AN ANALYTICAL APPROACH FOR SIMULATING EFFECTS OF AVALANCHES ON MOUNTAIN GOAT POPULATION DYNAMICS: IMPLICATIONS FOR MANAGEMENT AND CONSERVATION

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ABSTRACT: Mountain environments with snow avalanche hazard cover about 6% of Earth's land area and occur on all continents. Whereas human risks associated with avalanche hazard have been widely studied, little is known about how avalanche activity affects population dynamics in mountain wildlife. Globally, thirty-two species of mountain ungulates across 70 countries occupy avalanche-prone terrain. Avalanches comprise the leading cause of mortality in coastal Alaskan mountain goats (mean = 36%, range = 23 – 65%, depending on area), and disproportionately remove prime-aged individuals from populations. The implications of such rates and patterns of mortality on population growth rate are likely to be significant given the species' low reproductive productivity, but further clarity is needed. To fill this knowledge gap, we developed a sex- and age-specific population modeling approach that integrates both reproduction and mortality to simulate the effects of avalanche-caused mortality on population growth rate across a range of empirically-observed states of avalanche-caused mortality (minimum, mean, maximum). Simulations were conducted to illustrate model functionality, and also provide insight about potential avalanche impacts on population demographic processes. For example, when severe avalanche years occur populations can experience significant additive mortality and declines (up to 15%). Due to low reproductive rates and slow life-history strategy of the species, such impacts can lead to long demographic recovery times (up to 11 years). From a species conservation perspective, such impacts are striking, and highlight the utility of employing a quantitative modeling approach to predict possible effects of avalanches 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 associated implications for the cultural and ecological communities that depend on them.

KEYWORDS: avalanche, Alaska, mountain goat, Oreamnos americanus, population modeling

1. INTRODUCTION

Climate is changing rapidly in mountain environments and altering snow climate regimes in significant ways, catalyzing impacts on sensitive ecological communities and processes. Effects of snow on organisms are often mechanistically described through the lens of ecological and physiological processes. Snow impedes movement, increasing energetic costs of locomotion, buries herbivore food resources, and shifts plant growing seasons – factors that alter nutritional and population dynamics of mammalian and plant communities. Yet, snow can also impose major impacts through the direct physical process of avalanching.

Specialized mountain wildlife populations may be particularly prone to these impacts, with avalanches comprising a major source of mortality. Recent work indicates that annual mortality from avalanches can exceed 20% of mountain goat (Oreamnos americanus; Figure 1) populations in coastal Alaska (White et al., 2024). Avalanche mortalities differ from ecologically driven mechanisms where snow- linked mortalities are selective, removing poorer quality young and old animals more frequently than robust, prime-aged individuals. Avalanches, on the other hand, largely remove animals from a population at random, including a substantial fraction of reproductively

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critical, prime-aged females. The extreme environmental conditions species face in mountain ecosystems require specialized adaptation that typically involve conservative allocation of energetic resources to reproduction and thus low population growth rates and limited resilience to stochastic perturbations and extreme events. As a consequence, even small impacts can elicit deleterious changes and entail prolonged recovery periods presenting conservation challenges.

Figure 1: (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 Peak, near 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°) (adapted from White et al. 2024).

Stochastic environmental change can play an important role in population dynamics. In alpine ecosystems, populations often persist in small, isolated populations that are particularly vulnerable to stochastic events (i.e. due to Allee effects). 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). 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 (McClung and Schaerer, 2006; Schweizer et al., 2003). Avalanches occur across a range of spatiotemporal scales and can have outsized effects for alpine specialists such as mountain goats, given their slow life-history strategies and low resilience. Intrinsic growth rates of mountain goat populations are low (1- 4%) (Hamel et al., 2006; Rice and Gay, 2010; White et al., 2021b), relative to other northern ungulates. Consequently, mortality due to avalanches have the potential to elicit major population declines with resultant long recovery times (White et al., 2024). Yet, 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 potentially important driver of mountain ungulate population dynamics and viability, we describe a population dynamics modeling approach for simulating the effects of varying levels of avalanche-caused mortality on population growth and recovery times (in scenarios where declines occur). The modeling framework, parameterized based on long-term data collected in the study system (White et al., 2011, 2018, 2021b, 2024) is intended to fill an important knowledge gap by providing realistic insights about avalanche impacts on mountain goat population dynamics to inform management and conservation strategies.

2. METHODS:

2.1 Study System

Mountain goats were studied in four separate areas across a broad geographic range in coastal Alaska (5537 km2; Figure 2) from 2005- 2022. This area is within the Coast Mountains biogeographic region (Gallant et al., 1995).

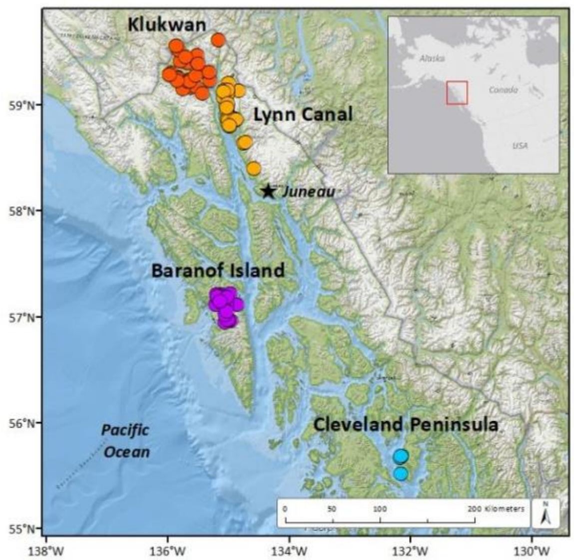

Fig. 2: Map depicting the four study areas and individual locations where radio-marked mountain goats were studied and died in avalanches during 2005 – 2022 in coastal Alaska (adapted from White et al. 2024).

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.

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 (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. Overall, 62% of the area used by mountain goats in this area is comprised of avalanche hazard terrain (White et al., 2024).

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). Populations exhibit a high degree of local-scale population genetic differentiation, with limited movement among geographically discrete mountain complexes (Shafer et al., 2012). Mountain goats are habitat specialists and select steep, rugged terrain in close proximity to cliffs and exhibit seasonal variation in altitudinal distribution (Shafer et al., 2012). Mountain goats are partially migratory, with some individuals, depending on study area, residing in alpine and subalpine habitats throughout the year (Shakeri et al., 2021).

2.2 Mountain goat monitoring

Adult male and female mountain goats were captured using standard helicopter darting techniques (White et al., 2021a). 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). 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).

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.

Mountain goat population modeling To examine demographic responses of mountain goat populations to simulated avalanche perturbations, we used a post-breeding, sex- and age-structured (20 age classes) population model (White et al., 2018, 2021b) (Figure 3). The population model projects population size through time based on sex-, age-, and climate-specific reproduction and survival estimates based on relationships derived from 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, 2021b, unpub. data) (Figure 3). Age-specific fecundity was estimated based on direct observations of radio-marked females (n = 180 females, 640 female-yrs) during the parturition period in subset of three study areas during a 16-yr period (2005-2021) (White et al. 2018, 2021b, unpub. data). Neonate survival was parameterized following (Houston et al., 1994; Houston and Stevens, 1988) and Rice and Gay (2010), as described in White et al. (2018). The model is designed to simulate population trajectories given user specified climate inputs (winter snowfall (m), summer temperature (C); White et al. 2018) and human removals (White et al. 2021b). For this analysis, natural baseline conditions were simulated by specifying average climate conditions and zero harvest. Such specifications were also used to derive the stable stage distribution for a given

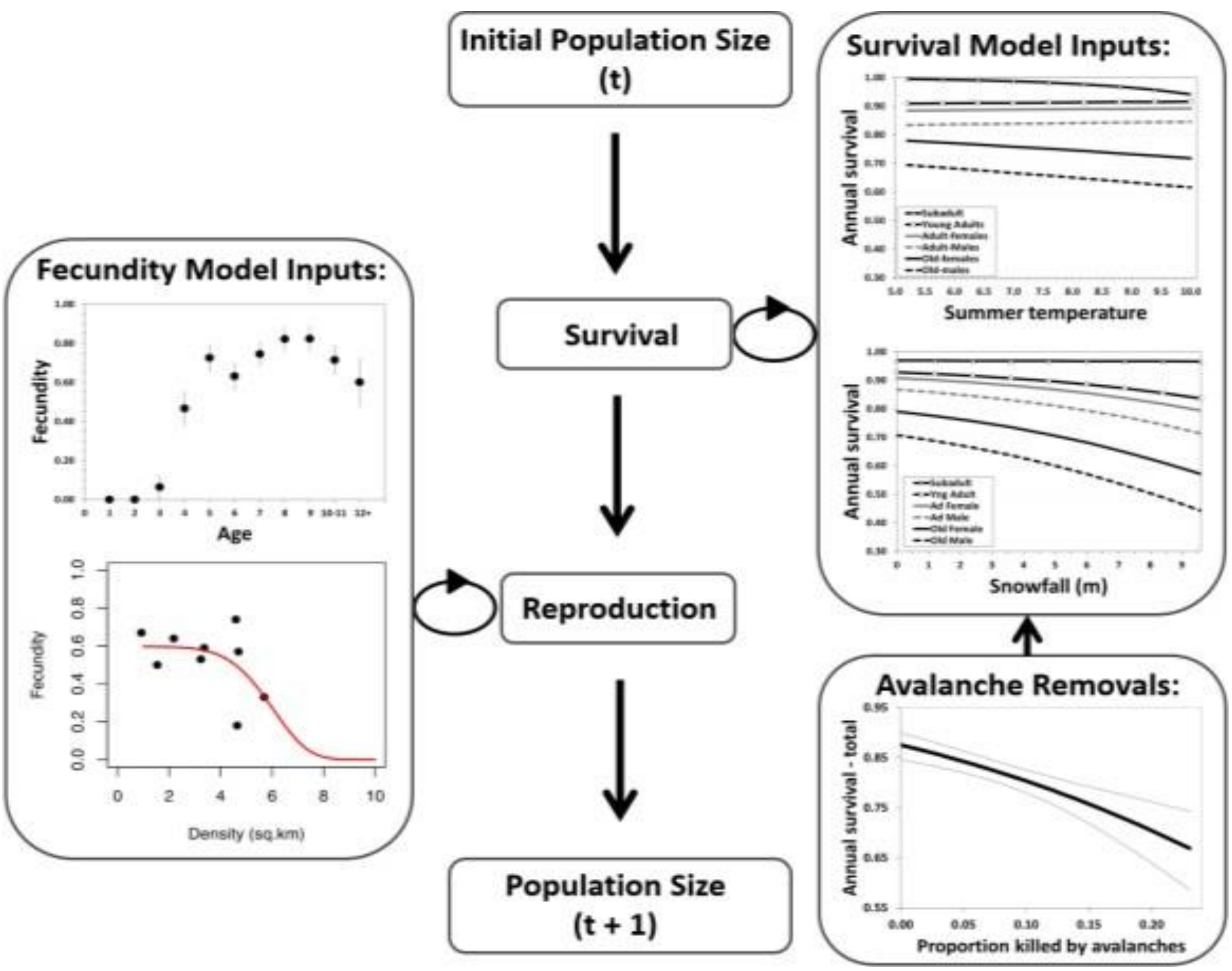

Figure 3: Conceptual diagram describing the dual-sex, post-breeding, age-structured population model. The model adjusts mountain goat survival for each sex and age class. Age- specific fecundity can be modified based on density-dependent relationships. The avalanche sub-model (bottom right) acts directly on mountain goat survival inputs to the model (adapted from White et al. 2018, 2021b).

initial population size input. Natural variability in population dynamics was simulated by sampling from within the error distribution of climate- specific survival estimates (i.e., accounting for uncertainty in the effect of summer temperature and winter snowfall on survival).

2.3 *Modeling effects of avalanche mortality on survival*

Avalanches risk is often difficult to predict, and avalanche mortality in goats is expected to be largely additive and remove animals from a population at random (White et al., 2024). However, 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 (defined following White et al. 2011) that died due to avalanches in relation to total annual survival using a generalized linear mixed modeling approach (package “lmer”, R version 4.3.1; Bates et al. 2014, R Core Team 2023).

Parameterizing this relationship enabled realistic simulation of avalanche impacts on a population recognizing that the fraction of avalanche mortalities that are additive may vary depending on the proportion of a population that dies due to avalanches (Figure 4). For example, we expected avalanche mortalities to be largely additive when occurring at high rates, whereas, at low rates of avalanche mortalities, we expected a small fraction would be impacting animals that would have died anyway (i.e. compensatory mortality).

Known-fate data from each individual animal (coded based on whether an animal died due to avalanches, other causes, or survived) were used to predict annual survival for each life stage based on the proportion of animals that died due to avalanches in a given population during a given year. These relationships were then used to adjust baseline annual survival inputs to simulate avalanche impacts on a population. For example, under average conditions we determined that 7% of a population dies due to avalanches. Thus, to simulate average avalanche conditions, no adjustment of survival inputs is required.

However, to simulate an above average avalanche mortality scenario, individuals are removed from the population by reducing annual survival. For below average avalanche mortality, annual survival is increased to augment the number of animals in a population. The ratio of the estimated annual survival at the baseline conditions in relation to annual survival at a given level of population-level avalanche mortality is calculated based on the empirical life-stage specific relationships described above, and used to adjust annual survival estimates according to specified avalanche scenarios.

Modeling effects of avalanche mortality using this approach allowed for accounting for variation in the extent that avalanche mortality is additive across a range of avalanche conditions. For example, under high avalanche mortality conditions it is more likely that such mortality is additive, as compared to a low avalanche mortality scenario (as described above; i.e. Figure 4).

2.4 *Simulating effects of avalanche mortality*

To illustrate the capability of the modeling approach, we conducted example simulations across a range of realistic scenarios using empirical estimates summarized by White et al (2024), as well as previously published estimates of population size and climate conditions (White et al. 2018). Specifically, we simulated avalanche mortality across a range of empirically derived percentiles (min = 0%, mean = 7%, max = 23%; based on White et al. 2024). We conducted 1000 simulations for each scenario (initial population size = 100 individuals) over a 30-yr time period (i.e. greater than 3 generations, IUCN 2012) and summarized average annual population growth rate (λ). In addition, in cases where populations declined, we estimated the amount of time required for a population to re-attain initial population size under average conditions (i.e. λ = 1.015; see below).

3. RESULTS

3.1 *Effects of avalanche mortality on survival*

We used generalized linear mixed effects modeling to characterize relationship between avalanche caused mortality and total annual survival of mountain goats in order to parameterize population modeling simulations. Our modeling results indicated similar avalanche caused mortality relationships among each sex and age class, even though baseline survival estimates varied (i.e. based on life-history expectations, sensu White et al. 2011). The overall 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 4). This finding indicates avalanche mortalities appear to be largely additive (i.e. killing animals that would not have otherwise died) when occurring at high rates. Whereas, at low rates, a small fraction of avalanche mortalities impact animals that would have died anyway (i.e. compensatory mortality).

3.2 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. We determined that under average conditions (7% of a population removed by avalanches), mountain goat populations were expected to exhibit relatively low rates of growth ($\lambda = 1.015$, $P_{25} = 1.012$, $P_{75} = 1.016$). Under conditions where no animals were killed by avalanches, populations were expected to exhibit 6.6% annual population growth ($\lambda = 1.066$, $P_{25} = 1.062$, $P_{75} = 1.068$). Whereas, during severe conditions (23% population-level avalanche mortality), populations were estimated to elicit a significant 14.8% decline ($\lambda = 0.852$, $P_{25} = 0.848$, $P_{75} = 0.852$). To understand the implications of the estimated population decline, we simulated a scenario involving a severe event followed by average conditions and determined that population recovery would not be attained for 10.8 years ($P_{25} = 8.1$, $P_{75} = 17.9$ years).

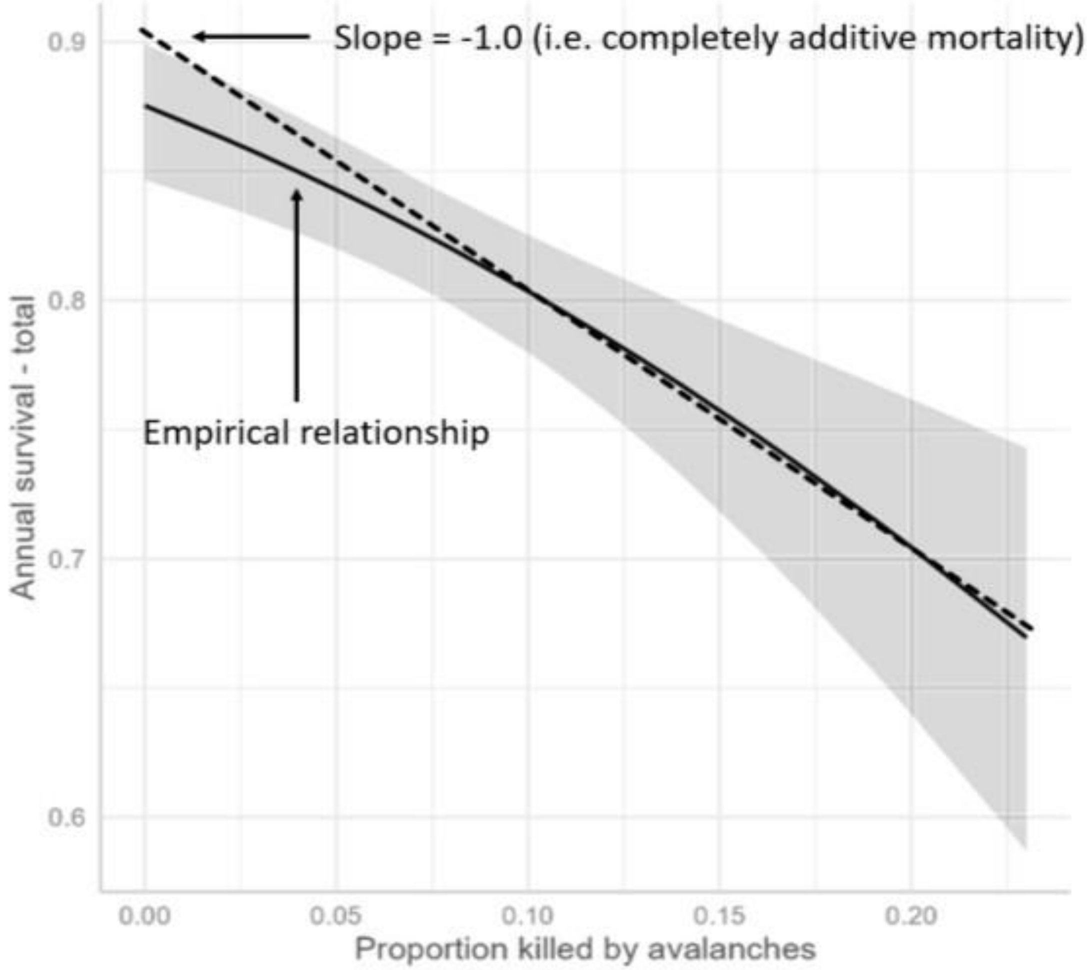

Figure 4: Conceptual diagram illustrating the relationship between the proportion of a sampled mountain goat population dying in avalanches in a given year and total annual survival. The dashed black line is provided for reference and illustrates a scenario where all avalanche caused mortalities are completely additive. The black solid line describes the empirical relationship based on radio-marked mountain goats monitored in coastal Alaska during 2005-2022.

4. DISCUSSION

Avalanches represent a major climate-linked driver of mountain goat populations. Previous analyses revealed that avalanches comprise 36% (and up to 65%) of mountain goat mortalities, and that prime-aged, reproductively critical individuals are heavily impacted (61% of all mortalities) (White et al., 2024). Translated to the population-level, 7% of a given population was estimated to be killed by avalanches annually, and over 22% in severe years (White et al., 2024). Understanding the implications of these findings on mountain goat population growth and viability is critical. In this study, we described a population modeling approach, using extensive long-term field data, that can be used for understanding demographic implications of avalanche mortality on mountain goat populations. A principal feature of our modeling work involved empirical determination that avalanche mortality is primarily additive, except at low levels. That is, avalanches largely kill animals that would have otherwise survived (and add to baseline mortality), 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 population simulations illustrated that populations experiencing average or low levels of avalanche mortality are capable of exhibiting relatively modest population growth for mountain goats. However, during severe conditions avalanche mortality is capable of eliciting significant population declines (~15%) that can require extended periods (~11 years) before populations recover to baseline levels, provided average conditions persist during the recovery phase. While such case studies only represent a subset of possible scenarios, they illustrate how our quantitative modeling approach can provide key ecological and conservation-relevant insight about the potentially major role avalanches can play in impacting mountain goat populations.

Specialization in extreme environments can come at a cost. Mountain goats are icons of rugged, remote mountain environments, exhibiting striking behavioral and morphological adaptations for life in steep, cliffy terrain where they can avoid the risk of predation by wolves and bears (Festa-Bianchet and Côté, 2008). Yet, mountain life requires enduring long winters and deep snow — conditions that strongly restrict nutritional condition and energy balance (Festa- Bianchet and Côté, 2008). Mountain goats cope with such extremes by employing a conservative reproductive strategy, favoring survival over reproduction, resulting in relatively low reproductive productivity and consequent population growth rates (Hamel et al., 2010; Festa-Bianchet et al., 2019). These characteristics, combined with a restricted distribution and geographic, genetic, and demographic isolation, predispose typically small, vulnerable populations to natural and anthropogenic perturbations — even if relatively minor (White et al., 2021b). Avalanches comprise sometimes major, stochastic perturbations that largely select individuals at random, including reproductively critical, prime- aged animals that normally escape predation or are otherwise resilient to malnutrition or disease (White et al., 2024). Identification of avalanches as a key climate-linked, stochastic agent of environmental change in mountain wildlife populations and ecosystems has important, broad reaching implications. If climate change alters the distribution and frequency of avalanches, as has been suggested (Ballesteros-Cánovas et al., 2018; Giacona et al., 2021), possible futures may include substantial restructuring of mountain wildlife communities.

5. CONCLUSION

Globally, thirty-two species of mountain ungulates across 70 countries occupy avalanche-prone terrain. That avalanches comprise a major pathway by which snow can elicit major demographic effects on slow-growing, mountain-adapted animal populations has only recently been described in detail (White et al. 2024). Integration of such knowledge into quantitative modeling approaches, such as those described here, represents a key tool for understanding the underlying demographic consequences of avalanches on population dynamics and examining conservation-relevant scenarios.

Such efforts carry important cultural and ecological implications. For example, Indigenous hunters have relied on mountain ungulate populations for millennia, a relationship involving important subsistence and cultural traditions (Jessen et al., 2022). Mountain ungulates are also highly regarded among contemporary sport hunters and recreational wildlife-viewers worldwide. Moreover, ungulate carcasses provide a key food resource for a diversity of avian and mammalian species, particularly in relatively unproductive mountain food webs.

Thus, advancing our capability for understanding how persistence of mountain ungulate populations relates to climate-linked natural hazards, such as avalanches, has far-reaching conservation, management, and cultural implications for mountain ecosystems and people.

DISCLAIMER

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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