DISSERTATION

ECOLOGICAL CONSEQUENCES OF WARMING CLIMES FOR COLD-ADAPTED SPECIES – EVIDENCE FROM MOUNTAIN GOATS

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ABSTRACT

ECOLOGICAL CONSEQUENCES OF WARMING CLIMES FOR COLD-ADAPTED SPECIES – EVIDENCE FROM MOUNTAIN GOATS

Global climate change from human activity is changing ecological communities at unprecedented rates. Coupled with recent and extraordinary loss of biodiversity, assessing the consequences for vulnerable species – and effecting proactive conservation – will be fundamental to stymieing these losses. Among the areas most strongly impacted by these changes are montane regions, which are warming at rates 2–5x the global average. Within those, cold-adapted organisms are among the most strongly impacted as they may experience thermal stress at moderate temperatures. Past species- and taxa-level responses to warming environs includes numerous concentrated extirpations at the southern peripheries of distributional ranges during the late Pleistocene. Less clear are localized capacities of cold-adapted species to mitigate thermal challenges against warming temperatures, especially through proximate behavioral and physiological adjustments. In this dissertation, I address three key tendrils of the ecological consequences of warming climes for cold-adapted species.

First, I evaluate the role of snow patches in mediating the physiological impacts of warming temperatures. Despite strong associations between many taxa and cold environs, great uncertainty remains about the biological benefits, if any, of using persistent snow during summer months. Contrary to the prevalent hypothesis that persistent snow provides thermal relief for cold-adapted species, I demonstrate that use of snow patches facilitates insect avoidance and not thermoregulatory gains. While the duration and spatial extent of snow declines globally as the climate warms, its diminishing availability is likely to have substantive impacts to populations given a general pattern of associations between insects and temperatures at high elevations and latitudes.

Next, I evaluate changes in spatial use relative to high temperatures and the influence of snow on resource selection. While thermal challenges to persistence are well evidenced through historical extirpations, attention to near-term shifts in resource use and snow as a driver of summer resource selection remains under-investigated. I found strong shifts in resource selection during periods of high temperature, with increased selection for cooler habitats, little effect from snow, and evidence of ecological tradeoffs in avoidance of heat. These results point to possible demographic consequences of changing behavior and illustrate the importance of proactive consideration of changing patterns of use in management policies.

Finally, I evaluate the importance of climate refugia and human translocation for the applied conservation of biodiversity. Despite a long history of relocating wildlife, translocations outside native ranges have rarely been conducted for conservation and populations introduced beyond their native ranges have seldom contributed to *in situ* species conservation within native ranges. Herein, I identify three cases of introductions to climate refugia and highlight the untapped conservation value of existing populations outside of native ranges. I report species in these refugia offer not only a reservoir for reintroductions but also a buffer against temperature-driven distributional change and may prove invaluable in stymieing current and future loss of biodiversity under continued climate challenges.

In concert, this dissertation addresses physiological and geographical consequences of warming climes for cold-adapted species, identifies the need for proactive conservation, and highlights one avenue through which meaningful conservation benefits may be achieved.

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SUMMARY

Conserving Earth's most rapidly changing biomes necessitates understanding biological consequences of altered climes. Past species- and taxa-level responses to warming environs includes numerous concentrated extirpations at the southern peripheries of distributional ranges during the late Pleistocene. Less clear are localized capacities of cold-adapted species to mitigate thermal challenges against warming temperatures, especially through proximate behavioral and physiological adjustments. Whereas snow patches persist in periglacial zones and elsewhere, broad reductions in seasonal snow raise concerns about how and why species continue to use them. If snow patches play a functional role to combat increasing thermal demands, we predicted individuals would display an array of autonomic responses to heightened temperatures modulated by wind, ambient temperature, and winter fur on and away from snow patches. We tested these predictions using a mammalian exemplar of high latitude and high elevation, mountain goats (*Oreamnos americanus*), using two sites in the northern Rocky Mountains, USA. Surprisingly, and contrary to expectations of reduced thermal stress, respiration rates were not decreased on snow patches but use of snow was strongly correlated with decreased metrics of insect harassment. As snow cover continues to decline in montane environs, persistence of cold-adapted species depends on navigating concurrent changes in biotic communities and thermal environments and balancing competing pressures on behavioral and biological responses.

INTRODUCTION

High elevation and high latitude environments are warming at rates 2–5x faster than Earth's average (Pörtner et al., 2021) resulting in temperatures which are now reshaping ecological communities. Among many documented changes are upward shifts in forest cover, shrubification, and movements of invertebrates and vertebrates northward and to higher elevation (Hughes, 2000; Eisen et al., 2008; Rowe et al., 2015). Historically, broad distributional shifts or site-specific extirpations in response to climatic change are not unusual and are reflected by Quaternary fossil deposits of cold-adapted mammals whose contemporary ranges are now situated at higher latitudes (Figure 1.1) (Grayson, 2011). Climate-related warming has been a driving force in the truncation of many species along their lower latitude periphery including those broadly associated with periglacial or cold climes such as mountain goats (*Oreamnos americanus*), pikas (*Ochotona* spp.), marmots (*Marmota* spp.), and lemmings (*Lemmus* spp.) (Pielou, 2008; McCain et al., 2021). Others of Holarctic distribution, including moose (*Alces alces*) and wolverines (*Gulo gulo*), are less restricted yet still reliant on environments with snow and cold temperatures (Karns, 2007; Lukacs et al., 2020).

Despite close association between species distributions and elements of climate, little is known about near-term responses by chionophiles (i.e., organisms reliant on cold wintery conditions) to rapidly warming temperatures especially given accentuated rates in mountainous and high latitude environments (Rowe et al., 2015). While the magnitude of immediate threats posed directly from humans (e.g., habitat loss, overhunting, and nonnative species) are primary threats (Tilman et al., 2017), warming temperatures are likely the paramount risk for cold-adapted organisms (Murali et al., 2023). Individual animals feel the immediacy of these changes, wherein behavioral and physiological mechanisms may play fundamental roles in capacities to adjust (McNab, 2012; Fuller et al., 2014).

Species of periglacial realms and of Earth's colder biomes are confronted by decreasing persistent snow (Pulliainen et al., 2020; Notarnicola, 2022). Yet, snow patches provide biological benefits to vertebrates (Rosvold, 2016), especially in summer (Table 1.1). Among these, grizzly bears (*Ursus arctos*) use snow-covered terrain for travel (French et al., 1994), and persistent ice or snow offer relief from heat across multiple mammalian orders (Table 1.1). Even during winter, remnant snow in arid regions of the Tibetan Plateau sustain lactating wild yaks (*Bos grunniens mutus*) (Berger et al., 2015).

Given the twin challenges of increasing temperatures and broad declines in snow, a critical test for species of arctic, subarctic, and otherwise wintry temperate environs will be their ability to reduce thermal stress. At a coarse scale, options include geographic choices of habitat and associated refuges (Parmesan, 2006; Lenoir et al., 2008; Rowe et al., 2015). At finer scales are behavioral responses, including use of persistent snow and ice (Rosvold, 2016), particularly because air over snow has lower ambient temperatures than above bare ground (Ion and Kershaw, 1989; Barry and Gan, 2022). Thus, we hypothesized that if snow patches provide thermal relief, individuals will exhibit reduced thermal load while on snow, and use of snow patches during warm periods would be strongly incentivized (Figure 1.2). Alternatively, snow patches may be unimportant thermally and confer quite different benefits: 1) reduced inimical insects, 2) sources of water, 3) playgrounds for young animals, and 4) travel corridors, or possibly none at all (Table 1.1). Herein we evaluate two hypotheses for snow patches – that it mitigates thermal exposure and/or insect harassment.

To assess these hypotheses, we used *in situ* measurements of well-established proxies: respiration rate and ear-flick rate for thermal stress and ectoparasitic harassment, respectively. We focus on mountain goats, a cold-adapted, high-elevation mammal of western North America

(Festa-Bianchet and Côté, 2008; White et al., 2018). Our primary study area, Glacier National Park, nears the southern periphery of the species current natural range (Figure 1.1) where 85% of the glaciers have been lost since 1850 (Hall and Fagre, 2003; Berger, 2018). Because of warming temperatures and the associated loss of glaciers we believe our choice of study site and organism well serves as an exemplar to evaluate potential benefits of snow patch use in other cold-reliant species (Figure 1.2). To evaluate our hypotheses, we present data from both Glacier National Park and an introduced population at a higher elevation 1,000 km to the south (Mount Evans, CO).

As the sustained increases global temperatures, species along the most vulnerable fronts are expected to experience the greatest stress (Rowe et al., 2015). Nowhere might this be more notable in North America than the contemporary southern edges of the Rocky Mountains where profound glacial loss and periglacial change is now occurring (Rangwala and Miller, 2012). With local extinction of populations of species such as pika, yellow-bellied marmot, and least weasel from such southern edges of past range (Figure 1.1), it appears that cold and snow are critical to the sustenance of chionophiles. The results we report are an initial attempt to disentangle the role played by a single component of periglacial zones – snow patches – in the ecology of a cold-adapted obligate.

RESULTS

Our major hypothesis – that use of snow patches reduces thermal stress – was not supported based on measurements of respiration rate (Figure 1.3, Table S1.4). In contrast, use of snow patches was strongly associated with reduced insect harassment. As a correlated variable, percent retention of winter coat contributed to both respiration rate and autonomic behaviors associated with insect deterrence and notably mediated by wind. The positive association for direct sun and temperature with respiration rate (Figure S1.5) provides key support for a foundational assumption of our study: that observed respiration rate is associated with increased thermal stress and that our field survey was able to capture this relationship.

Percent of winter coat shed was negatively correlated with respiration rate, suggesting increased shedding reduces thermal stress (Figure 1.4, Table S1.5). The mean effect size was, however, small leading to a small biological effect (Figure S1.5). Somewhat counterintuitively, laying on snow was not correlated with respiration rate, as reflected by the mean estimate of 0 and the credible interval equally split between positive and negative effects. Although thermoregulatory benefits of snow has previously been described for mountain goats (Sarmento et al., 2019), our greater sample size and improved methodology demonstrates a low probability of substantive thermal benefit. Perhaps the high albedo (i.e., reflectance) of snow increases animals exposure to solar radiation, offsetting and surpassing the cooling effects of snow (Vera et al., 1975; Ion and Kershaw, 1989).

With respect to hypothesized responses to endo-parasitic insects, percent winter coat shed and exposure to direct sun was positively associated with increased ear-flick rate (Figure 1.3, Table S1.4, Figure S1.6). Temperature and wind speed both had very small credible intervals and were negatively correlated with ear-flick rate, with temperature having a greater effect. In strong contrast to respiration rate, recumbency on snow had a substantive negative effect on ear-flick rate. The wider credible interval for the effect of laying on snow (relative to other climatic variables) can be ascribed to the relatively small sample size. Younger age cohorts (young-of-year and sub-adult) were also negatively correlated with ear-flick rate, but with higher uncertainty in estimated effects due to a smaller sample size. Our results support the hypothesis that snow patch use is greatly incentivized for insect relief.

Percent of winter coat shed was strongly correlated with week of year, elevation, and age class (Figure 1.4, Table S1.5). Week of year was associated with decreased percent of coat shed with small variance in estimated effect and is well supported by prior literature (Hibbs, 1966; Déry et al., 2019; Nowak et al., 2020). An increase in elevation (of 1,000 m) was associated with a large negative effect on percent coat shed suggesting winter coats are retained longer in cooler environs. Both sub-adult and adult male age classes were positively associated with shedding while adult females accompanied by young-of-year retained their winter coats for longer. Prior research suggests the variability in estimated effects for age class is likely a result of individual condition (Déry et al., 2019).

Overall, our results contribute to a broader picture of a possible functional response to a presently declining resource – snow patches. While the hypothesis that snow patches provide thermal relief was not supported, insect harassment declined substantively when animals were recumbent on snow. Strong linkages between the impacts of ectoparasitic insects and demography (Joly et al., 2020) indicate that reduced capacity for insect avoidance has wide ranging consequences for affected populations.

DISCUSSION

Changing climates have clear implications for species persistence as borne out by paleontological evidence. Where a general gradient of warming temperatures has proceeded from lower latitude (warmest) to higher latitude (less so), species or population extirpations are prominent from their southern extents (Figure 1.1). The ability for cold-adapted species to tolerate warm temperatures and associated biotic changes will be a key determinant of population trajectories and is a dominant concern for conservation planning (Meek et al., 2023). To date, many reported benefits of persistent snow are primarily observational or based on sparse empirical evidence (Table 1.1). The additional hypotheses we brought forth for snow patch use – as playgrounds, perhaps because running around in snow is fun, and as sources of accessible water – require additional investigation.

The results we offer represent a mixed picture for thermally sensitive species. On one hand, use of snow patches does not appear to reduce thermal stress, at least through our metric of respiration rate. This portends increased challenge for cold-adapted organisms, including mountain goats, which face projected population declines even at northern latitudes (White et al., 2018). By contrast, pika populations persist even in unexpected environments in part because they have adopted mechanisms to counter acute heat stress (Beever et al., 2010). Similar behavioral shifts to avoid increased temperature are well documented, with notable examples including moose and alpine ibex (Mason et al., 2017; Verzuh et al., 2021), although physiological benefits are rarely quantified (Table 1.1). However, species must additionally contend with changing resource availability and interspecific interactions which may be heightened under changing climate conditions (Berger et al., 2022).

As warming temperatures are creating more favorable conditions for insects, abundances are increasing even in areas where they were previously scarce and include a progressive expansion of activity in arctic and subarctic environs (Hughes, 2000; Eisen et al., 2008; Culler et al., 2015). Accordingly, there are greater consequences of direct effects (e.g., blood loss) which can dramatically impact body condition of mammals (Helle and Tarvainen, 1984; Joly et al., 2020). The demographic consequences of which can be dramatic; for instance increasing densities of winter ticks in some moose populations are responsible for >90% of calf mortality (Debow et al., 2021). Additionally, caribou are well known for behavioral changes, including foregoing foraging and interrupted lactation, to avoid of insects during summer months (Joly et al., 2020). Nevertheless, projected decreases in the availability of persistent snow and ice (Siirila-Woodburn et al., 2021; Rounce et al., 2023) will continue to challenge the extent to which species across geographically varied environments can use behavioral mechanisms and specific habitat components to evade insects.

Our research on a species of the periglacial zones highlights the complexity of understanding the dynamic relationship between cold-adapted species and snow. Particularly, concurrent changes in biotic communities and thermal environments may place competing pressures on behavioral and biological responses. The complexity of these interactions and the rapidity of current climate changes provide a clear mandate to understand impacts to today's southerly populations – lest our studies follow the recession of species to higher latitudes and altitudes.

METHODS

Study site

Glacier National Park (48.8° N, –113.8° W) is a large (4,100 km^2) protected area characterized by high elevation mountains (~3,000 m) with alpine tundra and glacial lakes, and lower elevation (~1,000 m) coniferous forests. Mountain goats are native to the region with an estimated population size of 2,000–3,000 in Montana (Festa-Bianchet and Côté, 2008). Predators included grizzly bears, black bears (*Ursus americanus*), mountain lions (*Puma concolor*), wolves, (*Canis lupus*), and coyotes (*Canis latrans*) (Sarmento and Berger, 2017; Anderson et al., 2023).

Mount Evans, Colorado (35.59° N, –105.64° W; 4,350 m) is located within a 300-km^2 protected wilderness and characterized by alpine tundra, exposed rocky slopes, and coniferous forests at lower elevations. Mountain goats were introduced to Colorado by the Colorado Parks and Wildlife (formerly Game, Fish, and Parks Department) in 1948 and at Mount Evans in 1961 where population estimates have since ranged from 60–200 individuals (Hibbs, 1966; Reed and Green, 1994) (Colorado Parks and Wildlife unpublished data). Predators included black bears, mountain lions, and coyotes (Gross et al., 2002).

Data collection

We used respiration rate, a physiological response to environmental heat stress (Appleman and Delouche, 1958; Wijffels et al., 2021), to evaluate whether use of snow patches had a cooling effect. Respiration rate is well suited to assessing changes in thermal environment as, under periods of heat stress, it is the first physiological mechanism used in many mammals to maintain body temperature (Berihulay et al., 2019). Dogs on warm days seek shade and breath more rapidly. Study of domestic ruminants also reveals that respiration rate increases due to heightened temperatures (Appleman and Delouche, 1958; Phulia et al., 2010). As such, measurements of respiration rate under variable conditions are one of the best methods for assessing relative levels and immediacy of heat stress (Wijffels et al., 2021).

We used ear-flick rate as a measure of insect disturbance (Mooring et al., 2003; Blank, 2020). Prior research in which insect abundances were quantified indicates ear-flicks are positively correlated with measures of insect abundance (Mooring et al., 2003) and is corroborated by decreased observations of ear-flicks in animals experimentally treated with insect repellents (Woollard and Bullock, 1987). We used relative levels of disturbance, as measured using ear-flick rates, to test the hypothesis that snow patch use provides refuge from insects. Avoidance of ectoparasitic insects is important as they have high direct costs in domestic and wild mammals including disease transmission, blood loss, and redirection of feeding behavior (Hart, 1990; Mooring et al., 2003; Joly et al., 2020).

We recorded *in situ* observations of autonomic responses (respiration rate and ear-flick rate) of mountain goats and variation in local weather (Figure 1.2) in Glacier National Park during May–September of 2020–2022 and at Mount Evans during July of 2022. We recorded data using telephoto lenses and spotting scopes, typically at distances of 200–500 m, to minimize disturbance to animals. We restricted observations to recumbent individuals to facilitate accurate measurement and to avoid confounding results because of additional energetic demands of standing or walking (Chappel and Hudson, 1979). Using the digitally recorded video observation, we counted the number of flank movements (Appleman and Delouche, 1958; Wijffels et al., 2021) and the number of ears-flicks per ear during the survey period (Mooring et al., 2003).

Under ideal conditions, visual observation of respiration rate and ear-flick rate may still be challenging and is prone to observation error and inter-observer variation (Wijffels et al., 2021). To enhance repeatability and accuracy of measures, we captured video imagery of study animals with digital cameras. We used cameras with long telephoto lenses (Canon Inc, Tokyo, Japan, model: EOS 7D with EF 300mm F/4L IS USM and Extender EF 1.4x II; EOS RP with RF 100-500mm F4.5-7.1 L IS USM, and Extender RF 1.4x) to capture 15-second videos of bedded individuals. The 15-second measure of respiration is commonly used (Wijffels et al., 2021), as behavior (e.g., transition to standing) or local weather conditions (e.g., cloud cover) are unlikely to change during the survey period. We additionally collected a small number of visual observations (i.e., not digitally recorded) from experienced wildlife technicians following the same observation protocol and accounted for the possibility of increased observation error within the statistical model (described below).

For each observation, we classified each recumbent mountain goat by sex and age group (Figure S1.7). We did not classify sex for juveniles as sexual dimorphism of mountain goats does not develop until the second summer (Festa-Bianchet and Côté, 2008). We also recorded the percent of winter coat shed for all individuals one year or older (Figure S1.7), the latter variable under the assumption that percent of winter coat is associated with dissipation of body heat (Déry et al., 2019; Nowak et al., 2020). Further, we recorded two binary variables: exposure to direct sun and use of snow patches while recumbent. Last, we recorded the date, time, and geographic coordinates where the animal was observed to match observations with climatic and geographic variables. To reduce pseudoreplication, we collected repeat observations only after ≥15 minutes had elapsed.

We recorded temperature (°C) and wind speed (km/h) at 20-second intervals using a portable weather station (Nielsen-Kellerman Company, Boothwyn, PA, model: Kestrel 5000 Environmental Meter) on a tripod at a height of 1 ft above ground. The weather station was placed level and allowed to freely rotate, guided by a weathervane, to provide an accurate wind speed reading. These weather metrics were gathered at observer locations because it was either too disruptive to hike near goats at the time of data collection or not possible without extreme danger due to their occupancy of precipitous terrain. Our sample consisted of 928 *in situ* observations of mountain goats during 2020–2022 in Glacier National Park and at Mount Evans (Table S1.3). Of these, digital video imagery accounted for >90% (n = 876).

Analytical methods

Respiration and ear-flick rate

To link recorded temperature and wind metrics with observation data we used the time of initiation for each observation (rounded down to minute) and calculated the average temperature and wind speed for that minute. We derived the number of ear-flicks/ear for the 15-second survey period by dividing the number of ear-flicks by the number of ears visible. We modeled respiration rate and ear-flick rates as independent response variables and centered and scaled continuous variables (e.g., percent shed, temperature, and wind speed) by subtracting their mean and dividing by their standard deviation to facilitate model fit and interpretation of results (Hayek and Buzas, 2010). We used a Bayesian framework for all models with 10,000 iterations and 5,000 iterations of burn in and concluded models had converged when $\hat{R} < 1.01$ (Gelman and Rubin, 1992). We analyzed both respiration and ear-flick rate as a function of local weather and biological condition using a generalized linear model:

$$\begin{aligned}Y_{(x1 \ldots n)} \sim\ & \beta 0 + \beta 1 \times \mathrm{coat}\ shed_{(x1 \ldots n)} + \beta 2 \times \mathrm{sun}\ exposure_{(x1 \ldots n)} + \beta 3 \times t\mathrm{emperature}_{(x1 \ldots n)} \\ & + \beta 4 \times \mathrm{wind}\ speed_{(x1 \ldots n)} + \beta 5 \times snow\ us\mathrm{e}_{(x1 \ldots n)} + \beta 6 \times age\ class_{(x1 \ldots n)} \\ & + \beta 7 \times visual\ observation_{(x1 \ldots n)}\end{aligned}$$

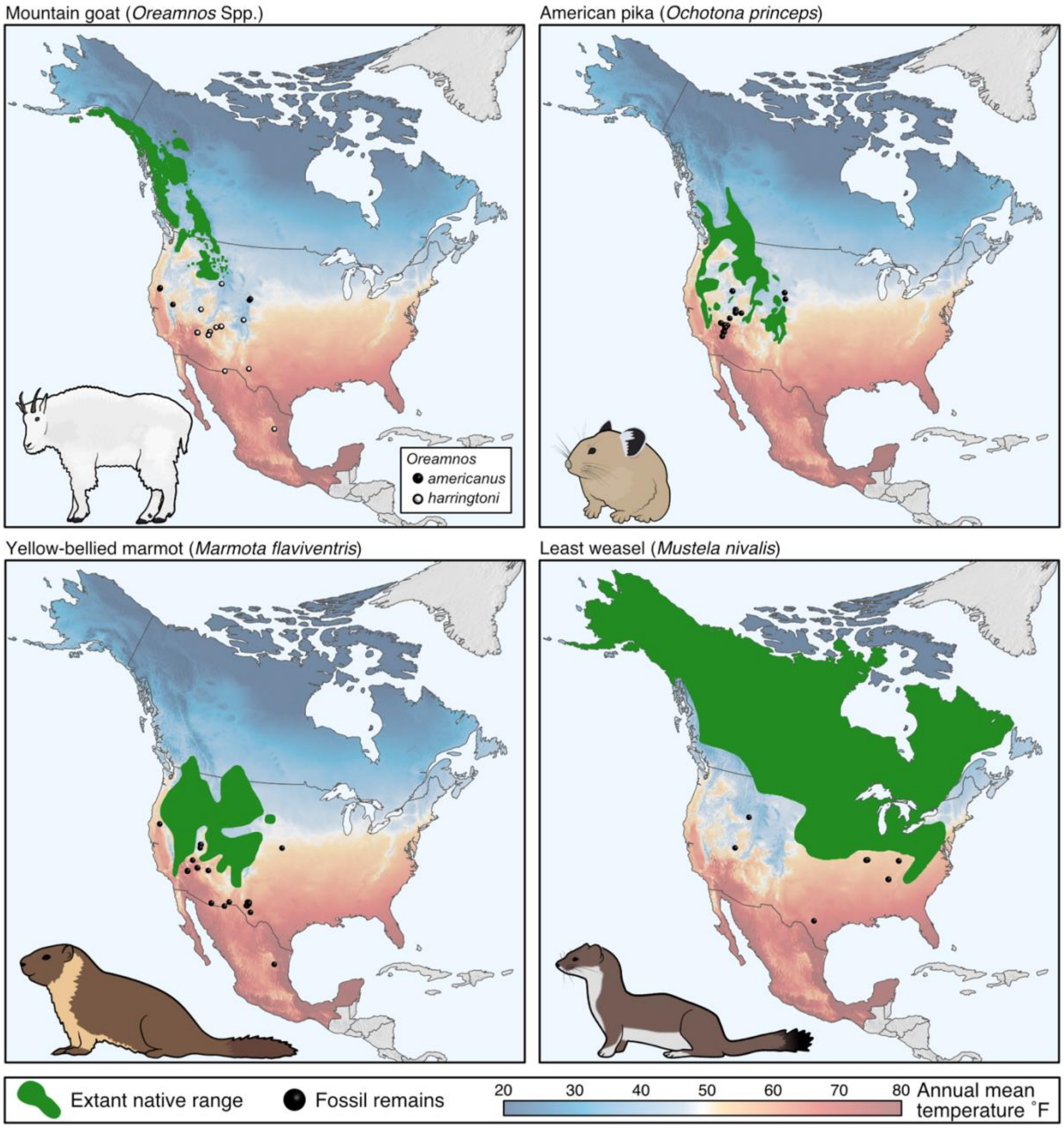
where *Y* represents the response variable (i.e., respiration rate or ear-flick rate), $x1 \ldots n$ represents observation 1 through n, *coat shed* was the percent of winter coat shed, *sun exposure* was whether the majority of the goat was exposed to direct sunlight, *temperature* was the ambient air temperature, *wind speed* was local wind speed (km/h), *snow use* was a binary variable for indicating bedding on snow, *age* was a categorical effect for young-of-year, and sub-adult (i.e., 1–2 years old), and *visual observation* was an additive effect for non-digital observations. Adult individuals (both male and female, age ≥ 3) are treated as the intercept. For ear-flick rate we used a Poisson regression to account for overdispersion of count data (Gelman and Hill, 2007). To incorporate information from observations without recorded temperature ($n = 69$) and wind data ($n = 68$) we interpolated unrecorded values by drawing samples from a distribution informed by observed data (Gelman and Hill, 2007).

Percent of winter coat shed

We derived the week of year for each observation by calculating the number of 7-day periods elapsed between January 1st and the observation date. We used the recorded geographic coordinates of the observation to obtain elevation from the USGS National Elevation Dataset (USGS 2005). We then centered and scaled elevation to evaluate the effect a change of 1,000 m by subtracting the mean observation elevation and dividing by 1,000. To evaluate biological and geographic factors influencing percent of winter coat shed we modeled shed as a linear model using a Bayesian framework:

$$\begin{aligned} shed_{(x1\ldots n)} \sim \beta 0 &+ \beta 1 \times elevation_{(x1\ldots n)} + \beta 2 \times \text{week}\ of\ year_{(x1\ldots n)} \\ &+ \beta 3 \times f\text{emale}\ with\ young_{(x1\ldots n)} + \beta 4 \times \text{age}/sex_{(x1\ldots n)} \end{aligned}$$

where *shed* was the observed percent of winter coat shed, $x_1 \ldots n$ indicates each observation, *elevation* was the elevation (m) of the observed individual, *week of year* was a numeric count of elapsed 7-day periods since January 1st, *female with young* was an added effect for adult females accompanied by young-of-year and *age/sex* was a categorical effect for young-of-year, juveniles (i.e., 1–2 years old), and adult males with adult females treated as the intercept.


Mountain goat (*Oreamnos* Spp.)

American pika (*Ochotona princeps*)

Yellow-bellied marmot (*Marmota flaviventris*)

Least weasel (*Mustela nivalis*)

Figure 1.1. Extant ranges of four exemplar cold-adapted species (mountain goats, American pika, yellow-bellied marmot, and least weasel) (IUCN, 2022) and selected locales in which fossilized remains have been found (references provided in Table S1.2). Mean annual temperature (map shading) (Thornton et al., 2022) illustrates that these species have been extirpated from warmer geographies but persist within cooler ecoregions.

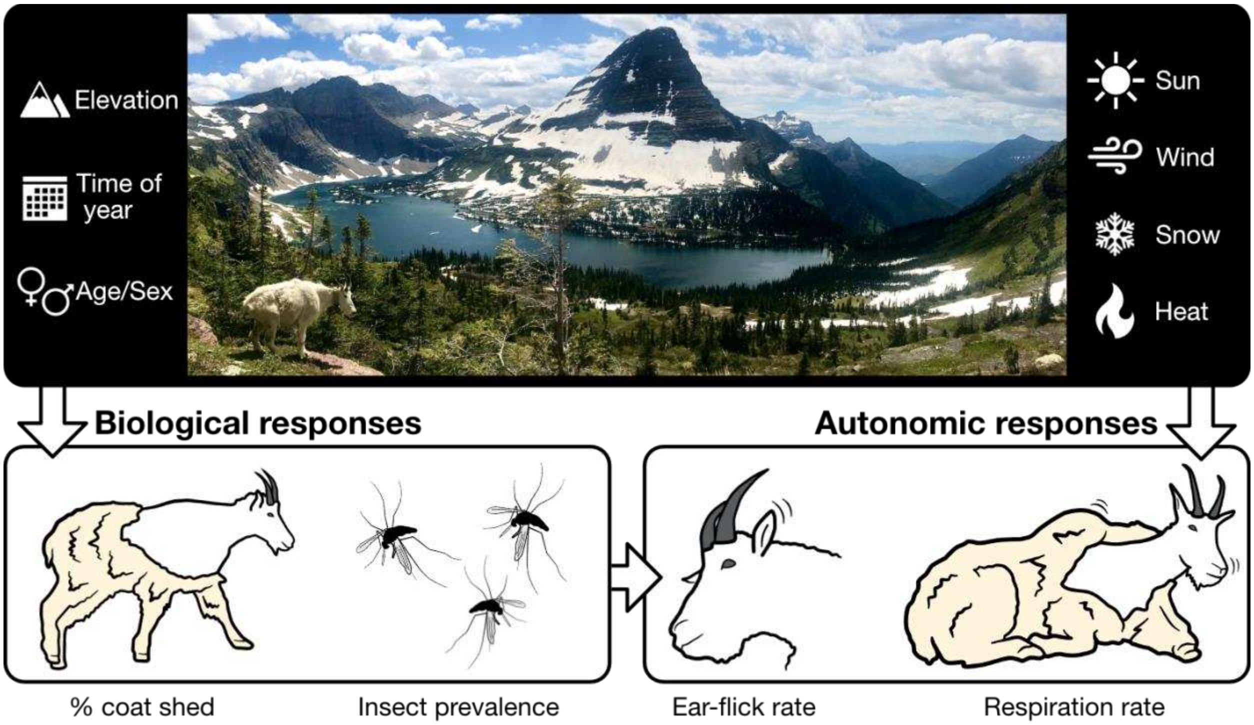


Figure 1.2. Overview of primary study region (top photograph; Glacier National Park, 2020) and schematic of investigated variables hypothesized to affect biological and autonomic responses. As depicted, biological responses are the amount of winter coat shed by a given individual and insect prevalence; autonomic responses are ear-flick and respiration rates. Time of year will of course be associated with snow and heat on a seasonal basis.

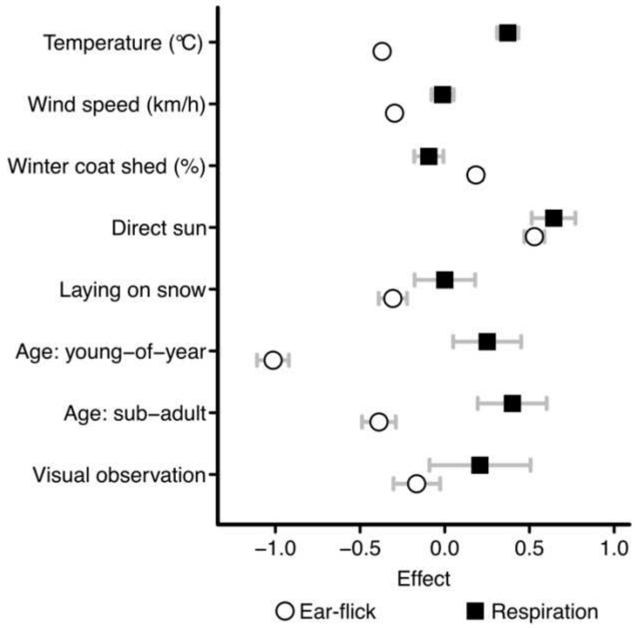


Figure 1.3. Effects of abiotic, weather, and biological variables (y-axis) on ear-flick and respiration rate of mountain goats from study sites in the Rocky Mountains, USA. Point estimates represent mean effect values, whiskers show 95% credible intervals. Effects of continuous variables (winter coat shed and wind speed) are standardized to reflect a change of one standard deviation. Categorical variables (direct sun, age, visual observation) are additive effects with adult individuals and video observations treated as the intercept.

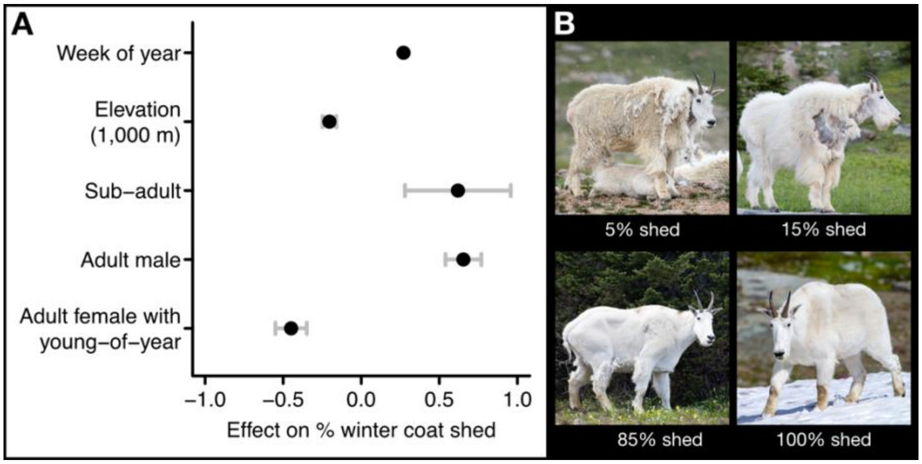


Figure 1.4. A) Effects of week of year, elevation, and age class on percent of winter coat shed. Mean estimates represented by dots, whiskers represent 95% credible intervals. The estimated effect for elevation represents an increase of 1,000 m. Categorical variables (age class and accompaniment by young-of-year) are additive effects with adult females (without young-of-year) treated as the intercept. B) Example of variation in mountain goat percent winter coat shed.

Table 1.1. Hypothesized benefits of use of snow patches during summer months by species for which benefits have been reported and strength of supporting evidence.

			Evidence and strength of benefit			
Benefit	**Observed in**		**Mentioned**	**Empirical**	**Strong**	**Reference**
Heat relief	Horse	*Equus caballus*	X			Keiper and Berger, 1982
	Mountain goat	*Oreamnos americanus*		X		Sarmento et al., 2019
	Muskoxen	*Ovibos moschatus*	X			Hall, 1964
	Caribou	*Rangifer tarandus*	X			Anderson and Nilssen, 1998
	Grizzly bear	*Ursus arctos*	X			French et al., 1994
Insect relief	Horse	*Equus caballus*	X			Keiper and Berger, 1982
	Mountain goat	*Oreamnos americanus*	X			Sarmento et al., 2019
	Caribou	*Rangifer tarandus*			X	Ion and Kershaw, 1989
Water	Horse	*Equus caballus*	X			Keiper and Berger, 1982
	Wild yak	*Bos grunniens mutus*		X		Berger et al., 2015
Play	Elk	*Cervus elaphus*	X			Altmann, 1956
	Horse	*Equus caballus*	X			Berger, 1986
	Bighorn sheep	*Ovis canadensis*	X			Berger, 1980
	Wolverine	*Gulo gulo*	X			Polley, 2022

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CHAPTER 2 – HOW HIGH SUMMER TEMPERATURES INFLUENCE SELECTION FOR SNOW IN COLD-ADAPTED SPECIES

SUMMARY

Rapid changes to climate in montane environments are reshaping ecological communities. Within these, cold-adapted organisms are among the most strongly impacted as they may experience thermal stress at moderate temperatures. Thermal challenges to persistence are evidenced by recent and historical extirpations at low elevations or the heated edges of former distributional ranges. The importance of adaptive mechanisms to thwart thermal and other stresses are well studied, but attention to snow as a driver of summer resource selection remains under-investigated. We hypothesized that 1) spatial use by cold-adapted species is modulated by the presence of persistent snow during summer months, and 2) avoidance of heat will result in increased use of snow during peak summer temperatures. We tested these posits using GPS location data spanning a decadal period for mountain goats (*Oreamnos americanus*) near the southern terminus of their present continental natural range. Contrary to expectations, mountain goats exhibited only modest selection for proximity to snow. During periods of peak temperatures, selection increased for areas associated with reduced thermal exposure and decreased for snow. Additionally, individuals used areas further from escape terrain during the warmest periods. Our results highlight that snow plays only a small role in the summer resource selection of mountain goats. More broadly, responses to warming temperatures may expose individuals to greater predation risk. Among other cold-adapted species the relationships between increasing temperatures and the consequences of behavioral modification remain less clear and warrants additional attention. As montane environments continue to warm,

understanding changes in resource selection during the warmest periods today offers an invaluable lens for understanding challenges for populations tomorrow.

INTRODUCTION

Human-caused increases in global temperatures are indelibly altering ecosystems and present a key threat to the long-term conservation of biodiversity (Lovejoy and Hannah, 2019). Prior to anthropogenic warming, periglacial zones have long provided refuge for cold-adapted species (Pielou, 2008; Rosvold, 2016). As Earth warms, species inevitably die out, shift ranges, or develop diverse adaptations to adjust to changing thermal conditions (Parmesan, 2006; Rowe et al., 2015; Wiens, 2016). In alpine ecosystems, temperatures are warming 2–5x more rapidly than elsewhere resulting in glacial mass losses, decreased snow persistence, and changes in seasonality (Choi et al., 2010; Hugonnet et al., 2021; Pörtner et al., 2021). Such cumulative alterations have resulted in range losses or shifts of cold-adapted species – notably mammals such as wolverines (*Gulo gulo*), American pikas (*Ochotona princeps*), and yellow-bellied marmots (*Marmota flaviventris*) (Frase and Hoffmann, 1980; Copeland et al., 2010; Billman et al., 2021).

The species that arguably best typifies a tight association between distribution and periglacial zones is the mountain goat (*Oreamnos americanus*). Their range is inextricably tied to North America's cold Pacific rugged mountain realm coupled with interior montane glaciated systems (Figure 2.1). Both the species itself and an associated con-generic (*O. harrgintoni*) have become extinct in warming Holocene climes from northern Mexico, Arizona, and Utah (Rideout and Hoffmann, 1975). Unlike the more widespread nature of ibex (*Capra* spp.), a goat relative distributed across Eurasia's cold biomes and into the hot deserts of northern Africa including Egypt and Ethiopia (Gross et al., 1995; Parrini et al., 2009), extant mountain goats have narrow ecological niches in relatively cold and snowy environs (Festa-Bianchet and Côté, 2008). While mountain goats have been introduced to more southerly latitudes and persist at high elevation (Figure 2.1), cold-adapted species found at low-latitude or low-elevation may fail to adjust to warming temperatures and are often the first to be impacted by a warming climate (Wiens, 2016).

In response to warming temperatures, cold-adapted species make both fine-scale alterations in resource use and broad-scale shifts in locality (Table 2.1). Moose (*Alces alces*), a Holarctic species, reduces movement and increases use of shaded areas and standing water for conductive cooling (Renecker and Hudson, 1990; Alston et al., 2020). Similarly, fine-scale changes in temporal activity patterns occur in alpine ibex (*C. ibex*) which change foraging patterns to utilize cooler daytime periods (Aublet et al., 2009). At broader scales both alpine vertebrates and invertebrates are shifting to higher elevations (Parmesan, 2006), with changes noted for mammals including pikas and crested porcupines (*Hystrix cristata*) (Moritz et al., 2008; Mori et al., 2018). Further, populations at the southern edge of species ranges have been extirpated, resulting in species-wide shifts in distribution (Chen et al., 2011; Hayes, Chapter 1 of this dissertation). Among others, marmots (*Marmota* spp.), caribou (*Rangifer tarandus*), and snowshoe hares (*Lepus americanus*) have all become regionally extinct from the southern portion of their historical ranges (Racey and Armstrong, 2000; Armitage, 2013; Wilson et al., 2022).

Recent global warming is associated with decreased duration of snow and greater seasonal variability in mountainous regions (Choi et al., 2010). A multitude of species are known to make use of snow which provides various ecological benefits including foraging habitat, relief from heat and insects, and water sources (Rosvold, 2016). Less clear, however, are the physiological and ecological costs associated with a lack of snow (Hayes, Chapter 1 of this dissertation). In contrast, the direct negative effects of snow are well established, and include increased energetic expenditure for locomotion, increased predation risk and death by avalanche (Parker et al., 1984; Huggard, 1993; White et al., 2011). Despite the putative benefits of snow, we have a poor understanding of the role of persistent snow in modulating habitat suitability and spatial resource selection under continued climate change.

Given the strong link between mountain goats and periglacial environs (Figure 2.1) the value, if any, of summer snow presence has not been well investigated (Stevens, 1979; Rosvold, 2016; Sarmento et al., 2019). Here we explore how snow cover during summer months affects resource selection at coarse- and fine-spatial scales. Specifically, we hypothesized that if snow dominated landscapes provide critical resources during summer months, then (1) mountain goats will exhibit positive selection for snow and (2) periods of higher temperature will be associated with increased strength of selection for cooler habitats. Understanding the relationship between declining summer snow and habitat selection is relevant to a broader framing of how animals respond to thermal challenges, whether at the edges or at the centers of their ranges (Pennington et al., 2021). And, although climate envelope modeling reflect a wide array of interpretations (Nogués-Bravo, 2009), site specific data are rarely at the resolution needed to understand niche relationships involving snow and summer temperature extremes (Hargreaves et al., 2014).

Here, we use high temporal resolution, remotely sensed snow presence data to capture and evaluate the effects of changing snow availability (Figure 2.2) for its potential use by a species highly associated with ‘cold.’ We included measures of topography, thermal exposure, and human presence, which are known to impact resource selection by mountain goats (Sarmento et al., 2019). By capitalizing on contrasts of habitat selection during the hottest days of the year with those of milder summer temperatures using a decadal-long data set, we evaluate adaptive resource selection to develop insights about potential shifts under future climate conditions. As high latitude and elevation environments are being reshaped by changing climate, informed conservation requires developing a more robust understanding of the consequences of warming temperatures for species putatively reliant on 'cold' (Hall and Fagre, 2003; White et al., 2018).

METHODS

Study site

Glacier National Park (48.8° N, −113.8° W) is a large (4,100 km^2) protected area characterized by rugged high-elevation mountains dominated by alpine tundra and glacial lakes. Lower elevations are typified by coniferous forests and intermittent open meadows. Extant predators included grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), mountain lions (*Puma concolor*), wolves (*Canis lupis*), and coyotes (*Canis latrans*) (Sarmento and Berger, 2017; Anderson et al., 2023). Mountain goats are native to the region with an estimated population size of 2,000–3,000 in Montana (Festa-Bianchet and Côté, 2008).

Spatial data and mountain goats

We coupled high temporal resolution optical satellite imagery with a decadal dataset of mountain goat GPS locations to generate a novel assessment of temperature driven changes in resource use while accounting for changing availability of snow. We captured mountain goats in Glacier National Park, USA using either Clover traps or ground darting and fitted satellite GPS collars during 2013–2014 (Sarmento et al., 2019) and 2018–2020 (Table S2.2). We sedated goats in Clover traps using ketamine (2 mg/kg) and xylazine (3mg/kg) and sedated darted goats using either carfentanil (3 mg/mL at a dosage of 0.035mg/kg) or thiafentanil (10mg/ml at a dosage of

0.1 mg/kg). Standard handling techniques included use of blindfolds to reduce stress and administering oxygen to minimize risks of hypoxia. After handling, we antagonized capture drugs using yohimbine (10mg/ml xylazine) or naltrexone (50mg/ml at a dosage of 100mg/mg carfentanil or 20mg/mg thiafentanil). All animal captures, handling, and monitoring was in accordance with approved Institutional Animal Care and Use Committee (IACUC) protocol (Glacier National Park IMR_GLAC_Biel_MtnGoat_2018.A3).

We recorded 67,215 GPS locations during 2013–2016 and 98,497 GPS locations during 2018–2022. For data collected between 2018–2022, which included horizontal location error, we censored 10,842 points with error exceeding the resolution of our spatial dataset (i.e., >30 m). We then created a subset of recorded locations for the summer period when snow is receding (Figure 2.2; May 15th and August 31st) resulting in a total of 47,950 observed locations.

We used elevation data with a 30 m spatial resolution from the USGS National Elevation Dataset (USGS, 2005) and derived slope and aspect from the elevation using the R package "raster" (Hijmans, 2021). We classified slopes ≥33° as escape terrain (Gross et al., 2002), and generated a distance-to-escape layer using the GRASS GIS (GRASS Development Team, 2019). Based on slope and aspect, we calculated daily solar radiation per unit area for each day $(watt - hour \times m^2)$ for the entire study region. First, we calculated visible horizon from the center of each 30m grid cell in 5° intervals based on the digital elevation model. We assumed a constant surface albedo (ground reflectance) of 0.22 and clear sky conditions (Marshall and Miller, 2020). We then calculated daily solar radiation for each grid cell with the "r.sun" function in GRASS GIS and used this as a representative measure of thermal exposure at a given location.

We used distance to roads and trails to incorporate measure of potential anthropogenic presence as a possible modifier of mountain goat behavior. We acquired vector data from Open

Street Map (www.openstreetmap.org) and converted them to 30 m resolution raster images. We then calculated least distance-to-feature for the center location of each grid cell using GRASS GIS.

Assessing snow cover

We used Google Earth Engine to develop a last-day-of-snow dataset based on daily Normalized Difference Snow Index (NDSI) imagery acquired by the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor at a 500 m resolution (Hall and Riggs, 2016). For each study year, we identified the last day (up to August 31st) a given pixel was classified as snow. We resampled the resulting last-day-of-snow dataset using a 30 m resolution and, for each day of the year, determined the closest distance to areas identified as snow on or after the date of use. As we were interested in the localized effects of snow, we truncated proximity to snow at 2 km (i.e., the effects of snow were considered not to selection at distances >2 km from snow covered areas).

Identifying warm periods

We used daily mean air temperature from a centrally located weather station (SNOTEL #482; 48.8° N, −113.85° W; 6,300 ft; www.nrcs.usda.gov). We identified the warmest days of each year by assessing those which exceeded the 85th percentile of temperatures per summer during the summer study period. We chose mean daily air temperature as it encapsulates warmth across an entire day; however, days with the top 15% minimum and maximum temperatures were similar (Figure S2.7). We subset used and available location data based on hot and cool days (i.e., days with mean temperatures >85th percentile and <85th percentile, respectively). Using these, we modeled selection independently, as described below, for both groups of data subsets.

Analytical methods

We assessed availability of resources at two spatial scales: 1) within an individual animal's home range and 2) proximate to used locations. We estimated the annual home range of each individual using a 95% minimum convex polygon using the R package "sp" (Bivand et al., 2013). We generated 10 random available locations for each recorded GPS location within each home range. To identify fine-scale availability (i.e., resources proximate to used locations), we used a step-selection process (Thurfjell et al., 2014). First, we created 4-hour steps using recorded locations, a minimum of three consecutive points, and a tolerance of 30 minutes using the R package "amt" (Signer et al., 2019). We then generated 10 available locations for each step based on a random step length and turning angle drawn from the distribution of observed values (Street et al., 2016).

We assessed resources based on availability at the date and time of observed locations as some spatial data were temporally variable. For both spatial scales, we extracted values for used and available locations based on the geographic coordinates and time stamp of each location. We modeled distance-based resources as distance-to-feature and, to facilitate interpretation, we evaluated selection as proximity-to-feature (i.e., the inverse effect of distance-to-feature) so that positive selection indicates increased proximity to the resource. For proximity-to-feature we transformed observed distance-to values using $log_{10}(x+1)$ to meet assumptions of normality and facilitate model fit. We centered and scaled all covariates by subtracting the mean and dividing by standard deviation.

We used a Bayesian hierarchical random effect resource selection model (Thomas et al., 2006) to evaluate summer (i.e., mid-May to the end of August) selection by mountain goats at two spatial scales and account for individual variation. We used a uniform distribution for the population-level hyperparameter (α) for each covariate (x):

$$\alpha_x = U(min = 0, max = 25)$$

with a population-level variance:

$$\tau_x = N(\mu = 0, \sigma = 0.001).$$

We treated individual (i) as a random effect with the prior distribution for each covariate (β_x) informed by population-level distributions:

$$\beta_{x,i} = N(\mu = \alpha_x, \sigma = \tau_x)$$

We modeled the relative probability (p) of selection for resources by each individual as

$$logit(p_{i,j,k}) = \beta_0 + \beta_{1,i,j,k} * x_{1,i,j,k} + \ \dots + \beta_{n,i,j,k} * x_{n,i,j,k}$$

where $p_{i,j,k}$ is the relative probability of selection by individual i at observation j, scale k, β_0 is the intercept, and $\beta_1 \dots \beta_n$ are coefficients estimated for covariates $x_1 \dots x_n$. We modeled the likelihood of use by individual i at observation j and scale k (i.e., $pres_{i,j,k}$) as a Bernoulli random variable:

$$pres_{i,j,k} = Bernoulli(p_{i,j,k}).$$

This model structure allows for sharing of information between individual-level effects while accounting for individual variation and differences in sample sizes (Thomas et al., 2006). For each spatial scale we determined population-level effects by taking mean of all individual-level effects (i.e., $\mu_{\beta x}$). We evaluated a single global model which included all covariates of interest and determined the effect based on the magnitude of beta estimates and the 95% credible interval. We ran models for 5,000 iterations and 2,500 iterations of burn in and concluded models had converged when $\hat{R} < 1.01$ (Gelman and Hill, 2007).

RESULTS

We tested the influence of snow on resource selection and alteration based on peak summer temperatures using the previously described decadal dataset. As hypothesized, snow cover influenced spatial use by mountain goats during summer months; the relative effect on selection was small (Figure 2.3). Additionally, we found individuals exhibited adaptive resource selection in response to high temperatures but, notably, selection for snow decreased during the warmest summer days (Figure 2.4, Figure 2.5). Perhaps most importantly, there were ecological tradeoffs associated with selection for cooler topographies during the warmest periods wherein use of cooler habitats may expose individuals to greater predation risk (Figure 2.4).

Home range scale selection

In agreement with previous literature (e.g., Gross et al., 2002; Poole et al., 2009; Richard and Côté, 2016), we found escape terrain, elevation, human presence, and solar radiation were the primary determinants of spatial use by mountain goats within their home range (Figure 2.3, Table S2.3). Human presence was strongly influential, with positive selection for proximity to both roads and trails. Snow had the smallest effect of any covariate considered at the home range scale (Figure 2.3). Habitat use was positively associated with topography characterized by increased thermal exposure, although, like proximity to snow, the relative effect size was small.

Our second hypothesis, that individuals exhibit adaptive resource selection and increased use of snowy areas in response to high temperatures, was only partially supported. Comparison of selection during the warmest 15% of summer days (i.e., hot days) and cooler days revealed decreased selection for proximity to escape, solar radiation, and snow and increased selection for elevation and proximity to anthropogenic features (Figure 2.4, Table S2.4). These differences are notable as they indicate a behavioral change in resource use during the hottest periods. The broader credible intervals for selection during the warmest days is likely a result of reduced data availability rather than increased variance in estimated individual effects.

Selection for topographic variables (escape terrain and elevation) had the greatest change between hot and cool days (Figure 2.4). Mountain goats demonstrated a substantial increase in selection for higher elevations during hot days, which are presumed to be cooler environs based on correlations between elevation and temperature (i.e., air temperature lapse rate) (Rolland, 2003). Strikingly, there was a concurrent substantial decreased selection for proximity to escape terrain, suggesting temperature driven changes in resource selection may expose mountain goats to higher levels of predation as they were no longer situated near steeply sloped topographies. Selection during hot days also included increased proximity to roads and trails, which may also influence predator presence and, thus, predation risk (Sarmento and Berger, 2017).

Selection for solar radiation showed a modest decrease in selection during the warmest days (Figure 2.4). While mountain goats still occupied terrain with higher solar exposure relative to availability, the strength of selection was reduced in comparison to cool days. This suggests increased thermal stress during high ambient temperatures may encourage selection for slopes with less solar exposure. Mountain goats also exhibited reduced selection for proximity to snow during hot days, suggesting use of areas near snow was not for thermoregulation.

Fine scale selection

Our first prediction was only partially supported by results from our analysis of fine scale selection. Specifically, proximity to snow had a minimal effect on spatial use (Figure 2.3). Negative selection for elevation and, to a lesser degree, escape terrain proximity contrast with strong positive selection at the home range scale. As the ecological benefits of these covariates are well established for mountain goats, this suggests that selection for these critical resources is occurring primarily at broader scales. In another noteworthy contrast, mountain goats exhibited avoidance of solar radiation at the fine scale, indicating localized behavior mitigating thermal exposure.

There were strong differences in fine-scale resource selection during the warmest days (Figure 2.5, Table S2.5). Markedly, changes in selection for proximity to escape terrain, elevation, and solar radiation were in the opposite direction of observed selection at the home range scale. This suggests changes in availability of local habitat (i.e., because of movement within their home range) may be key explanatory factors in the observed effect.

As in the home range comparison, our second hypothesis was not supported by changes in fine scale selection. During the warmest days mountain goats used habitats that were further away from areas identified as snow. The consistency of results at differing spatial scales strongly suggests that use of snow habitats is unlikely to increase under warming summer temperatures.

DISCUSSION

The importance of persistent snow, ice, and eponymous periglacial zones for cold-adapted species have been inadequately understood despite strong species associations with these environments (Morrison and Hik, 2007; Millar et al., 2014; Hayes, Chapter 1 of this dissertation; Figure 2.1). As contemporary alpine environments warm at previously unprecedented rates

(Pörtner et al., 2021) evaluating changing use of periglacial environs will help to inform species responses to future conditions.

Climate forcing and changes to the cryosphere in mountain environments have widespread impacts, particularly to hydrology, alpine stream ecosystems, and species phenological responses (McKelvey et al., 2011; Giersch et al., 2017). For populations of cold-adapted animals, including ptarmigan (*Lagopus leucura*), pika, and wolverines, forecasted climate warming is predicted to lead to population declines (Wang et al., 2002; Beever et al., 2010; McKelvey et al., 2011). Already warming temperatures have resulted in broad shifts in distribution and behavior of many montane species (McCain et al., 2021). At more local levels individuals may exhibit adaptive resource use in response to changing thermal exposure, such as changing temporal activity or seeking shade (Aublet et al., 2009; Alston et al., 2020). Our results show that mountain goats make both broad and fine scale adjustments to spatial use during warmer temperatures.

We found selection for snow is not increasing under hotter conditions as would have been expected if snow-dominated habitat (Figure 2.6) was providing a refuge from increased temperatures. Avoidance of deep snow occurs in large-bodied, cold-adapted species due to increased locomotion costs (Parker et al., 1984; Dailey and Hobbs, 1989; White and Gregovich, 2017), however, these effects are likely reduced during summer months when snow is less deep. Selection, however, may be occurring at the fine spatial scale which was not captured by either the temporal resolution of our spatial data or the spatial resolution of snow cover data. That said, recent research (Hayes, Chapter 1 of this dissertation) suggests little or undetectable thermal benefit for animals bedded on snow, as measured by respiratory responses. Thus, our findings that mountain goats do not select for areas characterized by snow during times of peak temperatures are less surprising. In concert, these studies provide strong evidence that a reduction of persistent snow and ice alone is unlikely to create increased thermal challenges for mountain goats.

We found support for temperature-mediated changes in resource selection, including shifts in elevation and reduced use of areas with high solar exposure (Figure 2.4, Figure 2.5). Elevational shifts concurrent with increased temperatures like those we identified are well supported across numerous taxa (Parmesan, 2006; Moritz et al., 2008). Reduced selection for thermal exposure at the home range scale suggests that observed changes are, at least in part, a result of increased ambient temperatures. Notably, with respect to mountain goats, there was a concurrent increase in use of areas associated with higher risk of disturbance or mortality (i.e., further from escape terrain and closer to humans), which carries potential demographic consequences.

Risk of death is strongly related to proximity to escape terrain with areas farther from steep slopes bringing increased mortality including predation by grizzly bears (Figure 2.6; see also Festa-Bianchet and Côté, 2008). The observed increase in use of areas farther from escape terrain during warm days suggests that temperature induced shifts in resource use may expose mountain goats to increased predation risk. However, we also noted a corresponding increase in selection strength for escape terrain at the fine scale which may partially offset these effects.

The relative costs and benefits of increased use of areas close to anthropogenic activity are less clear (Figure 2.6). On the positive side, mountain goats gain increased access to anthropogenic sources of salt (Singer, 1975) including human urine and the presence of people offers an apparent shield from predators (Sarmento and Berger, 2017). In reptiles for instance, habitat use shifts with increasing temperatures in part because of enhanced ability to avoid predators (Pearson and Bradford, 1976). However, a growing body of research into the effects of recreation related disturbance on wildlife populations suggests that anthropogenic disturbance (such as by hikers) may have substantial energetic costs (Neumann et al., 2011). Although we are unable to disentangle these effects in our work, the fact that use of areas proximate to anthropogenic activity increased during the hottest days of the year suggests a complicated tradeoff between predation risk and thermal costs that warrants additional attention.

Among other cold-adapted species of montane environments, changing relationships between summer temperatures and habitat use reflect important behavioral choices (Teitelbaum et al., 2021). Selection for shade and altered patterns of foraging during cooler periods of the day are prime examples (Aublet et al., 2009; Mason et al., 2017; Alston et al., 2020). However, use of summer snow patches and possible tradeoffs between thermal constraints and predation remain understudied – although they are critical to understanding potential adaptive responses to future climate challenge.

Our results point to temperature-modulated resource selection and indicate increased selection for snowy locales is unlikely, even as glaciers diminish and climes warm. Additionally, changes in behavior related to avoidance of thermal exposure can lead to increased use of high-risk habitats, heightening the chances of predation or energetically costly disturbance. As warmer temperatures reduce availability of cooler habitats, species will show shifts in resource use – and tradeoffs between thermal environment and safety – are likely. Under future climates the indirect effects of changing behavior, such as exposure to increased predation risk, are a key concern as elevational and geographic shifts in resource use are inexorable. As populations at the marginal edge of distributions will be most strongly impacted, evaluating responses to the warmest experienced conditions, as we have elected to do, provides insights about future population responses and challenges to long-term persistence.

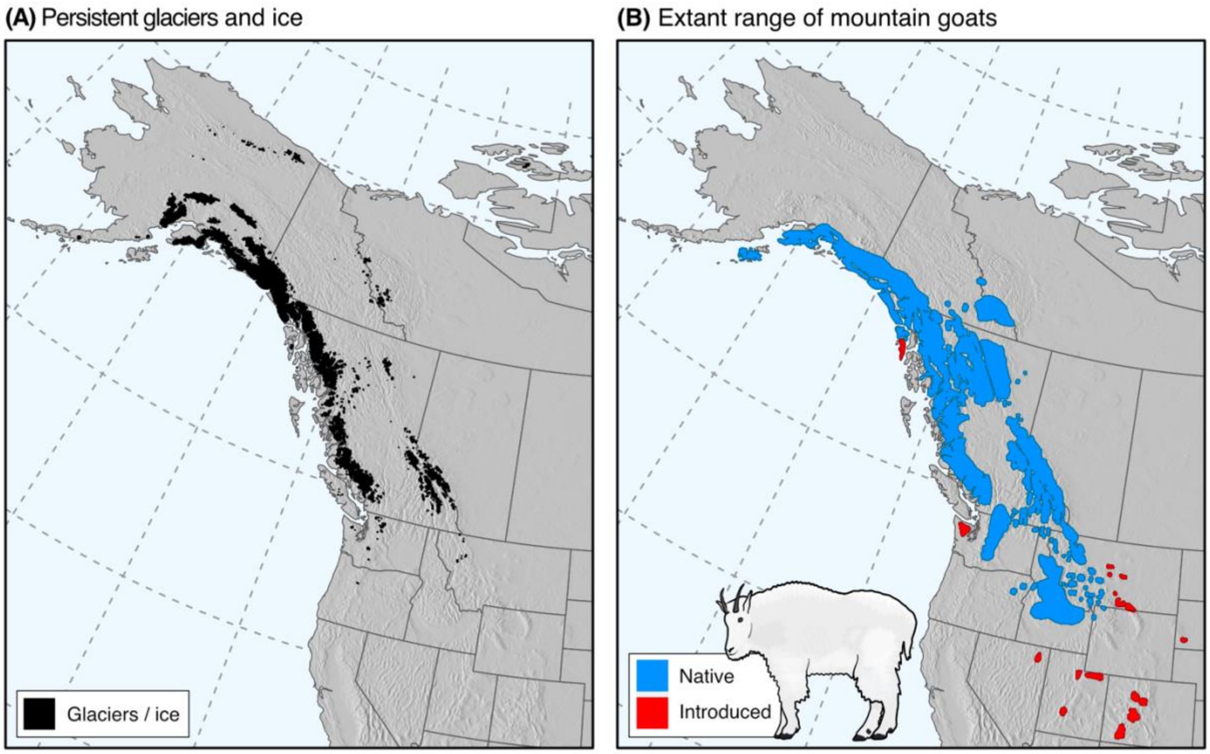

Figure 2.1. The native distribution of mountain goats (*Oreamnos americanus*) and periglacial zones; introduced populations persist at high elevations at lower latitudes (reflected in red). (A) The distribution of persistent glaciers and ice in western North America. (B) the extant range of mountain goats. Data on glaciers and mountain goats are from the North American Atlas and IUCN (www.iucnredlist.org), respectively.

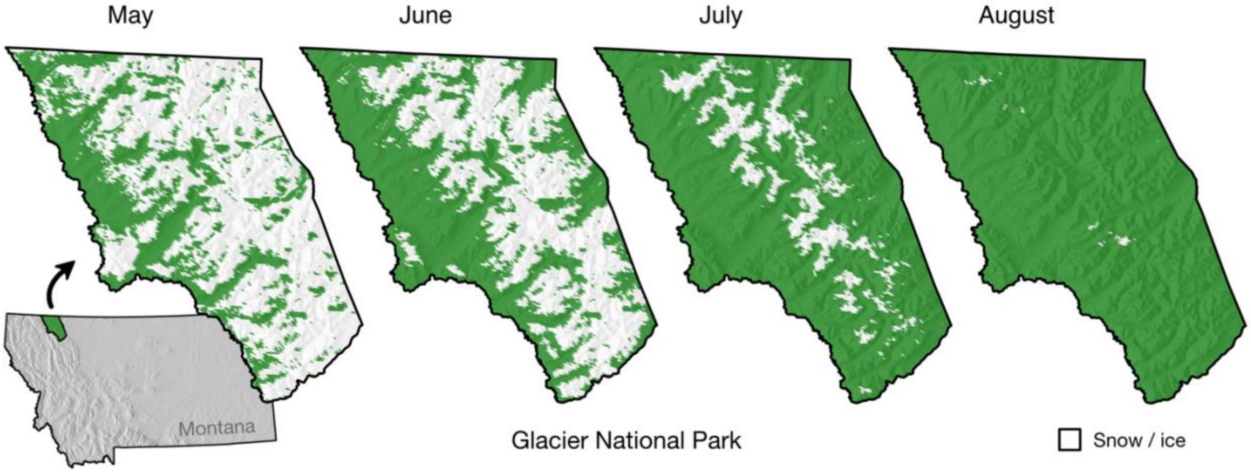

Figure 2.2. Phenology of snow and ice in Glacier National Park, MT during spring and summer months (May–August). Data are from the MODIS Terra Daily NDSI product and show pixels that were identified as snow on or after the first day of each month May–August of 2022.

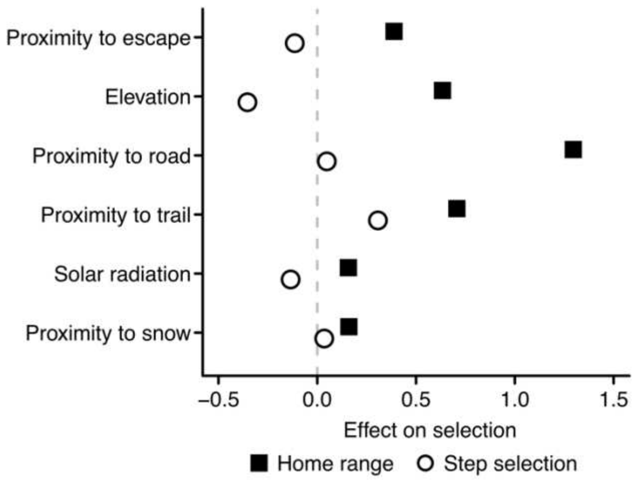

Figure 2.3. Modeled population-level effects of covariates on resource selection by mountan goats in Glacier National Park during May 15th to August 31st across a decade (2013–2022). Square points represent mean estimates of selection effects within home ranges, circles represent mean estimates of selection based on a step selection process. 95% credible intervals are not shown, as they would be obscured by points, and are provided in Table S2.3.

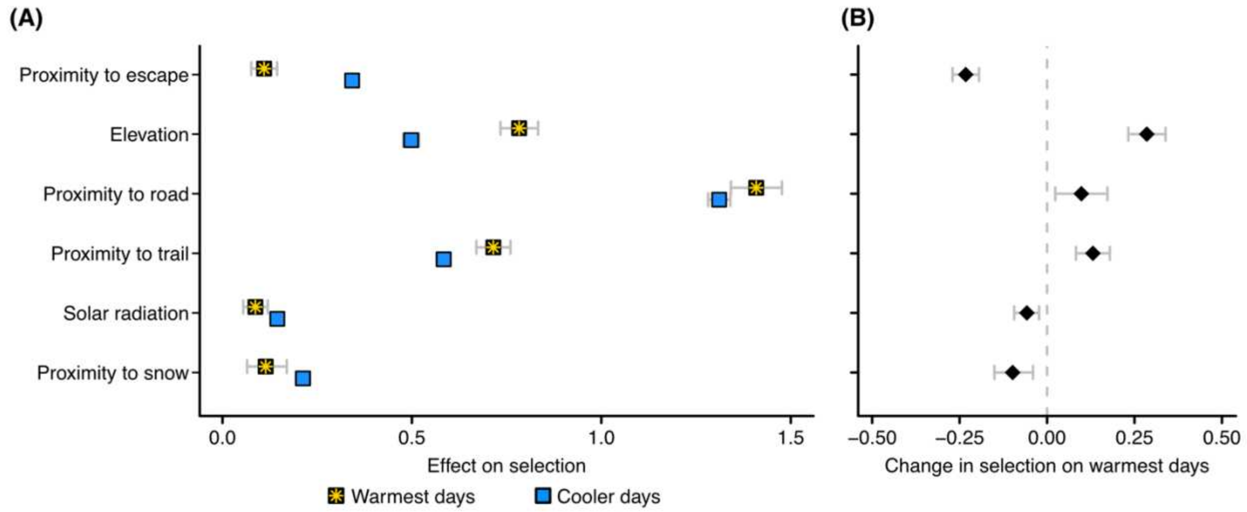

Figure 2.4. Contrasts between resource selection within home ranges during the warmest (> 85th percentile) and cooler (all other) days by mountan goats in Glacier National Park during May 15th to August 31st across a decade (2013–2022). (A) comparison between effects during warmest days and cooler days. (B) change in selection on warmest relative to selection on cool days. Points represent mean population effect estimates. Whiskers represent 95% credible intervals and, as some are not visible due to the narrow range, are provided in Table S2.4.

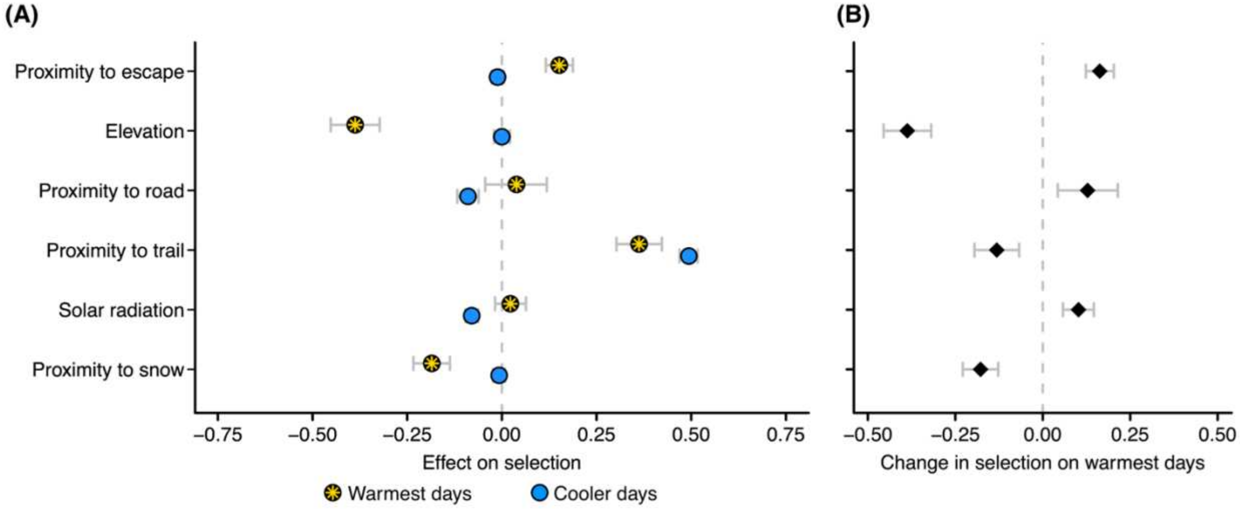

Figure 2.5. Contrasts between resource selection at a fine scale during the warmest (> 85th percentile) and cooler (all other) days by mountan goats in Glacier National Park during May 15th to August 31st across a decade (2013–2022). (A) comparison between effects during warmest days and cooler days. (B) change in selection on warmest relative to selection on cool days. Points represent mean population effect estimates. Whiskers represent 95% credible intervals and, as some are not visible due to the narrow range, are provided in Table S2.5.

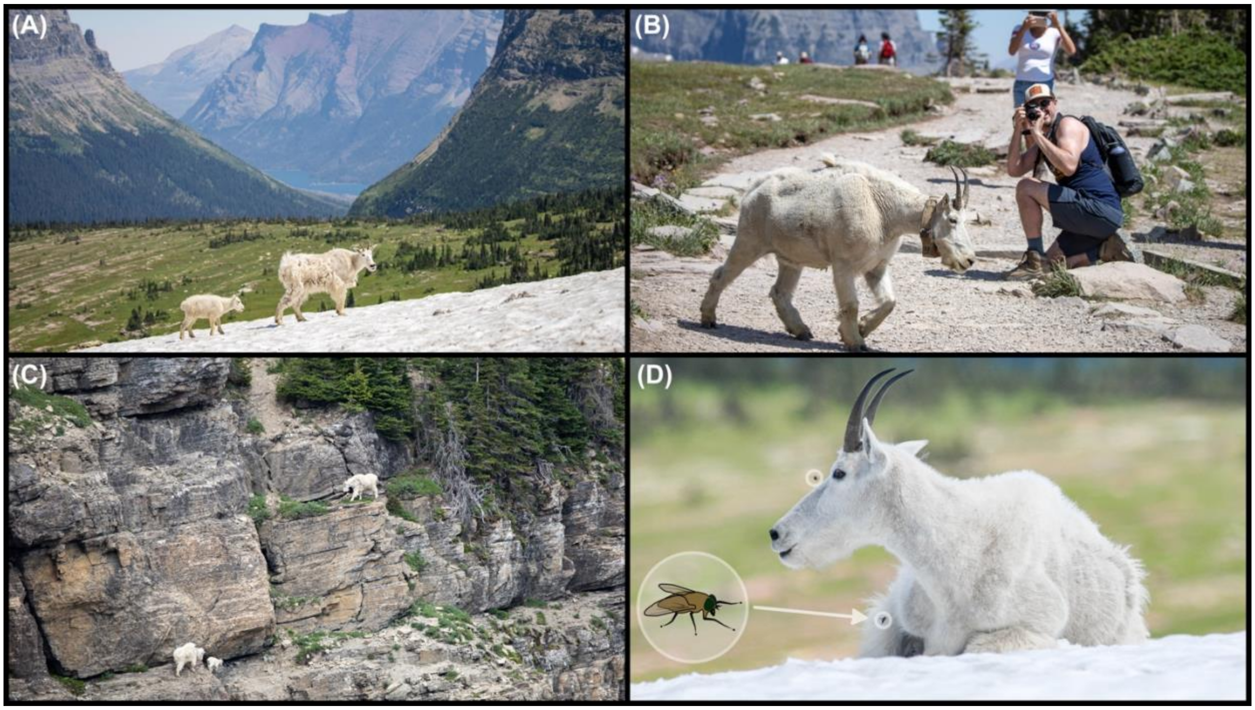

Figure 2.6. Key factors affecting resource selection by mountain goats. (A) elevation characteristics and, to a lesser extent, presence of snow. (B) presence of humans and anthropogenic resources (e.g., salt). (C) escape terrain and associated relative predation risk. (D) prevalence and disturbance by ectoparasitic insects. Photographs A, B, and C by Forest P. Hayes; D by Joel Berger.

Table 2.1. Selective cases representing numerous taxa of cold-adapted mammals employing behavioral responses to increased temperatures.

Common name	Latin name	Behavioral shift with increased temperature	Reference
Chamois	*Rupicarpa rupicarpa*	Reduced activity, upslope shift	Mason et al., 2014
Elk	*Cervus elaphus*	Increased use of shade	Merrill, 1991
Ibex	*Capra ibex*	Temporal change in activity, upslope shift	Aublet, et al., 2009
Ice rat	*Myotomys sloggetti*	Increased time in burrows	Hinze et al., 2006
Marmot	*Marmota flaviventris*	Reduced aboveground activity and foraging	Melcher et al., 1990
Moose	*Alces alces*	Temporal change in activity, use of thermal refuges	Dussault et al., 2004
Mountain goat	*Oreamnos americanus*	Upslope shift, avoidance of solar radiation	This study
Pika	*Ochotona princeps*	Temporal change in activity, use of cool crevices	Smith 2020

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CHAPTER 3 – INADVERTENT CLIMATE REFUGIA: UNTAPPED BENEFITS FOR CONSERVATION

SUMMARY

Rapidly warming climates are among the greatest challenges to the persistence of cold-adapted species. As the rapidity of climate change outpaces the ability of species to migrate or otherwise adapt to warming temperatures, assisted migration to areas offering climate refugia offer a key mechanism through which conservation can be accomplished. While few examples exist for assisted migration of mammals, humans have a long history of moving animals for other reasons. Herein, we capitalize on cases of anthropogenic species introductions to climate refugia – all outside of their native ranges – and the role these populations have played in species restoration and conservation. Stymieing current and future loss of biodiversity under climate change will likely require assisted migration of many species and necessitates novel valuation of introduced populations. Species moved generations ago into these refugia offer not only a reservoir for reintroductions but also a buffer against rapid shifts to suitable ranges.

INTRODUCTION

The ongoing extinction of species and resulting decline in global biodiversity is among the greatest long-term concerns for conservation (Barnosky et al., 2011; Ceballos et al., 2020). A key driver of species loss is unabated global climate change which is altering ecosystems at a rate that challenges the ability of species to adapt or relocate (Loarie et al., 2009; Bellard et al., 2012). Further, continued anthropogenic land conversion and habitat fragmentation decrease the possibility for species to make range shifts in pursuit of suitable climates (Kuipers et al., 2021). Addressing these threats is especially urgent for communities at high elevations and latitudes, which are warming at rates 2–5x faster than Earth's average (Pörtner et al., 2021). Moreover, many of the cold-adapted species (Table 3.1) which inhabit these environs have reduced tolerance for high temperatures and are limited in geographic range (e.g., Berger, 2018; Festa-Bianchet & Côté, 2008). Models of biodiversity indicate climate and anthropogenic impacts will result in catastrophic loss of species if the status quo continues (Caro et al., 2022; Morecroft et al., 2022), mandating an increase in proactive conservation (Wilkening et al., 2015). One tool for conservation of species is human-assisted migration (Table 3.1), however, the practice has been infrequently implemented, particularly for mammalian species, and remains controversial (Hewitt et al., 2011; Twardek et al., 2023).

Far more common are examples of species which have been introduced to novel regions across the globe for other reasons (Long, 2003). Many of these are to areas with favorable contemporary climates (Figure 3.1). The conservation value of these populations is largely unrealized but may prove an invaluable resource for ensuring the long-term persistence of these species.

Assisted migration

Although human-assisted migration as a conservation strategy in response to global climate change has only recently gained traction (e.g., Ste-Marie et al., 2011), humans have a long history of translocating wildlife for other reasons. Archeological evidence indicates long-distance transport of exotic wildlife by humans to Rome and Egypt around 2,500 BCE (MacKinnon, 2006). Far more recently and in greater number, many species have been translocated for the purpose of hunting and agriculture. The first clear recorded evidence of stocking wildlife is a delivery of 200 duck eggs for the purpose of propagation in 17th century England (Leopold, 1933). Over the past century alone, nearly 100 species have been introduced to Europe primarily for hunting purposes (Carpio et al., 2017). Today, agencies tasked with wildlife management routinely stock rivers and lakes with non-native species for recreational harvest (Eby et al., 2006; Halverson, 2008). Introduction of non-native terrestrial species is less frequent but not uncommon (Figure 3.1; Long 2003). In places like New Zealand and South Africa, the introductions have included Alpine chamois (*Rupicapra rupicapra*), wallabies (*Macropus* spp.), giraffes (*Giraffa camelopardalis*), and hedgehogs (*Erinaceus europaeus*) (Long, 2003).

Of concern whenever non-native species are introduced is the possibility they will become invasive (Mueller and Hellmann, 2008; Simberloff, 2013). Invasive species (Table 3.1) have become increasingly common as globalization has facilitated deliberate and unintentional introductions (Hulme, 2009). In North America, the number of species introduced has been closely correlated to the rate of human immigration from Europe (Jeschke and Strayer, 2005). As changing climate leads to geographical shifts in ecosystems, native species are likely to face increased competition from introduced species that are more strongly adapted to the contemporary local climate (Bradley, 2009). Moreover, evidence suggests that climate change will create progressively more favorable conditions for invasive species as altered climate may be more suitable for introduced species than native ones (Hiroyasu and Hellmann, 2019). Assisted migration is one mechanism through which species may be able to match shifts in geographic ranges with shifts in their climatic niche but understanding potential tradeoffs for native and introduced species will become increasingly important.

Assisted migration as a means of population restoration or the reestablishment of extirpated species to their historical ranges is no longer uncommon (Kleiman, 1989; Seddon et al., 2007). Among the first species for such endeavors were bison (*Bison bison*) beginning with their translocation to Oklahoma in 1907 (Kleiman, 1989; Hedrick, 2009). Reintroductions, especially of charismatic vertebrates, often garner broad public interest, including notable examples such as peregrine falcons (*Falco peregrinus*; Tordoff & Redig, 2001), Arabian oryx (*Oryx leucoryx;* Price, 1989), and gray wolves (Smith and Bangs, 2009). Not all reintroductions are successful; less than half of historical reintroductions of threatened, endangered, or sensitive species have resulted in established populations (Griffith et al., 1989). As ecoregions continue to shift due to climate change, restoration of ecosystems to historical ecological baselines may no longer be attainable (Kopf et al., 2015).

Far less common are examples of assisted migration as a means of facilitating range shifts or as a direct means of avoiding extinction. In one such case, cold-adapted trees (whitebark pine, *Pinus albicaulis*) have been successfully translocated to higher latitudes to avoid their extirpation under projected climate change (McLane and Aitken, 2012). In another, Owens pupfish (*Cyprinodon radiosus*) were rescued from sure extinction – in a bucket, solely by Phil Pister – by translocation to a nearby riparian area (Pister, 1993). Conversely, a few meager attempts at translocating American pika (*Ochotona princeps*), a cold-adapted species, have had only mixed success (Bunnell and Johnson, 1974; Wilkening et al., 2015).

Cold-adapted species

Numerous cold-adapted species are already geographically limited to areas of high elevations and latitudes. Even those of Holarctic distributions (e.g., moose, *Alces alces*) may experience thermal stress at what are relatively low temperatures (Renecker and Hudson, 1990). In response to warming climes species have already begun to shift in distribution to higher elevation and latitude (Parmesan, 2006). Fine-scale behavioral shifts in avoidance of increasing temperatures are also increasingly apparent (e.g., Aublet et al. 2009; Hayes, Chapter 2 of this dissertation). However, increasingly fragmented habitat and anthropogenic barriers to movement may greatly inhibit movement and dispersal (Fletcher et al., 2018). Additionally, isolation of suitable habitat, such as high-elevation mountain peaks separated by unsuitable habitat, often preclude natural movement between locales under current climate conditions (Suzette and Hooghiemstra, 2018). As global temperatures continue to warm, with especially pronounced changes in montane regions, the persistence of many cold-adapted species within historic ranges will be challenged.

Historic range recession and regional extirpation of cold-adapted species are well evidenced by fossils from the warming Holocene. Representatives from at least four mammalian taxa (mountain goat, *Oreamnos americanus*; pika; marmot, *Marmota flaviventris*; and weasel, *Mustela nivalis*) occurred at lower latitude and elevation during cooler epochs and became extirpated with increasing temperatures (Grayson 2011; Hayes, Chapter 1 of this dissertation). Their continued existence in isolated communities of cooler climes today indicates successful persistence within *in situ* refugia (Table 3.1) or shifts to geographies with suitable climate. Although this provides evidence of persistence during periods of warming, the rate of contemporary climate change far exceeds historical ones (e.g., during the Holocene; IPCC, 2022). Moreover, human land use has greatly reduced the availability of suitable habitat (Caro et al., 2022) and, where it exists, and fragmentation and barriers to movement may still preclude access by species. The difficulty for contemporary species to respond to rapidly changing climates – and uncertainty in ability for species to adapt – is subject to great concerns and has prompted increased focus on proactive biodiversity conservation.

Inadvertent climate refugia

Rather than reintroducing species to their historic range, in some cases conservation of biodiversity may be better achieved through introduction of species to novel areas with climates more closely matching historical conditions. In these environments populations may safely be propagated and later used to enhance conservation back in native areas (but see below for potential negative impacts). For three species – mountain goats, muskoxen (*Ovibos moschatus*) and bison – populations have already been established in areas outside their historic range where climates have proved favorable. Such exemplars highlight the conservation value of human-assisted migration in establishing populations of cold-adapted species outside of historic ranges – even when conservation was not the primary goal.

Human translocation of wildlife, with varied intents but none associated with climate, has resulted in inadvertent climate refugia (Table 3.1). In the three cases we highlight, each species was introduced to latitudes or elevations that differ from that of their native distributions. These locales have often been far from natural populations and span distances or habitats which would make natural dispersal highly unlikely if not impossible, such as beavers (*Castor canadensis*) to Patagonia or Himalayan tahr (*Hemitragus jemlahicus*) to New Zealand. In North America, the introduction of mountain goats to Colorado – some at elevations exceeding 4,000 m – is a case in point and has resulted in a distribution to lower latitudes and to substantially higher elevation.

WHAT IS THE CONSERVATION VALUE OF INADVERTENT REFUGIA?

While translocations out of a species range allow for their persistence, it is incumbent to know if any of these hold conservation value. We suggest at least two benefits arise from species moved to inadvertent refugia: 1) establishment of robust populations for species which are experiencing population declines within their historic ranges and 2) providing genetic reservoirs and source populations for species restoration. However, we note that introduction of species outside their native range can have additional unintended consequences (Simberloff and Stiling, 1996; Pearson et al., 2022). We offer three cases of species introductions into climate refugia – all outside of their natural range and with benefits to conservation.

Mountain goats

As an endemic to North America, this caprine is limited continentally to northwestern montane and periglacial regions. Notably, they have been introduced at high elevation south of their native distributions where they have now colonized national parks (Grand Teton, Yellowstone) and to numerous locations in Colorado, Utah, and Nevada (Festa-Bianchet and Côté, 2008). There is increasing concern about the persistence of marginal and low-elevation populations (Abeli et al., 2018) as recent and continued warming is predicted to decrease survival (White et al., 2018). Their strong association with periglacial regions and adaptations to cold raises further concern about their long-term persistence within their historic range (Déry et al., 2019; Hayes, Chapter 1 of this dissertation).

Among the earliest introduction of the species to a novel environment was to the Olympic Mountain range in Washington state during the 1920s, prior to the establishment of Olympic National Park (Moorhead and Stevens, 1982). Mountain goats subsequently spread throughout the Olympic Mountains, raising concerns over the growing ecological impacts of the nonnative population (Happe et al., 2020). During 2018–2020, the park embarked on removing 90% of the extant population (Happe et al., 2020). Of the mountain goats removed, 326 were relocated to other areas in the Cascades where native goats were in low abundances due, in part, to anthropogenic activity (Harris et al., 2020). These translocations serve as an example of how an inadvertent refuge with suitable climate has facilitated restoration of the species within its native range.

Muskoxen

Muskoxen have a circumpolar distribution in the northern hemisphere except in Europe, and are primarily limited to Arctic tundra habitats (Cuyler et al., 2020). Historic populations were more broadly distributed but declined following the retreat of glaciers in the Holocene and the last native populations in Alaska were extirpated by the early 1900s (Gunn and Adamczewski, 2003). Notably, muskoxen abundance is positively associated with cold and dry climate conditions (Lent, 1999) but experience high mortality during rain-on-snow events, which are becoming increasingly common (Berger et al., 2018).

Muskoxen were introduced outside their modern native range to Nunivak Island in southwestern Alaska in the 1930s. Because the species had been hunted to extinction in Alaska, the intent was to reintroduce the species, primarily for hunting and for food (Spencer and Lensink, 1970). The population on Nunivak grew steadily and stabilized at ~500 individuals. The Nunivak founders have now been reintroduced to other areas of Arctic Alaska (Wald, 2009) with all ~4,000 muskoxen descended from the single introduction outside their native range (Cuyler et al., 2020), as well as the one on Wrangel Island, Chukotka, Russia (Berger et al., 2018). The deliberate restoration effort of a population highlights the high potential conservation value of *ex situ* climate refuges.

American bison

Bison were formerly widespread across much of North America but largely extirpated by human hunting. Today they occur as geographically isolated populations (Sanderson et al., 2008). Bison were transplanted outside their historically native range to the Henry Mountains in Utah between 1941–1942 from a source population in Yellowstone National Park (Van Vuren and Bray, 1986). There is no evidence that they previously occupied the region (Berger and

Cunningham, 1994), and the introduction there was to establish a harvestable population (Nelson, 1965).

Relevant from a conservation perspective, bison from the introduced Henry Mountain population were translocated back to native areas on the Uintah and Ouray Reservation by the Ute Indian Tribe (Utah Wildlife Board, 2007). This reintroduction– from a refuge at higher elevation – has aided in the continued restoration of the species, which has high cultural value for indigenous and other Americans (Plumb and Sucec, 2006). As efforts mount to expand restoration of the species to formerly occupied reaches (USDOI Order #3410, 2023), the presence of multiple source populations will facilitate this endeavor.

CONCLUSIONS

As suitable habitat for many species shifts geographically, climate refugia will play a key role in determining future distributions whether species are rare, threatened, or otherwise declining (Ceballos and Ehrlich, 2002; Rosenberg et al., 2019; Wagner et al., 2021). As these shifts occur, restoration of diminished or extirpated populations to historic ranges will become increasingly difficult and less likely to succeed (Thorpe and Stanley, 2011), except perhaps to the more climate-appropriate parts of ranges or to *ex situ* climate refugia. This latter tact will have conservation benefit for the species itself but will entail unknown ecological consequence at the community level. Such introductions necessitate serious planning discussions, as has been the case for whitebark pine and certain extensions for cold-adapted fish (Harig et al., 2000; McLane and Aitken, 2012). Inadvertent climate refugia have netted conservation value for a few large mammals (Figure 3.2), but the majority of organisms vulnerable to warming temperatures in their native habitats has only recently become part of the discussion.

Despite clear conservation value, much trepidation persists about assisted migration and the consequences of introducing non-native species (Hewitt et al., 2011). A cursory understanding of the environmental impacts of the Emerald ash borer (*Agrilus planipennis*), Burmese python (*Python bivittatus*), or wild pig (*Sus scrofa*) illustrates potential hazards (Herms and McCullough, 2014; Strickland et al., 2020; Guzy et al., 2023), though none of these species were introduced for ecological benefit**.** Additionally, changing climate conditions may increase rates of interspecific conflict (Berger et al., 2022). However, the majority of introduced species are not highly disruptive (Simberloff, 2013). If species are introduced for their ecological benefits, we must be mindful of balancing the needs of already climate-stressed native species.

As Earth's climate continue to warm, there is a clear need to reassess management of species based solely on historical baselines – which may no longer reflect current ecological realities (Lovejoy and Hannah, 2019). While assisted migration remains controversial (Hewitt et al., 2011), many similar translocations have already taken place (Figure 3.1), although often without the direct intent to conserve biodiversity. The conservation value of these introduced populations is largely untapped in efforts to mitigate unprecedented climate challenges and loss of biodiversity.

We have identified not only the anthropogenic creation of inadvertent refugia for cold-adapted species but also realized conservation benefit for at least three cold-adapted mammals. There are certainly additional cases in need of reporting but the more pressing issue for future generations is how to structure realistic plans for the management of biological diversity and organisms that dictate a system's ecological dynamics and ultimately human endurance. Increased recognition is needed of both already realized value (and costs) of species introductions and the even greater potential for conservation benefit, especially when translocations are to be conducted with a conservation goal.

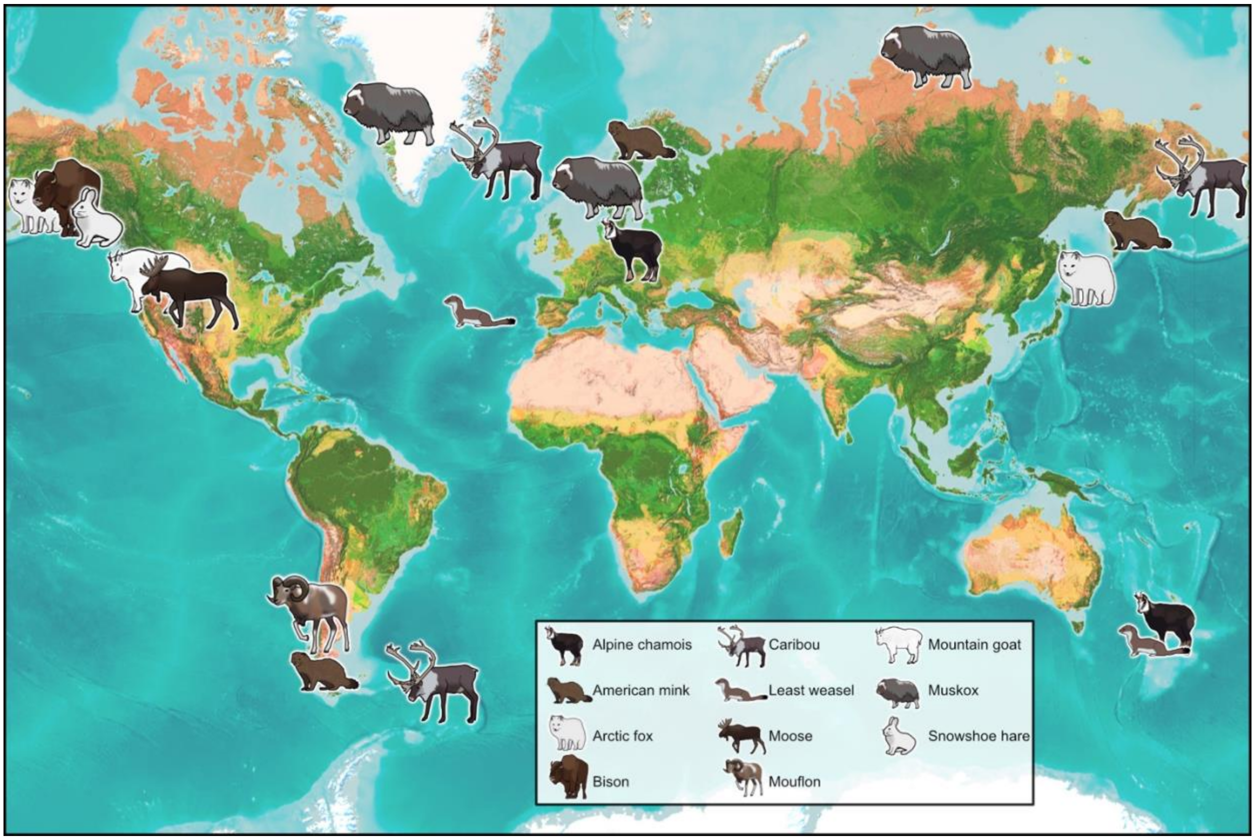

Figure 3.1. Humans have introduced many cold-adapted mammal species to geographies with favorable climates outside of native distributions. Globally highlighted extant introduced populations are shown on this map, depicted by icons for each species. Species, regions, and references are provided in Table S3.2.

Figure 3.2. Examples of conservation success – species which have been introduced to climate refugia and later used to restore or bolster populations in native ranges. (A) Bison, (B) mountain goats, (C) muskoxen. Photographs A and B by Forest P. Hayes, C by Joel Berger.

Table 3.1. Operational definitions for key terms.

Term	Definition	Reference
Cold-adapted species	Species that occur and persist at high elevations and/or latitudes. *Although distributions of many cold-adapted species are limited to specific climatic conditions, others may be more broadly distributed at lower elevation or more southerly latitudes.*	
Assisted migration	The purposeful movement of species to facilitate or mimic natural range expansion as a direct management response to climate change. *This term includes both translocation with the intent of hastening return or repopulation of a species within historic ranges and the translocation of species to areas outside their range.*	Vitt et al., 2010
Invasive species	Species which have been recently introduced and exert substantial negative impacts on other biota. *A more simplistic definition would be "introduced species that establish and spread," however, climate change will cause range shifts in both native and introduced species and alter the balance of positive and negative impacts, thus we characterize invasive species as only those with substantial negative impacts.*	Hellmann et al., 2008
Climate refugia	An area or region that is large enough to sustain a population that provides suitable conditions for populations/species during periods of climate change. *These may include both in situ refugia (a subset of currently occupied areas) and ex situ refugia (areas with favorable habitat which were not previously occupied by the species). In this manuscript we focus on refugia from anthropogenic climate change (i.e., as opposed to refugia during glacial or interglacial periods).*	Ashcroft 2010
Inadvertent refugia	An *ex situ* climate refugia which was not established by naturally dispersing populations or through assisted migration.	This paper

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SUPPLEMENTAL MATERIALS

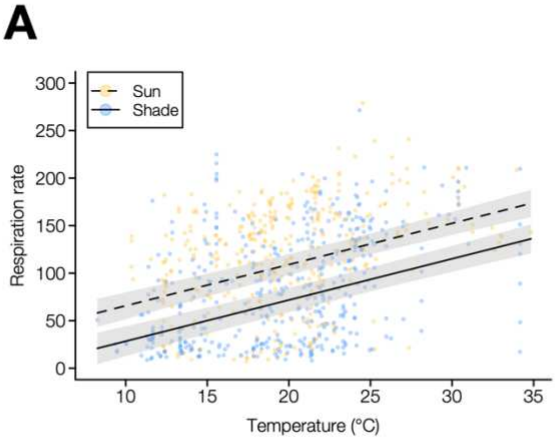


Figure S1.5. Estimated biological effects of respiration rate in response to A) temperature and B) percent of winter coat shed. Points represent *in situ* measurements of respiration and explanatory variables. Lines represent modeled respiration response based on temperature and percent of winter coat in and out of direct sun, shaded regions represent 95% credible intervals.

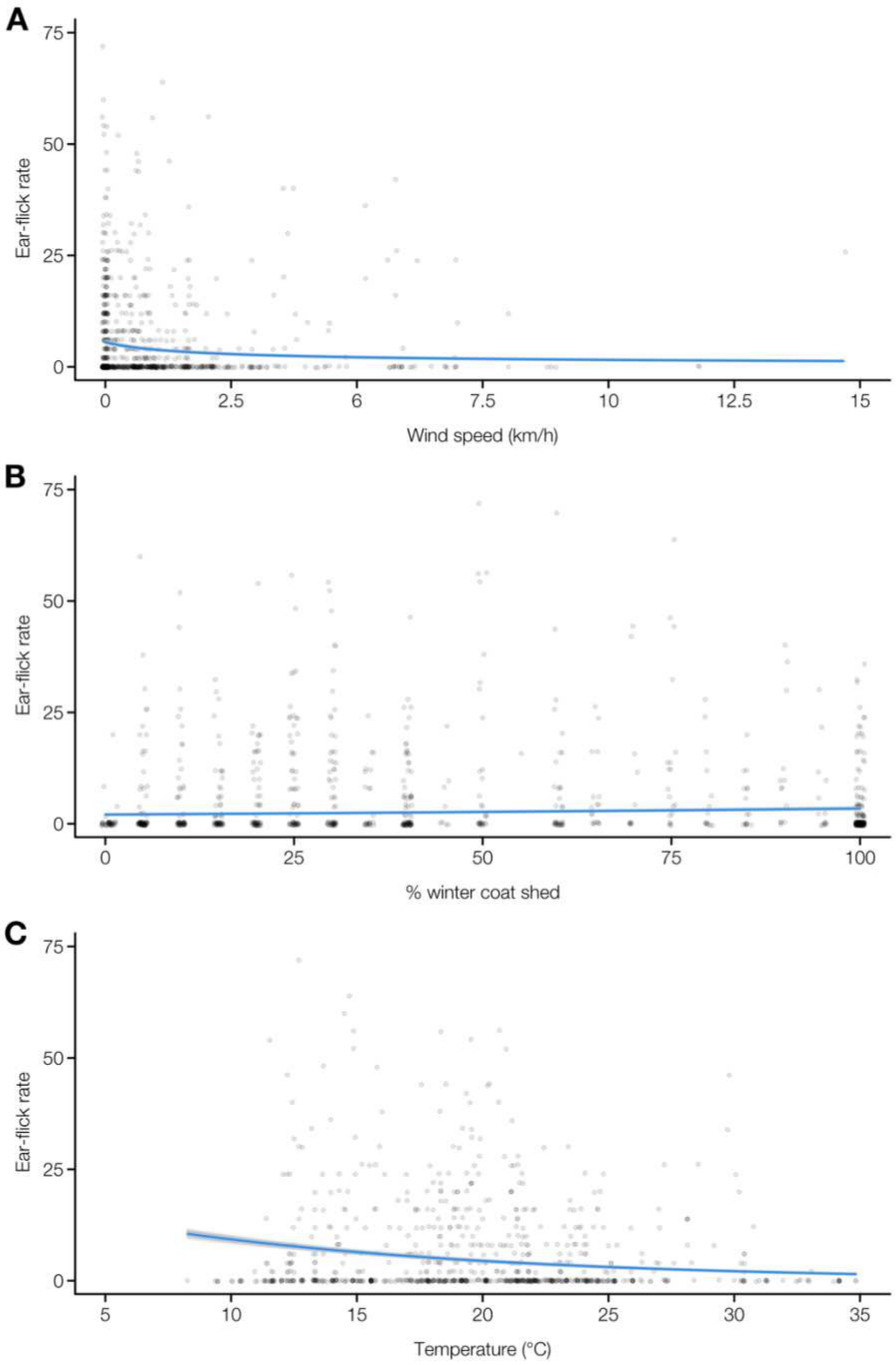


Figure S1.6. Estimated biological effects of ear-flick rate (number of ear-flicks per ear per minute) in response to A) wind speed, B) percent of winter coat shed, and C) temperature. Points represent *in situ* measurements of ear-flick rate and explanatory variables. Lines represent modeled ear-flick response based on wind speed, % of winter coat shed, and temperature. Shaded regions represent 95% credible intervals.

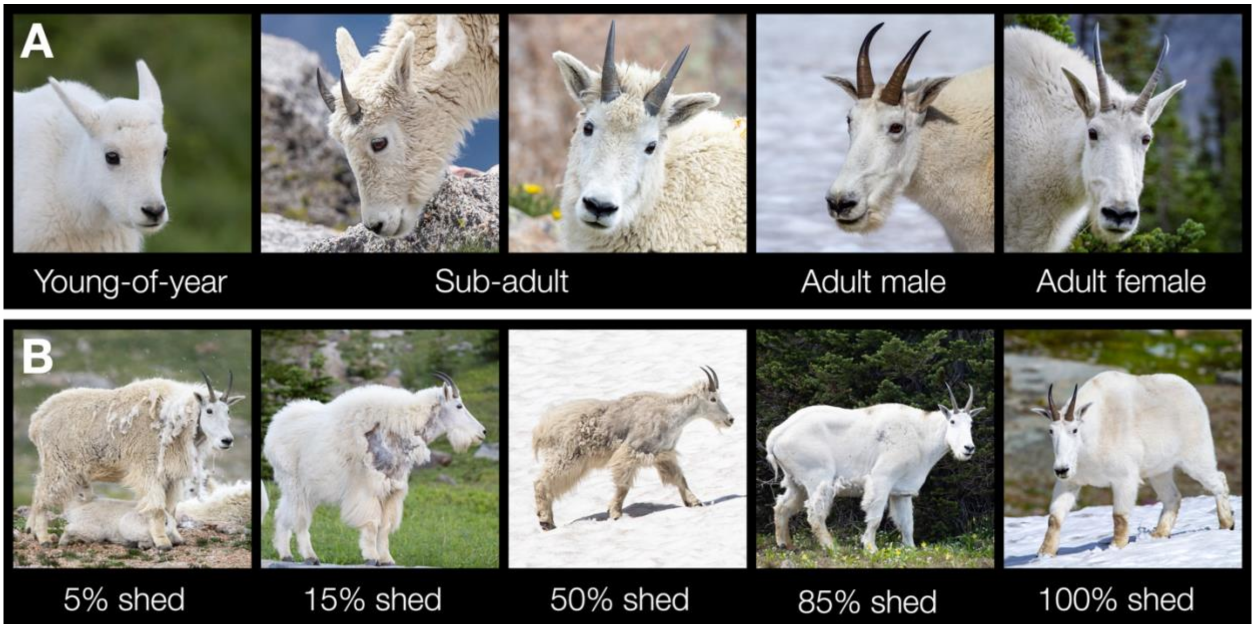
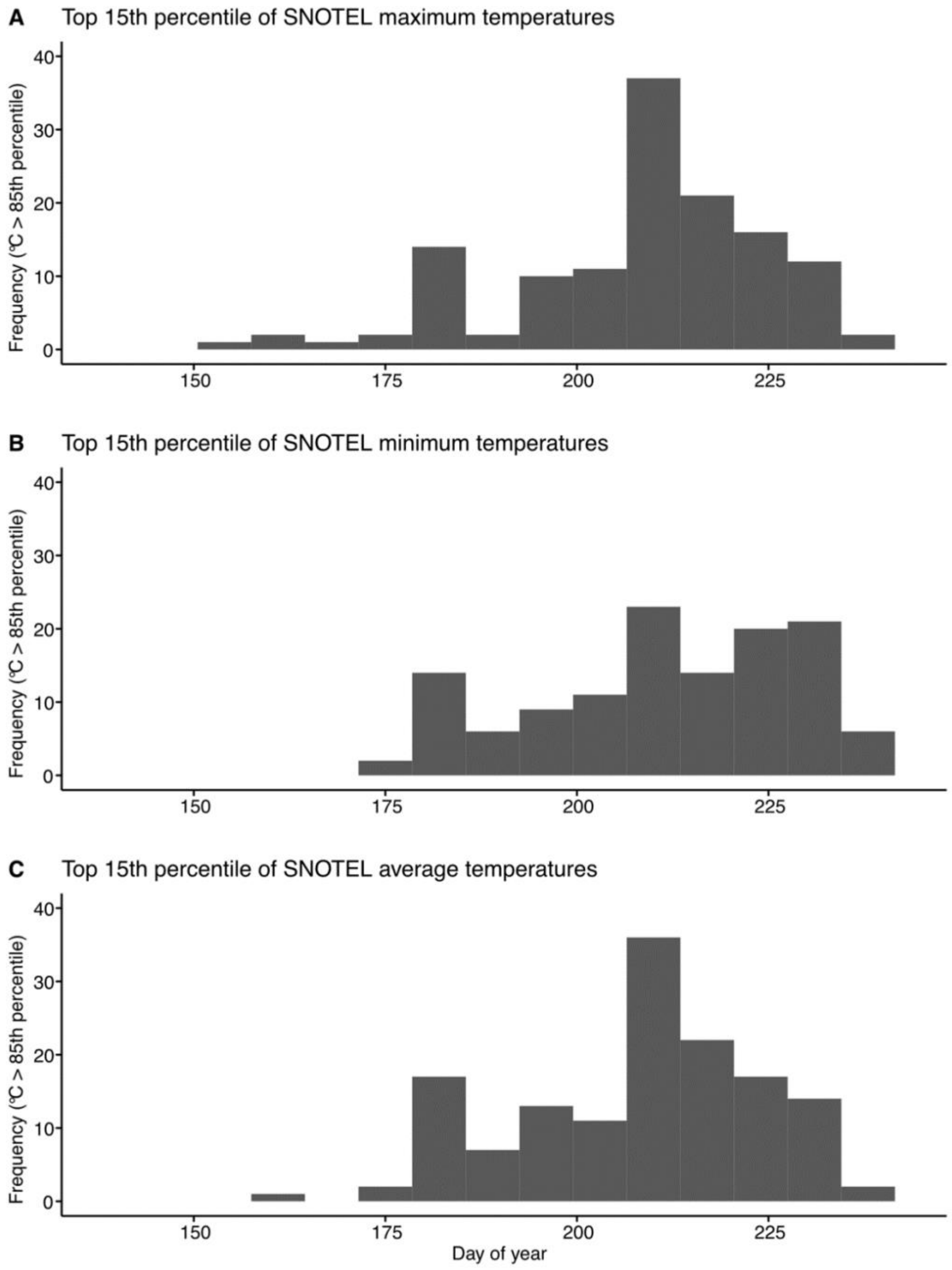


Figure S1.7. A) Classification categories for age and sex of mountain goats. Individuals classified as either young-of-year (< 1 year old), sub-adult (1 or 2 years old), adult male (≥ 3 years old) or adult female (≥ 3 years old). B) Examples of estimated percent of winter coat shed.



Top 15th percentile of SNOTEL maximum temperatures

Top 15th percentile of SNOTEL minimum temperatures

Top 15th percentile of SNOTEL average temperatures

Figure S2.7. Comparison of metrics that reflect the warmest periods of year (temperatures > 85th percentile). Data are from (SNOTEL #482; 48.8° N, −113.85° W). Counts represent the frequency of days during each 7-day period during 2013–2016 and 2018–2022 which were identified as being in the top 15th percentile. (A) days identified using daily maximum temperature. (B) days identified using daily minimum temperatures. (C) days identified using daily average temperatures.

Table S1.2. Information on fossil location for mountain goats (*Oreamnos americanus* and *Oreamnos harringtoni*), pika (*Ochotona princeps*), marmot (*Marmota flaviventris*) and weasel (*Mustela nivalis*). Site, geographic coordinates, age, and literature citations were obtained from the FAUNAP database (Graham and Lundelius, 1994).

Species	Site	Longitude	Latitude	Min age	Max age	Citation
Oreamnos americanus	Adrian Valley [LACM 6228]	-119.22194	39.15556	35000	400000	Jefferson, G.T., H.G. McDonald, and S.D. Livingston. 2004. Catalogue of Late Quaternary and Holocene fossil vertebrates from Nevada. Occasional Papers 6. Nevada State Museum, Carson City, Nevada, USA.
Oreamnos americanus	Bell Cave [48AB304]	-105.36667	41.75	10000	13500	Walker, D. N. 1987. Late Pleistocene/Holocene environmental changes in Wyoming: the mammalian record. Pages 334-393 in Late Quaternary mammalian biogeography and environments of the Great Plains and prairies (R. W. Graham, H. A. Semken, Jr., and M. A. Graham, editors), Illinois State Museum Scientific Papers 22.
Oreamnos americanus	Bell Cave [48AB304]	-105.36667	41.75	10000	13500	Zeimans, G., and D. N. Walker. 1974. Bell Cave, Wyoming: preliminary archaeological and paleontological investigations. Wyoming Geological Survey, Report of Investigations 10:88-90.
Oreamnos americanus	Horned Owl Cave [48AB305]	-105.51667	41.56667	10000	35000	Gebhard, D., D. A. Agogino, and V. Haynes. 1964. Horned Owl Cave, Wyoming. American Antiquity 29(3):360-368.
Oreamnos americanus	Horned Owl Cave [48AB305]	-105.51667	41.56667	10000	35000	Guilday, J. E., H. W. Hamilton, and E. K. Adam. 1967. Animal remains from Horned Owl Cave, Albany County, Wyoming. Contributions to Geology, University of Wyoming 6(2):97-99.
Oreamnos americanus	Horned Owl Cave [48AB305]	-105.51667	41.56667	10000	35000	Walker, D. N. 1987. Late Pleistocene/Holocene environmental changes in Wyoming: the mammalian record. Pages 334-393 in Late Quaternary mammalian biogeography and environments of the Great Plains and prairies (R. W. Graham, H. A. Semken, Jr., and M. A. Graham, editors), Illinois State Museum Scientific Papers 22.
Oreamnos americanus	Potter Creek Cave [5357,1055]	-122.28083	40.78389	11500	110000	Kurtén, B.O.L, and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York, New York, USA.
Oreamnos americanus	Potter Creek Cave [5357,1055]	-122.28083	40.78389	11500	110000	Lundelius, E. L., Jr., R. W. Graham, E. Anderson, J. Guilday, J. A. Holman, D. W. Steadman, and S. D. Webb. 1983. Terrestrial vertebrate faunas. Pages 311-353 in Late-Quaternary environments of the United States: volume 1, The late Pleistocene (S. C. Porter, editor), University of Minnesota Press, Minneapolis, Minnesota, USA.
Oreamnos americanus	Potter Creek Cave [5357,1055]	-122.28083	40.78389	11500	110000	Stock, C. 1918. The Pleistocene fauna of Hawver Cave. University of California Publications, Bulletin of the Department of Geology 10(24):462-515.
Oreamnos americanus	Samwel Cave	-122.2318	40.9171	19063	25605	Harris, A.H. 1985. Late Pleistocene Vertebrate Paleoecology of the West. University of Texas Press, Austin, Texas, USA.
Oreamnos americanus	Samwel Cave	-122.2318	40.9171	19063	25605	Feranec, R.S., E.A. Hadley, J.L. Blois, A.D. Barnosky, and A. Paytan. 2007. Radiocarbon dates from the Pleistocene fossil deposits of Samwel Cave, Shasta County, California, USA. Radiocarbon 49(Nr 1):117-121.
Oreamnos americanus	Samwell Cave	-122.23787	40.91691	11500	110000	Kurtén, B.O.L, and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York, New York, USA.
Oreamnos americanus	Samwell Cave	-122.23787	40.91691	11500	110000	Furlong, E.L. 1906. The exploration of Samwel Cave. American Journal of Science 22:235-247.
Oreamnos americanus	Samwell Cave	-122.23787	40.91691	11500	110000	Lundelius, E. L., Jr., R. W. Graham, E. Anderson, J. Guilday, J. A. Holman, D. W. Steadman, and S. D. Webb. 1983. Terrestrial vertebrate faunas. Pages 311-353 in Late-Quaternary environments of the United States: volume 1, The late Pleistocene (S. C. Porter, editor), University of Minnesota Press, Minneapolis, Minnesota, USA.
Oreamnos americanus	Samwell Cave	-122.23787	40.91691	11500	110000	Payen, L. A., M. C. Hall, and M. D. Kelley. 1978. Radiocarbon and obsidian hydration studies of Samwell Cave. American Quaternary Association Abstracts, 5th Biennial Meeting, University Alberta, Edmonton.
Oreamnos harringtoni	Booth Canyon Local Fauna	-111.12889	43.29972	11800	29000	Anderson, E. 1998. Quaternary wolverines (Gulo gulo) from Idaho. Pages 173-185 in W.A. Akerston, H.G. McDonald, D.J. Meldrum, and M.E.T. Flint, editors. And whereas ... Papers on the vertebrate paleontology of Idaho honoring John A. White, Volume 1. Occasional Paper 36. Idaho Museum of Natural History, Pocatello, Idaho, USA.
Oreamnos harringtoni	Booth Canyon Local Fauna	-111.12889	43.29972	11800	29000	Mead, J.I., and M.C. Lawler. 1994. Skull, mandible, and metapodials of the extinct Harrington's mountain goat (Oreamnos harringtoni). Journal of Vertebrate Paleontology 14(4):562-576.
Oreamnos harringtoni	Booth Canyon Local Fauna	-111.12889	43.29972	11800	29000	Akersten, W.A., S.J. Miller, and C.A. Repenning. 2002. The Booth Canyon Local Fauna, a depauperate mammalian assemblage from the Late Pleistocene of eastern Bonneville County, Idaho. Pages 101-130

						in W.A. Akersten, M.E. Thompson, D.J. Meldrum, R.A. Rapp, and H.G. McDonald, editors. And Whereas,Ä¶Papers on the Vertebrate Paleontology of Idaho Honoring John A. White, Volume 2. Occasional paper 37. Idaho Museum of Natural History, Pocatello, Idaho, USA.
Oreamnos harringtoni	Chuar Valley Midden 8b	-111.91667	36.18333	18000	19600	Cole, K., and J.I. Mead. 1981. Late Quaternary animal remains from packrat middens in the eastern Grand Canyon, Arizona. Journal of the Arizona-Nevada Academy of Science 16:24-25.
Oreamnos harringtoni	Chuar Valley Midden 8b	-111.91667	36.18333	18000	19600	Mead, J. I. 1981. The last 30,000 years of faunal history within the Grand Canyon, Arizona. Quaternary Research 15:311-326.
Oreamnos harringtoni	Hooper's Hollow [873]	-110.86667	37.25	10630	18840	Mead, J. I., and L. D. Agenbroad. 1992. Isotope dating of Pleistocene dung deposits from the Colorado Plateau Arizona and Utah. Radiocarbon 34(1):1-19.
Oreamnos harringtoni	Muskox Cave	-104.5	32.11667	1	35000	Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin.
Oreamnos harringtoni	Muskox Cave	-104.5	32.11667	1	35000	Logan, L. E. 1981. The mammalian fossils of Muskox Cave, Eddy County, New Mexico. Proceedings Eighth International Congress of Speleology 1:159-160.
Oreamnos harringtoni	Muskox Cave	-104.5	32.11667	1	35000	Jass, C. N., J. I. Mead, and L. E. Logan. 2000. Harrington's extinct mountain goat (Oreamnos harringtoni Stock 1936) from Muskox Cave, New Mexico. Texas Journal of Science 52(2):121-132.
Oreamnos harringtoni	Natural Bridges National Monument	-110	37.5	22000	25000	Mead, J.I., L.D. Agenbroad, A.M. Phillips III, and L.T. Middleton. 1987. Extinct mountain goat (Oreamnos harringtoni) in southeastern Utah. Quaternary Research 27(3):323-331. [DOI: 10.1016/0033-5894(87)90087-1]
Oreamnos harringtoni	Rampart Cave	-113.93333	36.1	13000	11000	Hansen, R. M. 1978. Shasta ground sloth food habits, Rampart Cave, Arizona. Paleobiology 4:302-319.
Oreamnos harringtoni	Rampart Cave	-113.93333	36.1	13000	11000	Long, A., and P.S. Martin. 1974. Death of American ground sloths. Science 186:638-640..
Oreamnos harringtoni	Rampart Cave	-113.93333	36.1	13000	11000	Martin, P. S., B. E. Sabels, and D. Shutler, Jr. 1961. Rampart Cave coprolite and ecology of the Shasta ground sloth. American Journal of Science 259:102-127.
Oreamnos harringtoni	Rampart Cave	-113.93333	36.1	13000	11000	Mead, J. I. 1981. The last 30,000 years of faunal history within the Grand Canyon, Arizona. Quaternary Research 15:311-326.
Oreamnos harringtoni	Rampart Cave	-113.93333	36.1	13000	11000	Mead, J. I., L. D. Agenbroad, O. K. Davis, and P. S. Martin. 1986. Dung of Mammuthus in the arid southwest, North America. Quaternary Research 25:121-127.
Oreamnos harringtoni	Rampart Cave	-113.93333	36.1	13000	11000	Van Devender, T. R., A. M. Phillips, III, and J. I. Mead. 1977. Late Pleistocene reptiles and mammals from the lower Grand Canyon of Arizona. Southwestern Naturalist 22:49-66.
Oreamnos harringtoni	Smith Creek Cave [26WP46]	-114.08333	39.33333	12600	35000	Bryan, A. L. 1979. Smith Creek Cave. Pages 164-251 in The archaeology of Smith Creek Canyon, eastern Nevada (D. R. Tuohy and D. L. Rendall, editors), Nevada State Museum Anthropological Papers 17.
Oreamnos harringtoni	Smith Creek Cave [26WP46]	-114.08333	39.33333	12600	35000	Mead, J.I., C.J. Bell, and L.K. Murray. 1992. Mictomys borealis (northern bog lemming) and the Wisconsin paleoecology of the east-central Great Basin. Quaternary Research 37(2):229-238. [DOI: 10.1016/0033-5894(92)90084-V]
Oreamnos harringtoni	Smith Creek Cave [26WP46]	-114.08333	39.33333	12600	35000	Mead, J. I., R. S. Thompson, and T. R. Van Devender. 1982. Late Wisconsinan and Holocene fauna from Smith Creek Canyon, Snake River Range, Nevada. Transactions of the San Diego Society of Natural History 20(1):1-26.
Oreamnos harringtoni	Stanton's Cave [Ariz C:5:3]	-111.83333	36.5	1	17300	Euler, R.C., editor. 1984. The archaeology, geology and paleobiology of Stanton's Cave. Grand Canyon Natural History Association Monograph 6.
Oreamnos harringtoni	Stanton's Cave [Ariz C:5:3]	-111.83333	36.5	1	17300	Harington, C. R. 1984. Ungulate remains from Stanton's Cave and identification list. Pages 69-75 in The archaeology, geology, and paleobiology of Stanton's Cave (R. C. Euler, editor), Grand Canyon Natural History Association, Monograph No. 6.
Oreamnos harringtoni	Stanton's Cave [Ariz C:5:3]	-111.83333	36.5	1	17300	Mead, J. I., L. D. Agenbroad, O. K. Davis, and P. S. Martin. 1986. Dung of Mammuthus in the arid southwest, North America. Quaternary Research 25:121-127.
Oreamnos harringtoni	Stanton's Cave [Ariz C:5:3]	-111.83333	36.5	1	17300	Olsen, J. W., and S. J. Olsen. 1984. Zooarchaeological analysis of small vertebrates from Stanton's Cave, Arizona. Pages 49-57 in The archaeology, geology, and paleobiology of Stanton's Cave (R. C. Euler, editor), Grand Canyon Natural History Association, Monograph 6.
Oreamnos harringtoni	Stanton's Cave [Ariz C:5:3]	-111.83333	36.5	1	17300	Robbins, E. I., P. S. Martin, and A. Long. 1984. Paleoecology of Stanton's Cave. Pages 115-130 in The archaeology, geology, and paleobiology of Stanton's Cave (R. C. Euler, editor), Grand Canyon Association Monograph 6.
Oreamnos harringtoni	Tse'an Bida Cave	-111.95	36	11000	13000	Mead, J. I. 1981. The last 30,000 years of faunal history within the Grand Canyon, Arizona. Quaternary Research 15:311-326.
Oreamnos harringtoni	Tse'an Bida Cave	-111.95	36	11000	13000	Mead, J. I., L. D. Agenbroad, O. K. Davis, and P. S. Martin. 1986. Dung of Mammuthus in the arid southwest, North America. Quaternary Research 25:121-127.

Oreamnos harringtoni[*]	San Josecito Cave	-99.91	23.95	11000	40000	Jachowski, D., Kays, R., Butler, A., Hoylman, A. M., and Gompper, M. E. (2021). Tracking the decline of weasels in North America. PLoS ONE 16, e0254387. doi: 10.1371/journal.pone.0254387.
Oreamnos harringtoni[*]	U-Bar Cave	-108.4337	31.4745	25000	40000	Harris, A. H. (1993). Quarternary vertebrates of New Mexico. *New Mexico Museum of Natural History and Science, Bulletin* 2, 179–198.
Ochotona princeps	Antelope Cave [SBC1.10.10]	-115.5	35.36667	10000	20000	Jefferson, G.T. 1991. Rancholabrean age vertebrates from the Southeastern Mojave Desert, California. Pages 163-175 in R.E. Reynolds and J. Reynolds, editors. Crossing the borders: Quaternary studies in eastern California and Southwestern Nevada. Special Publication. San Bernardino County Museum Association, Redlands, California, USA.
Ochotona princeps	Antelope Cave [SBC1.10.10]	-115.5	35.36667	10000	20000	Reynolds, R. E., R. L. Reynolds, C. J. Bell, and B. Pitzer. 1991. Vertebrate remains from Antelope Cave, Mescal Range, San Bernardino County, California. Pages 107-109 in Crossing the borders: Quaternary studies in eastern California and southwestern Nevada (R. E. Reynolds, editor), San Bernardino County Museum Association, Redlands.
Ochotona princeps	Arch Cave	-114.08333	39.11667	34040	34040	Grayson, D.K. 1987. The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years. Journal of Mammalogy 68(2):359-375.
Ochotona princeps	Bell Cave [48AB304]	-105.36667	41.75	10000	13500	Walker, D. N. 1987. Late Pleistocene/Holocene environmental changes in Wyoming: the mammalian record. Pages 334-393 in Late Quaternary mammalian biogeography and environments of the Great Plains and prairies (R. W. Graham, H. A. Semken, Jr., and M. A. Graham, editors), Illinois State Museum Scientific Papers 22.
Ochotona princeps	Bell Cave [48AB304]	-105.36667	41.75	10000	13500	Zeimans, G., and D. N. Walker. 1974. Bell Cave, Wyoming: preliminary archaeological and paleontological investigations. Wyoming Geological Survey, Report of Investigations 10:88-90.
Ochotona princeps	Corn Creek Spring, Corn Creek PR 3, Las Vegas Valley	-115.35722	36.43917	13500	15100	Jefferson, G.T., H.G. McDonald, and S.D. Livingston. 2004. Catalogue of Late Quaternary and Holocene fossil vertebrates from Nevada. Occasional Papers 6. Nevada State Museum, Carson City, Nevada, USA.
Ochotona princeps	Council Hall Cave [26WP229]	-114.16667	39.33333	4220	23900	Bryan, A. L. 1979. Council Hall Cave. Pages 257-268 in The archaeology of Smith Creek Canyon, eastern Nevada (D. R. Tuohy and D. L. Rendall, editors), Nevada State Museum Anthropological Papers 17.
Ochotona princeps	Council Hall Cave [26WP229]	-114.16667	39.33333	4220	23900	Mead, J. I., R. S. Thompson, and T. R. Van Devender. 1982. Late Wisconsinan and Holocene fauna from Smith Creek Canyon, Snake River Range, Nevada. Transactions of the San Diego Society of Natural History 20(1):1-26.
Ochotona princeps	Council Hall Cave [26WP229]	-114.16667	39.33333	4220	23900	Miller, S. J. 1979. The archeological fauna of four sites in Smith Creek Canyon. Pages 273-329 in The archeology of Smith Creek Canyon, eastern Nevada (D. R. Tuohy and D. L. Randall, editors), Nevada State Museum Anthropological Papers 17.
Ochotona princeps	Council Hall Cave [26WP229]	-114.16667	39.33333	4220	23900	Thompson, R. S., and J. I. Mead. 1982. Late Quaternary environments and biogeography in the Great Basin. Quaternary Research 17:39-55.
Ochotona princeps	Crystal Ball Cave	-113	39	10000	23000	Heaton, T.H. 1985. Quaternary paleontology and paleoecology of Crystal Ball Cave, Millard County, Utah: with emphasis on the mammals and the description of a new species of fossil skunk. Great Basin Naturalist 45:337-390.
Ochotona princeps	Deer Creek Cave [EL-25]	-115.36667	41.75	10085	10085	Heaton, T.H. 1985. Quaternary paleontology and paleoecology of Crystal Ball Cave, Millard County, Utah: with emphasis on the mammals and the description of a new species of fossil skunk. Great Basin Naturalist 45:337-390.
Ochotona princeps	Deer Creek Cave [EL-25]	-115.36667	41.75	10085	10085	Ziegler, A. C. 1963. Unmodified mammal and bird remains from Deer Creek Cave, Elko County, Nevada. Pages 15-24 in Deer Creek Cave, Nevada (M. E. Shutler and R. Shutler, Jr., editors), Nevada State Museum Anthropological Papers 11.
Ochotona princeps	Eleana Range ER2-10	-116.23417	37.12167	17100	17100	Grayson, D.K. 1987. The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years. Journal of Mammalogy 68(2):359-375.
Ochotona princeps	Eleana Range ER2-11r	-116.23417	37.12167	10800	14310	Grayson, D.K. 1987. The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years. Journal of Mammalogy 68(2):359-375.
Ochotona princeps	Eleana Range ER2-7	-116.23417	37.12167	14760	14760	Grayson, D.K. 1987. The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years. Journal of Mammalogy 68(2):359-375.
Ochotona princeps	Hendries Cave [26PLn5]	-114.87528	38.00028	1	71000	Jefferson, G.T., H.G. McDonald, and S.D. Livingston. 2004. Catalogue of Late Quaternary and Holocene fossil vertebrates from Nevada. Occasional Papers 6. Nevada State Museum, Carson City, Nevada, USA.
Ochotona princeps	Kokoweef Cave [SBC1.11.13]	-115.5	35.41667	10000	20000	Goodwin, H. T., and R. E. Reynolds. 1989. Late Quaternary Sciuridae from Kokoweef Cave, San Bernardino County, California. Bulletin of the Southern California Academy of Sciences 88(1):21-32.
Ochotona princeps	Kokoweef Cave [SBC1.11.13]	-115.5	35.41667	10000	20000	Reynolds, R. E., R. L. Reynolds, C. J. Bell, N. J. Czaplewski, H. T. Goodwin, J. I. Mead, and B. Roth. 1991. The Kokoweef Cave faunal assemblage. Pages 97-103 in Crossing the borders: Quaternary

						studies in eastern California and southwestern Nevada (R. E. Reynolds, editor), San Bernardino County Museum Association, Redlands.
Ochotona princeps	Little Box Elder Cave [48CO287]	-105.61667	42.61667	9250	9250	Anderson, E. 1968. Fauna of the Little Box Elder Cave, Converse County, Wyoming: the Carnivora. University of Colorado Studies Series in Earth Science 6.
Ochotona princeps	Little Box Elder Cave [48CO287]	-105.61667	42.61667	9250	9250	Indeck, J. 1987. Sediment analysis and mammal faunal remains from Little Box Elder Cave, Wyoming. Ph.D. dissertation, University of Colorado, Boulder.
Ochotona princeps	Little Box Elder Cave [48CO287]	-105.61667	42.61667	9250	9250	Walker, D. N. 1987. Late Pleistocene/Holocene environmental changes in Wyoming: the mammalian record. Pages 334-393 in Late Quaternary mammalian biogeography and environments of the Great Plains and prairies (R. W. Graham, H. A. Semken, Jr., and M. A. Graham, editors), Illinois State Museum Scientific Papers 22.
Ochotona princeps	Mescal Cave [SBC1.10.12]	-115.5	35.36667	10000	20000	Brattstrom, B.H. 1958. New records of Cenozoic amphibians and reptiles from California. Bulletin of the Southern California Academy of Sciences 57:5-12.
Ochotona princeps	Mescal Cave [SBC1.10.12]	-115.5	35.36667	10000	20000	Grayson, D.K. 1987. The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years. Journal of Mammalogy 68(2):359-375.
Ochotona princeps	Mescal Cave [SBC1.10.12]	-115.5	35.36667	10000	20000	Jefferson, G.T. 1991. Rancholabrean age vertebrates from the Southeastern Mojave Desert, California. Pages 163-175 in R.E. Reynolds and J. Reynolds, editors. Crossing the borders: Quaternary studies in eastern California and Southwestern Nevada. Special Publication. San Bernardino County Museum Association, Redlands, California, USA.
Ochotona princeps	Mescal Cave [SBC1.10.12]	-115.5	35.36667	10000	20000	Mehringer, P.J., Jr., and C.W. Ferguson. 1969. Pluvial occurrence of bristlecone pine (Pinus aristata) in a Mohave Desert mountain range. Journal of the Arizona Academy of Science 5(4):284-292.
Ochotona princeps	Mormon Mountain Cave [V6702A]	-115	37	8000	35000	Jefferson, G. T. 1982. Late Pleistocene vertebrates from a Mormon Mountain cave in southern Nevada. Bulletin of the Southern California Academy of Sciences 81(3):121-127.
Ochotona princeps	Owl Cave 2	-114.05	38.9	10000	35000	Turnmire, K. L. 1987. An analysis of the mammalian fauna from Owl Cave One and Two, Snake Range, east central Nevada. Master's thesis, University of Maine, Orono.
Ochotona princeps	Pintwater Cave	-115.56139	36.94056	7285	32372	Jefferson, G.T., H.G. McDonald, and S.D. Livingston. 2004. Catalogue of Late Quaternary and Holocene fossil vertebrates from Nevada. Occasional Papers 6. Nevada State Museum, Carson City, Nevada, USA.
Ochotona princeps	Pintwater Cave	-115.56139	36.94056	7285	32372	Hockett, B.S. 2000. Paleobiogeographic changes at the Pleistocene-Holocene boundary near Pintwater Cave, southern Nevada. Quaternary Research 53:263-269.
Ochotona princeps	Potosi Mine Cave, Potosi Mountain 2A-2 Spring Range [1547]	-115.50028	35.96583	14050	15080	Jefferson, G.T., H.G. McDonald, and S.D. Livingston. 2004. Catalogue of Late Quaternary and Holocene fossil vertebrates from Nevada. Occasional Papers 6. Nevada State Museum, Carson City, Nevada, USA.
Ochotona princeps	Potosi Mountain Midden 2	-115.38333	36	12000	16500	Mead, J. I., and L. K. Murray. 1991. Late Pleistocene vertebrates from the Potosi Mountain Packrat Midden, Spring Range, Nevada. Pages 124-126 in Crossing the borders: Quaternary studies in eastern California and southwestern Nevada (compiled by R. E. Reynolds), San Bernardino County Museum Association, Special Publication Redlands.
Ochotona princeps	Smith Creek Cave [26WP46]	-114.08333	39.33333	1	10000	Bryan, A. L. 1979. Smith Creek Cave. Pages 164-251 in The archaeology of Smith Creek Canyon, eastern Nevada (D. R. Tuohy and D. L. Rendall, editors), Nevada State Museum Anthropological Papers 17.
Ochotona princeps	Smith Creek Cave [26WP46]	-114.08333	39.33333	1	10000	Mead, J.I., C.J. Bell, and L.K. Murray. 1992. Mictomys borealis (northern bog lemming) and the Wisconsin paleoecology of the east-central Great Basin. Quaternary Research 37(2):229-238. [DOI: 10.1016/0033-5894(92)90084-V]
Ochotona princeps	Smith Creek Cave [26WP46]	-114.08333	39.33333	1	10000	Mead, J. I., R. S. Thompson, and T. R. Van Devender. 1982. Late Wisconsinan and Holocene fauna from Smith Creek Canyon, Snake River Range, Nevada. Transactions of the San Diego Society of Natural History 20(1):1-26.
Ochotona princeps	Spires SP2	-115.3	36.58333	18830	18830	Grayson, D.K. 1987. The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years. Journal of Mammalogy 68(2):359-375.
Marmota flaviventris	Antelope Cave [SBC1.10.10]	-115.5	35.36667	10000	20000	Jefferson, G.T. 1991. Rancholabrean age vertebrates from the Southeastern Mojave Desert, California. Pages 163-175 in R.E. Reynolds and J. Reynolds, editors. Crossing the borders: Quaternary studies in eastern California and Southwestern Nevada. Special Publication. San Bernardino County Museum Association, Redlands, California, USA.
Marmota flaviventris	Antelope Cave [SBC1.10.10]	-115.5	35.36667	10000	20000	Reynolds, R. E., R. L. Reynolds, C. J. Bell, and B. Pitzer. 1991. Vertebrate remains from Antelope Cave, Mescal Range, San Bernardino County, California. Pages 107-109 in Crossing the borders: Quaternary studies in eastern California and southwestern Nevada (R. E. Reynolds, editor), San Bernardino County Museum Association, Redlands.

Marmota flaviventris	Baldy Peak Cave [MALB 29]	-107.75	32.11667	10000	35000	Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin.
Marmota flaviventris	Burnet Cave	-104.75	32.36667	10900	11300	Churcher, C. S. 1984. Sangamona: the furtive deer. Pages 316-331 in H. H. Genoways and M. R. Dawson, editors. Contributions in Quaternary vertebrate paleontology: a volume in memorial to John E. Guilday. Special Publication of Carnegie Museum of Natural History 8, Pittsburgh, Pennsylvania, USA.
Marmota flaviventris	Burnet Cave	-104.75	32.36667	10900	11300	Harris, A. H. 1977. Wisconsin age environments in the northern Chihuahuan desert evidence from the higher vertebrates. Pages 23-52 in Transactions of the symposium on the biological resources of the Chihuahuan Desert Region, United States and Mexico (R. H. Wauer and D. H. Riskind, editors), National Park Service Transactions and Proceedings Series 3.
Marmota flaviventris	Burnet Cave	-104.75	32.36667	10900	11300	Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin.
Marmota flaviventris	Burnet Cave	-104.75	32.36667	10900	11300	Schultz, C. B., and E. B. Howard. 1935. The fauna of Burnet Cave, Guadalupe Mountains, New Mexico. Proceedings of the Academy of Natural Sciences of Philadelphia 87:273-298.
Marmota flaviventris	Council Hall Cave [26WP229]	-114.16667	39.33333	4220	23900	Bryan, A. L. 1979. Council Hall Cave. Pages 257-268 in The archaeology of Smith Creek Canyon, eastern Nevada (D. R. Tuohy and D. L. Rendall, editors), Nevada State Museum Anthropological Papers 17.
Marmota flaviventris	Council Hall Cave [26WP229]	-114.16667	39.33333	4220	23900	Mead, J. I., R. S. Thompson, and T. R. Van Devender. 1982. Late Wisconsinan and Holocene fauna from Smith Creek Canyon, Snake River Range, Nevada. Transactions of the San Diego Society of Natural History 20(1):1-26.
Marmota flaviventris	Council Hall Cave [26WP229]	-114.16667	39.33333	4220	23900	Miller, S. J. 1979. The archeological fauna of four sites in Smith Creek Canyon. Pages 273-329 in The archeology of Smith Creek Canyon, eastern Nevada (D. R. Tuohy and D. L. Randall, editors), Nevada State Museum Anthropological Papers 17.
Marmota flaviventris	Council Hall Cave [26WP229]	-114.16667	39.33333	4220	23900	Thompson, R. S., and J. I. Mead. 1982. Late Quaternary environments and biogeography in the Great Basin. Quaternary Research 17:39-55.
Marmota flaviventris	Dark Canyon Cave	-104.5	32.25	20120	25000	Harris, A. H. 1977. Wisconsin age environments in the northern Chihuahuan desert evidence from the higher vertebrates. Pages 23-52 in Transactions of the symposium on the biological resources of the Chihuahuan Desert Region, United States and Mexico (R. H. Wauer and D. H. Riskind, editors), National Park Service Transactions and Proceedings Series 3.
Marmota flaviventris	Dark Canyon Cave	-104.5	32.25	20120	25000	Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin.
Marmota flaviventris	Dry Cave	-104.48194	32.37361	13500	20000	Harris, A. H. 1984. Two new species of late Pleistocene woodrats (Cricetidae: Neotoma) from New Mexico. Journal of Mammalogy 65:560-566.
Marmota flaviventris	Dry Cave	-104.48194	32.37361	13500	20000	Harris, A. H. 1970. The Dry Cave mammalian fauna and late pluvial conditions in southeastern New Mexico. Texas Journal of Science 22(1):3-27.
Marmota flaviventris	Dry Cave	-104.48194	32.37361	13500	20000	Harris, A. H. 1980. The paleontology of Dry Cave, New Mexico. National Geographic Society Research Report 12:331-338.
Marmota flaviventris	Dry Cave	-104.48194	32.37361	13500	20000	Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin.
Marmota flaviventris	Dry Cave	-104.48194	32.37361	13500	20000	Harris, A. H. 1987. Reconstruction of Mid-Wisconsin environments in southern New Mexico. National Geographic Research 3(2):142-151.
Marmota flaviventris	Dry Cave	-104.48194	32.37361	10730	14470	Harris, A. H. 1984. Two new species of late Pleistocene woodrats (Cricetidae: Neotoma) from New Mexico. Journal of Mammalogy 65:560-566.
Marmota flaviventris	Dry Cave	-104.48194	32.37361	10730	14470	Harris, A. H. 1970. The Dry Cave mammalian fauna and late pluvial conditions in southeastern New Mexico. Texas Journal of Science 22(1):3-27.
Marmota flaviventris	Dry Cave	-104.48194	32.37361	10730	14470	Harris, A. H. 1980. The paleontology of Dry Cave, New Mexico. National Geographic Society Research Report 12:331-338.
Marmota flaviventris	Dry Cave	-104.48194	32.37361	10730	14470	Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin.
Marmota flaviventris	Dry Cave	-104.48194	32.37361	10730	14470	Harris, A. H. 1987. Reconstruction of Mid-Wisconsin environments in southern New Mexico. National Geographic Research 3(2):142-151.
Marmota flaviventris	Dust Cave [C-09]	-104.75	31.86667	13000	13000	Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin.
Marmota flaviventris	Dust Cave [C-09]	-104.75	31.86667	13000	13000	Van Devender, T.R., P.S. Martin, A.M. Phillips III, and W.G. Spaulding. 1975. Late Pleistocene biotic communities from the Guadalupe Mountains, Culberson County, Texas. Pages 107-113 in R.H. Wauer and D.H. Riskind, editors. Transactions of the Symposium on the Biological Resources of the Chihuahuan Desert Region United States and Mexico, Sul Ross State University, Alpine, Texas, 17-18

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Marmota flaviventris	Fowlkes Cave	-104.11667	31	10000	35000	Dalquest, W. W., and F. B. Stangl, Jr. 1984. Late Pleistocene and early Recent mammals from Fowlkes Cave, southern Culberson County, Texas. Pages 432-455 in Contributions in Quaternary vertebrate paleontology: a volume in memorial to John E. Guilday (H. H. Genoways and M. R. Dawson, editors), Carnegie Museum of Natural History Special Publications 8.
Marmota flaviventris	Fowlkes Cave	-104.11667	31	10000	35000	Dalquest, W. W., and F. B. Stangl, Jr. 1986. Post-Pleistocene mammals of the Apache Mountains, Culberson County, Texas, with comments on zoogeography of the Trans-Pecos Front Range. Occasional Papers of the Museum of Texas Tech University 104:2-35.
Marmota flaviventris	Kokoweef Cave [SBC1.11.13]	-115.5	35.41667	10000	20000	Goodwin, H. T., and R. E. Reynolds. 1989. Late Quaternary Sciuridae from Kokoweef Cave, San Bernardino County, California. Bulletin of the Southern California Academy of Sciences 88(1):21-32.
Marmota flaviventris	Kokoweef Cave [SBC1.11.13]	-115.5	35.41667	10000	20000	Reynolds, R. E., R. L. Reynolds, C. J. Bell, N. J. Czaplewski, H. T. Goodwin, J. I. Mead, and B. Roth. 1991. The Kokoweef Cave faunal assemblage. Pages 97-103 in Crossing the borders: Quaternary studies in eastern California and southwestern Nevada (R. E. Reynolds, editor), San Bernardino County Museum Association, Redlands.
Marmota flaviventris	Lower Sloth Cave	-104.86667	31.86667	1	11590	Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin.
Marmota flaviventris	Lower Sloth Cave	-104.86667	31.86667	1	11590	Logan, L. E. 1983. Paleoecological implications of the mammalian fauna of Lower Sloth Cave Guadalupe Mountains, Texas. National Speleological Society Bulletin 45:3-11.
Marmota flaviventris	Lower Sloth Cave	-104.86667	31.86667	1	11590	Van Devender, T.R., P.S. Martin, A.M. Phillips III, and W.G. Spaulding. 1975. Late Pleistocene biotic communities from the Guadalupe Mountains, Culberson County, Texas. Pages 107-113 in R.H. Wauer and D.H. Riskind, editors. Transactions of the Symposium on the Biological Resources of the Chihuahuan Desert Region United States and Mexico, Sul Ross State University, Alpine, Texas, 17-18 October 1974. United States Department of the Interior, National Park Service Transactions and Proceedings Series 3.
Marmota flaviventris	Mormon Mountain Cave [V6702A]	-115	37	8000	35000	Jefferson, G. T. 1982. Late Pleistocene vertebrates from a Mormon Mountain cave in southern Nevada. Bulletin of the Southern California Academy of Sciences 81(3):121-127.
Marmota flaviventris	Muskox Cave	-104.5	32.11667	1	35000	Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin.
Marmota flaviventris	Muskox Cave	-104.5	32.11667	1	35000	Logan, L. E. 1981. The mammalian fossils of Muskox Cave, Eddy County, New Mexico. Proceedings Eighth International Congress of Speleology 1:159-160.
Marmota flaviventris	Muskox Cave	-104.5	32.11667	1	35000	Jass, C. N., J. I. Mead, and L. E. Logan. 2000. Harrington's extinct mountain goat (Oreamnos harringtoni Stock 1936) from Muskox Cave, New Mexico. Texas Journal of Science 52(2):121-132.
Marmota flaviventris	North Cove [25HN164]	-99.36667	40.11667	12965	14700	Stewart, J. D. 1987. Prehistoric and historic cultural resources of selected sites at Harlan County Lake, Harlan County, Nebraska. U.S. Army Corps of Engineers, Final Report, Kansas City.
Marmota flaviventris	Papago Springs Cave	-110.61667	31.61667	1	1	Czaplewski, N. J., J. I. Mead, T. L. Ku, and L. D. Agenbroad. 1989. Radiometric age assignment for Papago Springs Cave deposits, southeastern Arizona. Southwestern Naturalist 34(2):278-281.
Marmota flaviventris	Papago Springs Cave	-110.61667	31.61667	1	1	Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin.
Marmota flaviventris	Papago Springs Cave	-110.61667	31.61667	1	1	Lindsay, E.H. 1978. Late Cenozoic vertebrate faunas, southeastern Arizona. Pages 269-275 in J.F. Callender, J.C. Wilt, R.E. Clemons, and H.L. James, editors. Land of Cochise (southeastern Arizona). New Mexico Geological Society\r\r\nGuidebook. New Mexico Geological Society, Socorro, New Mexico, USA.
Marmota flaviventris	Papago Springs Cave	-110.61667	31.61667	1	1	Skinner, M.F. 1942. The fauna of Papago Springs Cave, Arizona, and a study of Stockoceros; with three new antilocaprines from Nebraska and Arizona. Bulletion of the American Museum of Natural History 80(6):143-220.
Marmota flaviventris	Papago Springs Cave	-110.61667	31.61667	1	1	Czaplewski, N. J., W. D. Peachey, J. I. Mead, T.-L. Ku, and C. J. Bell. 1999. Papago Springs Cave revisited part I; geologic setting, cave deposits, and radiometric dates. Occasional Papers of the Oklahoma Museum of Natural History 3:1-25.
Marmota flaviventris	Papago Springs Cave	-110.61667	31.61667	1	1	Czaplewski, N.J., J.I. Mead, C.J. Bell, W.D. Peachey, and T.-L. Ku. 1999. Papago Springs Cave revisited, part II: vertebrate paleofauna. Occasional Papers of the Oklahoma Museum of Natural History 5:1-41.
Marmota flaviventris	Papago Springs Cave	-110.61667	31.61667	31000	110000	Czaplewski, N. J., J. I. Mead, T. L. Ku, and L. D. Agenbroad. 1989. Radiometric age assignment for Papago Springs Cave deposits, southeastern Arizona. Southwestern Naturalist 34(2):278-281.
Marmota flaviventris	Papago Springs Cave	-110.61667	31.61667	31000	110000	Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin.

Marmota flaviventris	Papago Springs Cave	-110.61667	31.61667	31000	110000	Lindsay, E.H. 1978. Late Cenozoic vertebrate faunas, southeastern Arizona. Pages 269-275 in J.F. Callender, J.C. Wilt, R.E. Clemons, and H.L. James, editors. Land of Cochise (southeastern Arizona). New Mexico Geological Society\r\r\nGuidebook. New Mexico Geological Society, Socorro, New Mexico, USA.
Marmota flaviventris	Papago Springs Cave	-110.61667	31.61667	31000	110000	Skinner, M.F. 1942. The fauna of Papago Springs Cave, Arizona, and a study of Stockoceros; with three new antilocaprines from Nebraska and Arizona. Bulletion of the American Museum of Natural History 80(6):143-220.
Marmota flaviventris	Papago Springs Cave	-110.61667	31.61667	31000	110000	Czaplewski, N. J., W. D. Peachey, J. I. Mead, T.-L. Ku, and C. J. Bell. 1999. Papago Springs Cave revisited part I; geologic setting, cave deposits, and radiometric dates. Occasional Papers of the Oklahoma Museum of Natural History 3:1-25.
Marmota flaviventris	Papago Springs Cave	-110.61667	31.61667	31000	110000	Czaplewski, N.J., J.I. Mead, C.J. Bell, W.D. Peachey, and T.-L. Ku. 1999. Papago Springs Cave revisited, part II: vertebrate paleofauna. Occasional Papers of the Oklahoma Museum of Natural History 5:1-41.
Marmota flaviventris	Potter Creek Cave [5357,1055]	-122.28083	40.78389	11500	110000	Kurtén, B.O.L, and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York, New York, USA.
Marmota flaviventris	Potter Creek Cave [5357,1055]	-122.28083	40.78389	11500	110000	Lundelius, E. L., Jr., R. W. Graham, E. Anderson, J. Guilday, J. A. Holman, D. W. Steadman, and S. D. Webb. 1983. Terrestrial vertebrate faunas. Pages 311-353 in Late-Quaternary environments of the United States: volume 1, The late Pleistocene (S. C. Porter, editor), University of Minnesota Press, Minneapolis, Minnesota, USA.
Marmota flaviventris	Potter Creek Cave [5357,1055]	-122.28083	40.78389	11500	110000	Stock, C. 1918. The Pleistocene fauna of Hawver Cave. University of California Publications, Bulletin of the Department of Geology 10(24):462-515.
Marmota flaviventris	Pratt Cave [TMM-41172]	-104.75	31.86667	1420	2820	Lundelius, E. L., Jr. 1979. Post-Pleistocene mammals from Pratt Cave and their environmental significance. Pages 239-257 in Biological investigations in the Guadalupe Mountains National Park, Texas, (H. H. Genoways and R. J. Baker, editors), National Park Service, Proceedings and Transactions Series 4.
Marmota flaviventris	Rampart Cave	-113.93333	36.1	10000	13000	Hansen, R. M. 1978. Shasta ground sloth food habits, Rampart Cave, Arizona. Paleobiology 4:302-319.
Marmota flaviventris	Rampart Cave	-113.93333	36.1	10000	13000	Long, A., and P.S. Martin. 1974. Death of American ground sloths. Science 186:638-640..
Marmota flaviventris	Rampart Cave	-113.93333	36.1	10000	13000	Martin, P. S., B. E. Sabels, and D. Shutler, Jr. 1961. Rampart Cave coprolite and ecology of the Shasta ground sloth. American Journal of Science 259:102-127.
Marmota flaviventris	Rampart Cave	-113.93333	36.1	10000	13000	Mead, J. I. 1981. The last 30,000 years of faunal history within the Grand Canyon, Arizona. Quaternary Research 15:311-326.
Marmota flaviventris	Rampart Cave	-113.93333	36.1	10000	13000	Mead, J. I., L. D. Agenbroad, O. K. Davis, and P. S. Martin. 1986. Dung of Mammuthus in the arid southwest, North America. Quaternary Research 25:121-127.
Marmota flaviventris	Rampart Cave	-113.93333	36.1	10000	13000	Van Devender, T. R., A. M. Phillips, III, and J. I. Mead. 1977. Late Pleistocene reptiles and mammals from the lower Grand Canyon of Arizona. Southwestern Naturalist 22:49-66.
Marmota flaviventris	Smith Creek Cave [26WP46]	-114.08333	39.33333	9280	12150	Bryan, A. L. 1979. Smith Creek Cave. Pages 164-251 in The archaeology of Smith Creek Canyon, eastern Nevada (D. R. Tuohy and D. L. Rendall, editors), Nevada State Museum Anthropological Papers 17.
Marmota flaviventris	Smith Creek Cave [26WP46]	-114.08333	39.33333	9280	12150	Mead, J.I., C.J. Bell, and L.K. Murray. 1992. Mictomys borealis (northern bog lemming) and the Wisconsin paleoecology of the east-central Great Basin. Quaternary Research 37(2):229-238. [DOI: 10.1016/0033-5894(92)90084-V]
Marmota flaviventris	Smith Creek Cave [26WP46]	-114.08333	39.33333	9280	12150	Mead, J. I., R. S. Thompson, and T. R. Van Devender. 1982. Late Wisconsinan and Holocene fauna from Smith Creek Canyon, Snake River Range, Nevada. Transactions of the San Diego Society of Natural History 20(1):1-26.
Marmota flaviventris	Snake Creek Burial Cave	-114.11667	38.86667	10000	35000	Heaton, T. H. 1987. Initial investigation of vertebrate remains from Snake Creek Burial Cave, White Pine County, Nevada. Current Research in the Pleistocene 4:107-109.
Marmota flaviventris	Snake Creek Burial Cave	-114.11667	38.86667	10000	35000	Mead, E. M., and J. I. Mead. 1989. Snake Creek Burial Cave and a review of the Quaternary mustelids of the Great Basin. Great Basin Naturalist 49(2):143-154.
Marmota flaviventris	Tse'An Kaetan Cave-Grand Canyon	-112	36	14220	30600	Agenbroad, L. D., and J. I. Mead. 1987. Late Pleistocene alluvium and megafauna dung deposits of the central Colorado Plateau. Pages 68-84 in G. H. Davis and E. M. VandenDolder, editors. Geologic diversity of Arizona and its margins: excursions to choice areas Arizona Bureau of Geology and Mineral Technology Special Paper 5.
Marmota flaviventris	Tse'An Kaetan Cave-Grand Canyon	-112	36	14220	30600	Emslie, S. 1987. Age and diet of fossil California condors in Grand Canyon, Arizona. Science 237:768-770.
Marmota flaviventris	Tse'An Kaetan Cave-Grand Canyon	-112	36	14220	30600	Mead, J. I., and L. D. Agenbroad. 1992. Isotope dating of Pleistocene dung deposits from the Colorado Plateau Arizona and Utah. Radiocarbon 34(1):1-19.

Marmota flaviventris	U-Bar Cave [LA5689]	-108.4337	31.4745	25000	40000	Bense, J. A. 1972. Cascade phase: a study in the effect of the altithermal on a cultural system. Ph.D. dissertation, Washington State University, Pullman.
Marmota flaviventris	U-Bar Cave [LA5689]	-108.4337	31.4745	25000	40000	Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin.
Marmota flaviventris	U-Bar Cave [LA5689]	-108.4337	31.4745	25000	40000	Harris, A. H. 1987. Reconstruction of Mid-Wisconsin environments in southern New Mexico. National Geographic Research 3(2):142-151.
Marmota flaviventris	Upper Sloth Cave [TTu-Tex-2]	-104.75	31.86667	11000	11760	Harris, A. H. 1985. Late Pleistocene vertebrate paleoecology of the west. University of Texas Press, Austin.
Marmota flaviventris	Upper Sloth Cave [TTu-Tex-2]	-104.75	31.86667	11000	11760	Logan, L. E., and C. C. Black. 1979. The Quaternary vertebrate fauna of Upper Sloth Cave, Guadalupe Mountains National Park, Texas. Pages 141-158 in Biological investigations in the Guadalupe Mountains National Park, Texas (H. H. Genoways and R. J. Baker, editors), National Park Service, Proceedings and Transactions Series 4.
Marmota flaviventris	Upper Sloth Cave [TTu-Tex-2]	-104.75	31.86667	11000	11760	Van Devender, T.R., P.S. Martin, A.M. Phillips III, and W.G. Spaulding. 1975. Late Pleistocene biotic communities from the Guadalupe Mountains, Culberson County, Texas. Pages 107-113 in R.H. Wauer and D.H. Riskind, editors. Transactions of the Symposium on the Biological Resources of the Chihuahuan Desert Region United States and Mexico, Sul Ross State University, Alpine, Texas, 17-18 October 1974. United States Department of the Interior, National Park Service Transactions and Proceedings Series 3.
Marmota flaviventris	Vulture Cave	-113.93333	36.1	1	13500	Mead, J.I., and A.M. Phillips III. 1981. The late Pleistocene and Holocene fauna and flora of Vulture Cave, Grand Canyon, Arizona. Southwestern Naturalist 26:257-288.
*Marmota flaviventris**	San Josecito Cave	-99.91	23.95	11000	40000	Jachowski, D., Kays, R., Butler, A., Hoylman, A. M., and Gompper, M. E. (2021). Tracking the decline of weasels in North America. PLoS ONE 16, e0254387. doi: 10.1371/journal.pone.0254387.
Mustela nivalis	Cheek Bend Cave [40MU261]	-86.86667	35.5	12500	16500	Klippel, W.E., and P.W. Parmalee. 1982. The paleontology of Cheek Bend Cave, Maury County, Tennessee: phase II report. Report to the Tennessee Valley Authority.
Mustela nivalis	Crankshaft Cave	-90.5	38.36667	11500	110000	Parmalee, P.W., R.D. Oesch, and J.E. Guilday. 1969. Pleistocene and recent vertebrate faunas from Crankshaft Cave, Missouri. Report of Investigations 14. Illinois State Museum, Springfield, Illinois.
Mustela nivalis	Meyer Cave	-90.25389	38.39667	1	11450	Parmalee, P.W. 1967. A recent cave bone deposit in southwestern Illinois. National Speleological Society Bulletin 29(4):119-147.
Mustela nivalis	Moonshiner	-112.61667	43.36667	8000	10000	Kurtén, B.O.L, and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York, New York, USA.
Mustela nivalis	Moonshiner	-112.61667	43.36667	8000	10000	Mullican, T. R., and L. N. Carraway. 1990. Shrew remains from Moonshiner and Middle Butte caves, Idaho. Journal of Mammalogy 71(3):351-356.
Mustela nivalis	Moonshiner	-112.61667	43.36667	8000	10000	White, J. A., H. G. McDonald, E. Anderson, and J. M. Soiset. 1984. Lava blisters as carnivore traps. Pages 241-256 in Contributions in Quaternary vertebrate paleontology: a volume in memorial to John E. Guilday (H. H. Genoways and M. R. Dawson, editors), Carnegie Museum of Natural History Special Publications 8.
Mustela nivalis	Snake Creek Burial Cave	-114.11667	38.86667	10000	35000	Heaton, T. H. 1987. Initial investigation of vertebrate remains from Snake Creek Burial Cave, White Pine County, Nevada. Current Research in the Pleistocene 4:107-109.
Mustela nivalis	Snake Creek Burial Cave	-114.11667	38.86667	10000	35000	Mead, E. M., and J. I. Mead. 1989. Snake Creek Burial Cave and a review of the Quaternary mustelids of the Great Basin. Great Basin Naturalist 49(2):143-154.
Mustela nivalis	Welsh Cave [15WD13]	-84.74722	37.87361	12950	12950	Guilday, J. E., H. W. Hamilton, and A. D. McCrady. 1971. The Welsh Cave peccaries (Platygonus) and associated fauna, Kentucky Pleistocene. Annals of the Carnegie Museum 43:249-320.
*Mustela nivalis**	Hall's Cave	-99.42	30.05	14700	20000	Seersholm, F. V., Werndly, D. J., Grealy, A., Johnson, T., Keenan Early, E. M., Lundelius, E. L., et al. (2020). Rapid range shifts and megafaunal extinctions associated with late Pleistocene climate change. Nat Commun 11, 2770. doi: 10.1038/s41467-020-16502-3.

*These data were separately acquired and not included in the FAUNMAP database.

Table S1.3. Numeric summary of mountain goat observations by year on and off snow in Glacier National Park, USA, during 2020–2022 and at Mt. Blue Sky, CO, USA during July of 2022.

	Glacier National Park			Mount Evans	
	2020	**2021**	**2022**	**2022**	**Total**
On snow	19	128	5	0	152
Not on snow	329	268	92	87	776
Total	348	396	97	87	928

Table S1.4. Numeric summary of the effects of biological condition and local weather on mountain goat respiration rate (breaths/minute) and ear-flick rate (flicks/ear/minute) of mountain goats in Glacier National Park, USA, during 2020–2022 and at Mt. Blue Sky, CO, USA.

	Effect on respiration rate				**Effect on ear twitch rate**			
	Mean	**SD**	**2.5%**	**97.5%**	**Mean**	**SD**	**2.5%**	**97.5%**
Temperature (°C)	0.37	0.03	0.31	0.43	–0.37	0.01	–0.40	–0.34
Wind speed (km/h)	–0.01	0.03	–0.08	0.05	–0.30	0.01	–0.32	–0.27
Winter coat shed (%)	–0.09	0.04	–0.18	-0.01	0.18	0.02	0.15	0.22
Direct sun	0.64	0.07	0.51	0.77	0.53	0.03	0.47	0.59
Laying on snow	0.00	0.09	–0.18	0.18	–0.31	0.04	–0.39	–0.22
Age: young-of-year	0.25	0.10	0.05	0.45	–1.01	0.05	–1.11	–0.92
Age: sub-adult	0.40	0.10	0.19	0.60	–0.39	0.05	–0.49	–0.29
Visual observation	0.21	0.15	–0.09	0.51	–0.17	0.07	–0.30	–0.03

Table S1.5. Numeric summary of the effects of biological condition and local weather on percent of winter coat shed by mountain goats in Glacier National Park, USA, during 2020–2022 and at Mt. Blue Sky, CO, USA.

	Mean	**SD**	**2.5%**	**97.5%**
Week of year	0.27	0.01	0.26	0.29
Elevation (1,000 m)	–0.20	0.02	–0.24	–0.15
Sub-adult	0.62	0.18	0.28	0.97
Adult male	0.65	0.06	0.54	0.77
Adult female with young-of-year	–0.45	0.05	–0.55	–0.35

Table S2.2. Numeric summary of collared mountain goats in Glacier National Park by year and sex between 2013–2020.

Year	Sex	Number	Collar make	Collar model	GPS fix rate
2013	F	2	Lotek[1]	Iridium Track 2D	2-hour
	M	-			
2014	F	3			
	M	3			
2018	F	8	Telonics[2]	TGW-3477-4	4-hour
	M	-			
2019	F	4			
	M	-			
2020	F	7			
	M	5			
TOTAL		32			

[1] Lotek Wireless Inc., Seattle, WA, USA
[2] Telonics, Inc., Mesa, AZ, USA

Table S2.3. Summary of modeled population-level effects of covariates on resource selection by mountan goats in Glacier National Park during May 15th to August 31st across a decade (2013–2022).

Scale	Variable	Lower CI	Mean	Upper CI
Home range	Elevation	0.62	0.63	0.65
	Proximity to escape	0.37	0.39	0.40
	Proximity to road	1.27	1.30	1.32
	Proximity to trail	0.69	0.71	0.72
	Solar radiation	0.14	0.16	0.17
	Proximity to snow	0.14	0.16	0.18
Fine scale (SSF)	Elevation	−0.38	−0.35	−0.33
	Proximity to escape	−0.13	−0.11	−0.10
	Proximity to road	0.02	0.05	0.07
	Proximity to trail	0.29	0.31	0.33
	Solar radiation	−0.15	−0.13	−0.12
	Proximity to snow	0.02	0.04	0.05

Table S2.4. Summary of contrasts between resource selection at a coarse scale (within home range) during the warmest (> 85th percentile) and cooler (all other) days by mountan goats in Glacier National Park during May 15th to August 31st across a decade (2013–2022). Under temperature, "difference" represents the change in selection from cooler to warmest days.

Temperature	Variable	Lower CI	Mean	Upper CI
Cooler	Proximity to escape	0.33	0.34	0.36
Cooler	Elevation	0.48	0.50	0.52
Cooler	Proximity to road	1.28	1.31	1.34
Cooler	Proximity to trail	0.57	0.58	0.60
Cooler	Solar radiation	0.13	0.14	0.16
Cooler	Proximity to snow	0.19	0.21	0.23
Warmest	Proximity to escape	0.08	0.11	0.14
Warmest	Elevation	0.73	0.78	0.83
Warmest	Proximity to road	1.34	1.41	1.48
Warmest	Proximity to trail	0.67	0.71	0.76
Warmest	Solar radiation	0.05	0.09	0.12
Warmest	Proximity to snow	0.07	0.11	0.17
Difference	Proximity to escape	−0.27	−0.23	−0.19
Difference	Elevation	0.23	0.29	0.34
Difference	Proximity to road	0.02	0.10	0.17
Difference	Proximity to trail	0.08	0.13	0.18
Difference	Solar radiation	−0.09	−0.06	−0.02
Difference	Proximity to snow	−0.15	−0.10	−0.04

Table S2.5. Summary of contrasts between resource selection at a fine scale (step selection) during the warmest (> 85th percentile) and cooler (all other) days by mountan goats in Glacier National Park during May 15th to August 31st across a decade (2013–2022). Under temperature, “difference” represents the change in selection from cooler to warmest days.

Temperature	Variable	Lower CI	Mean	Upper CI
Cooler	Proximity to escape	−0.03	−0.01	0.00
Cooler	Elevation	−0.02	0.00	0.02
Cooler	Proximity to road	−0.12	−0.09	−0.06
Cooler	Proximity to trail	0.47	0.49	0.52
Cooler	Solar radiation	−0.10	−0.08	−0.06
Cooler	Proximity to snow	−0.02	−0.01	0.01
Warmest	Proximity to escape	0.12	0.15	0.19
Warmest	Elevation	−0.45	−0.39	−0.32
Warmest	Proximity to road	−0.04	0.04	0.12
Warmest	Proximity to trail	0.30	0.36	0.42
Warmest	Solar radiation	−0.02	0.02	0.06
Warmest	Proximity to snow	−0.23	−0.19	−0.14
Difference	Proximity to escape	0.12	0.16	0.20
Difference	Elevation	−0.46	−0.39	−0.32
Difference	Proximity to road	0.04	0.13	0.21
Difference	Proximity to trail	−0.20	−0.13	−0.07
Difference	Solar radiation	0.06	0.10	0.15
Difference	Proximity to snow	−0.23	−0.18	−0.13

Table S3.2. Summary of introduced cold-adapted species (depicted in Figure 3.1) to areas outside of their native ranges.

		Translocated to		
Common name	**Latin name**	**Country**	**Region**	**Reference**
Alpine chamois	*Rupicapra rupicapra*	New Zealand	Kaikoura mountains	Martínková et al., 2012
		Czech Republic	Lysatuan Mountains (Lužické hory)	Martínková et al., 2012
American mink	*Mustela vison*	Argentina	Tierra del Fuego	Novillo and Ojeda 2008
		Sweden	Numerous locales, widely distributed	Gerell 1970
		Russia	Khabarovsk Krai area	Long 2003
Arctic Fox	*Vulpes lagopus*	Russia	Kuril Islands (Kuril'skiye Ostrova)	Khlyap et al., 2010
	Vulpes lagopus	United States	Alaska	MacDonald and Cook 2009
Bison	*Bison bison*	United States	Alaska, Copper River	MacDonald and Cook 2009
Caribou	*Rangifer tarandus*	United Kingdom territory	Falkland Islands	Bell and Dieterich 2010
		United States	Aleutian Islands, Adak Island	Jones 1966
		Iceland	Reykjanes Peninsula	Thórisson 1984
Least weasel	*Mustela nivalis*	New Zealand	Numerous locales, widely distributed	King 2017
		Portugal	Azores archipelago	Mathias et al., 1998
Moose	*Alces alces*	United States	Western Colorado	Duvall and Schoonveld 1988
Mouflon sheep	*Ovis aries*	Chile	Osorno region	
Mountain goat	*Oreamnos americanus*	United States	Washington, Olympic Mountain Range	Moorhead and Stevens 1982
Muskox	*Ovibos moschatus*	Greenland	Kangerlussuaq (Søndre Strømfjord)	Boertmann et al., 1992
		Norway	Dovre Mountains	Lønø 1960
		Russia	Poluostrov Taymyr	Yakushkin and Barr 1988
Snowshoe hare	*Lepus americanus*	United States	Southeastern Alaska, Douglass Island	MacDonald and Cook 2009