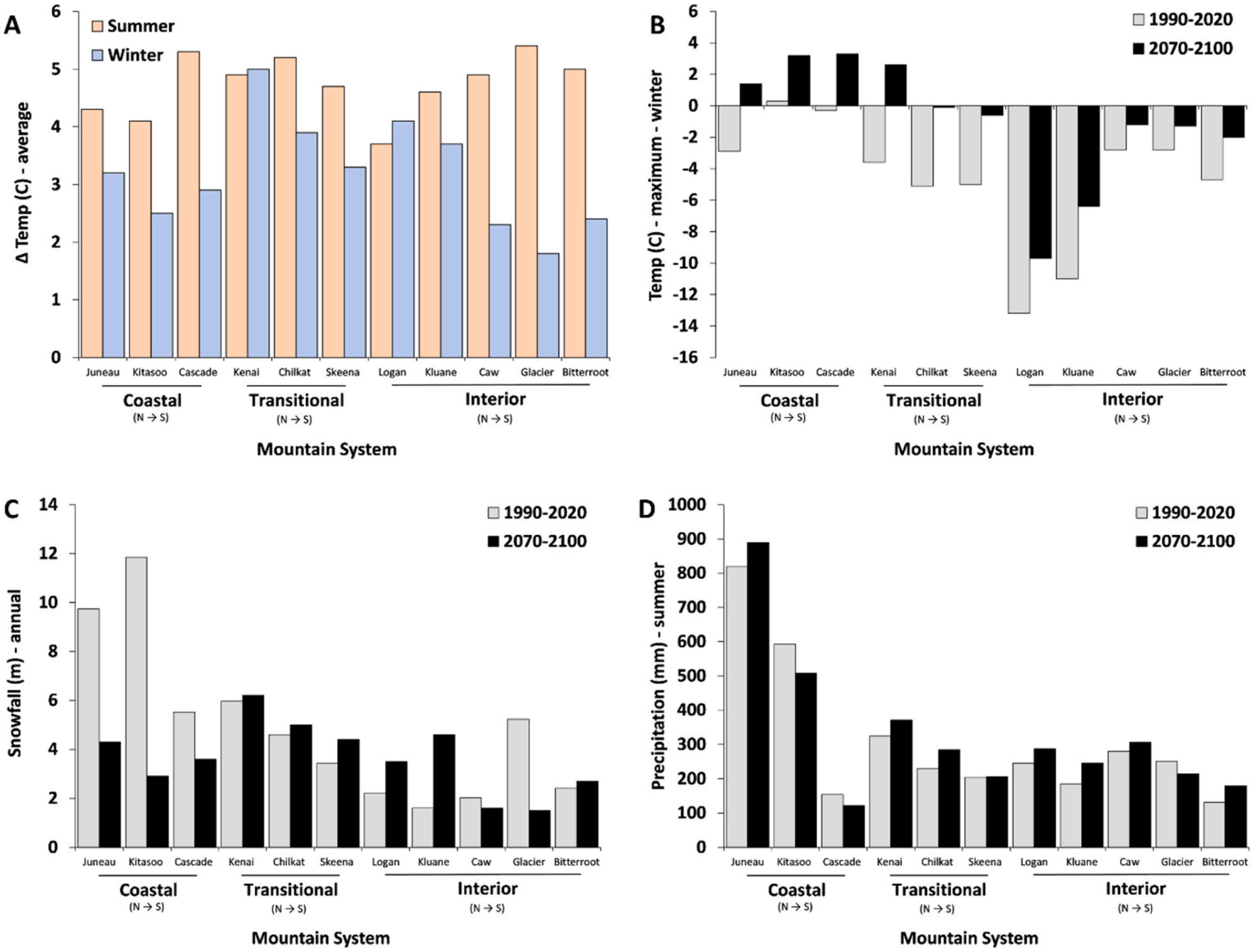

Fig. 5. Projected change in climate for 11 representative mountain regions (spanning ecotonal and latitudinal gradients; see Appendix for description) inhabited by mountain goats throughout their North American distribution. Baseline historical climate conditions (1990–2020) and estimated future conditions (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).

facilitated population expansions (Johnson, 1983; Houston et al., 1994).

3.3. *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

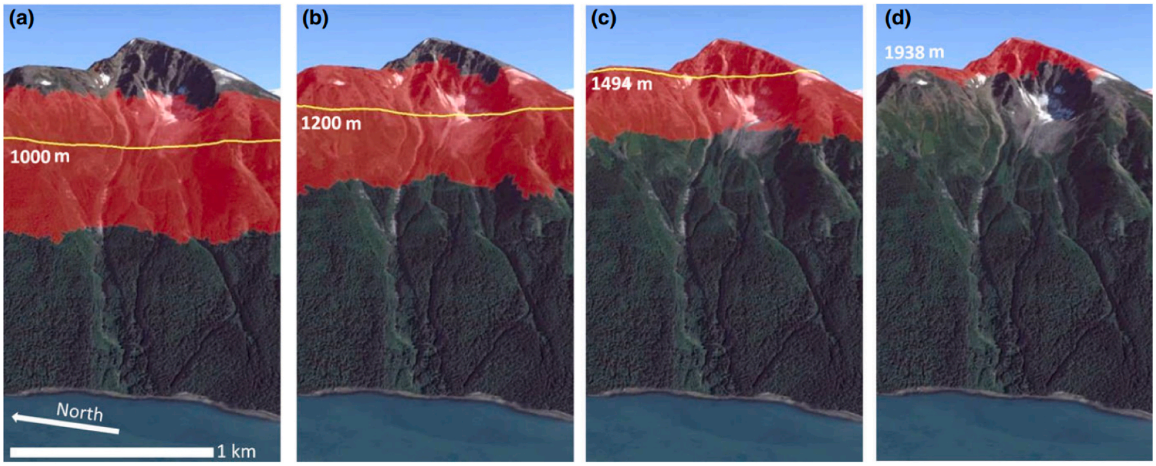

Fig. 6. Resource selection function modeling output describing predicted changes in mountain goat summer habitat distribution in Lynn Canal, Alaska for four scenarios: (a) current distribution (2005–2015 baseline conditions), (b) year 2085, GCM-GISS-RCP4.5 ("best case scenario"), (c) year 2085, GCM-MRI-RCP8.5/GCM-GFDL-RCP4.5 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)). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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 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 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).

3.4. 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., 2024). 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., 2024). 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 % and 4 % (Hamel et al., 2006; Rice and Gay, 2010; White et al., 2021), 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., 2024). 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., 2024).

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).

3.5. 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

Table 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.

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., 2020). 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).

3.6. 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).

4. Conclusions: mountain sentinels in a changing alpine world

4.1. 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 (Fig. 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.

4.2. 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., 2021), 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).

4.3. 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 (Fig. S1). 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 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., 2017, 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 spatio-temporal 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.

4.4. 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 (Jessen et al., 2022; Rofkar, 2014; 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.

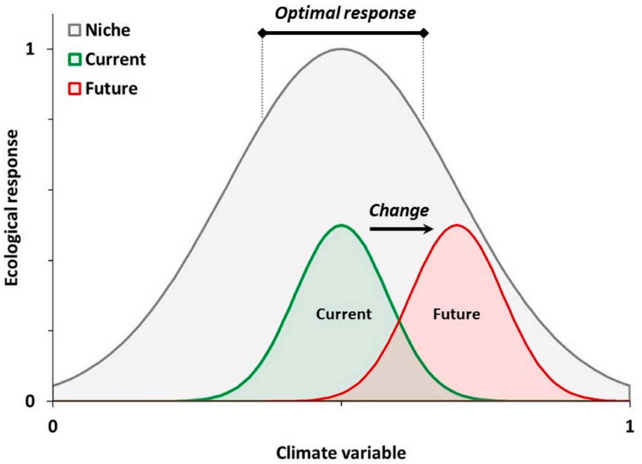

Fig. 7. Schematic of ecological niche of mountain goats in relation to variation in climate. The current distribution is characterized as an optimal response to current climate conditions. Due to climate change, observed responses may contract and shift toward the extreme of the niche (outside of the optimal zone), which may result in increased stress and reduced performance (adapted from Antão et al. (2022)).

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.

Ethics statement

Not applicable: This manuscript does not include human or animal research.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03364.

Data availability

Data will be made available on request.

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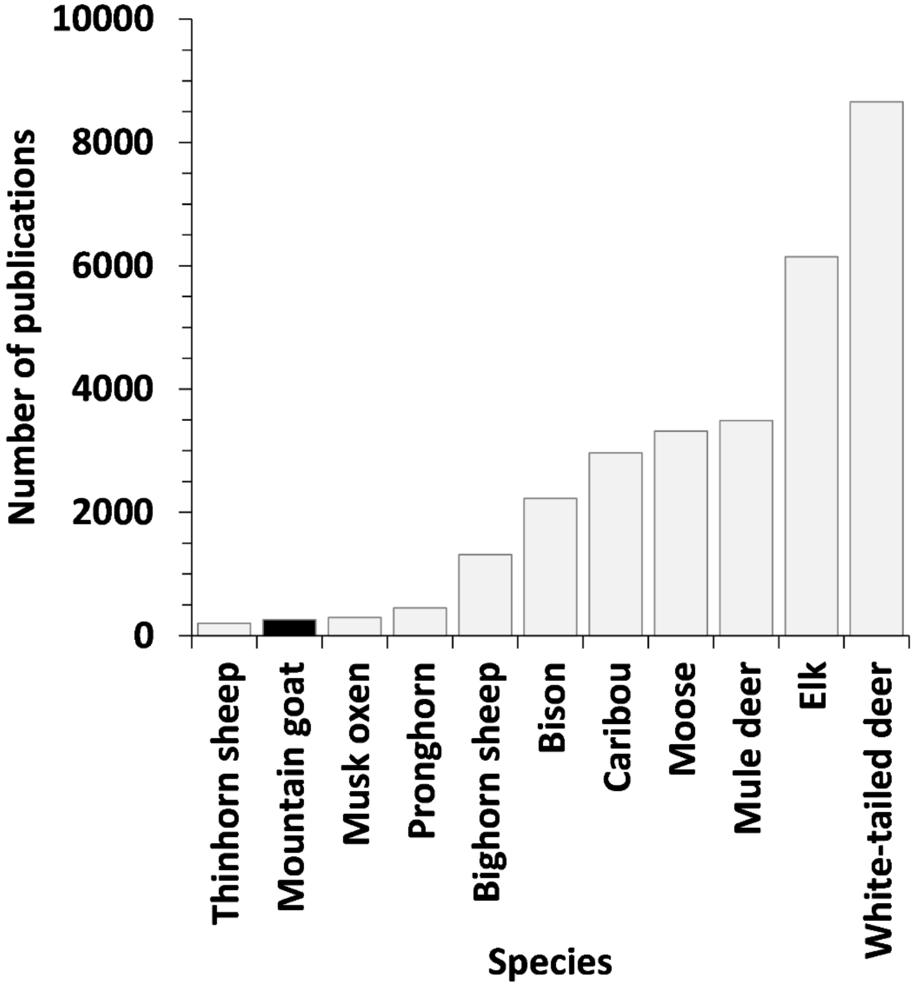
Appendix A. Supplementary material

Fig. S1. 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 B. 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, Fig. 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 S2. 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

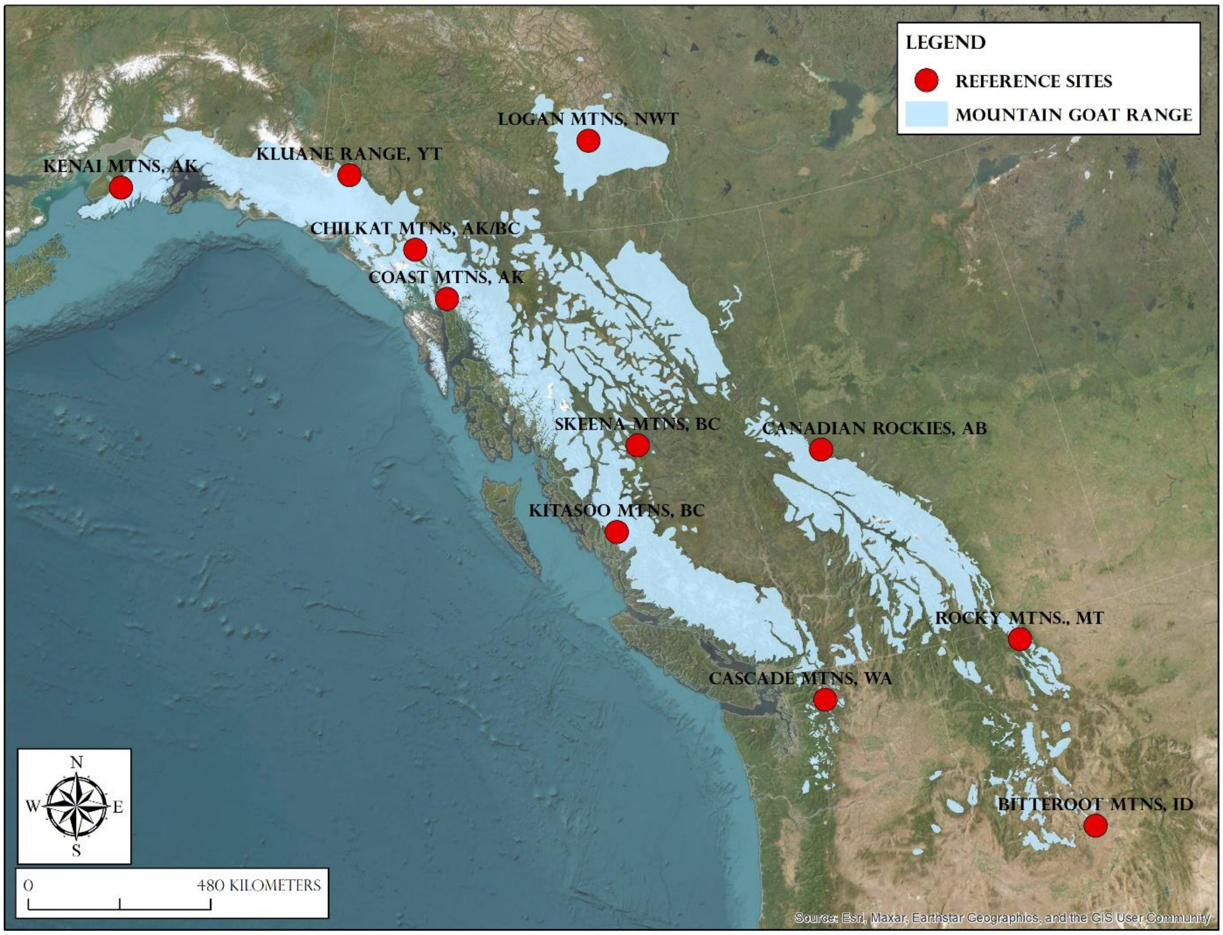
Table S3a. Projected change in climate in 11 representative mountain regions (spanning ecotonal and latitudinal gradients) inhabited by mountain goats throughout their North American distribution. Baseline historical climate conditions (1990-2020) and estimated future conditions (2070-2100) are summarized 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 S3b. 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

Fig. S2. 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.



Source: Esri, Maxar, Earthstar Geographics, and the GIS User Community

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