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Environmental Determinants of American Pika (*Ochotona princeps*) Distribution and Abundance Across the Northern Portion of the Greater Yellowstone Ecosystem

Kaitlyn Hanley
Clemson University, kaitlyn.hanley1@gmail.com

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ENVIRONMENTAL DETERMINANTS OF AMERICAN PIKA (*OCHOTONA PRINCEPS*) DISTRIBUTION AND ABUNDANCE ACROSS THE NORTHERN PORTION OF THE GREATER YELLOWSTONE ECOSYSTEM

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by
Kaitlyn Hanley
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Accepted by:
Dr. Saara DeWalt, Committee Chair
Dr. David Tonkyn, Committee Co-Chair
Dr. Michael Sears

ABSTRACT

Over the next century, temperatures are expected to rise by 1–4 °C in the Greater Yellowstone Ecosystem of the American West, and by even larger amounts in montane habitats. This warming may cause species that live there to acclimate, adapt, move, or disappear. Understanding the degree to which species' distributions are tied to temperature and other aspects of the environment is key to developing effective conservation plans. American pikas (*Ochotona princeps*) are small alpine lagomorphs restricted to cooler talus habitats. Pikas have exhibited varying responses across their range to the changing climate, suggesting that their distributions are not simply limited by climate. In this thesis, I explored how landscape, climate, vegetation, habitat connectivity and activity constraints are related to pika distribution and abundance in the northern range of the Greater Yellowstone Ecosystem including the Beartooth Plateau, Washburn Mountain, and Bunsen-Hoodoo area.

To determine the environmental variables that best explain pika distribution and abundance, I compared statistical models with different sets of environmental variables and field measurements of occupancy and pika latrine densities, as a proxy for pika density. The strongest predictor of pika occupancy was the timing of peak vegetation cover (measured as the maximum Normalized Difference Vegetation Index), with higher occupancy at sites with later peaks in vegetation cover. Habitat connectivity, measured by the percentage of talus within 1 km of each site, was the second strongest predictor of occupancy, with occupancy increasing with the amount of nearby talus. Neither maximum summer temperatures nor the number of hours pikas could be active during the summer were strong predictors of occupancy. Overall, there was a higher probability of occupancy at sites with increased connectedness to surrounding talus, peak primary productivity later in the year, and large amounts of seasonal precipitation. The necessity of large seasonal precipitation may be detrimental for pika populations because, under future climate scenarios, this area is expected to become drier.

The two strongest predictors of latrine density, and likely pika density, were the area of talus sites and the forage quality, as measured by the ratio of forbs to graminoids. Latrine density was greater in areas of higher amounts of forbs compared to graminoids, flatter slopes and smaller talus areas. As with site occupancy, summer temperatures and activity hours were not the strongest predictors of latrine density. Instead, winter temperatures and winter and summer precipitation were the strongest climate predictors of latrine density.

In conclusion, forage quality and habitat connectivity appear to drive the distribution and abundance of pikas in the Greater Yellowstone Region. In particular, the Beartooth Plateau appears to provide a refugia for pikas under the present and potentially the future climate. Summer temperatures do not appear to limit pikas in this region; instead they are limited by winter climate. Ultimately, identifying areas of large connectivity, such as the Beartooth Plateau, and high forage quality, will be necessary for future protection of this species.

DEDICATION

I would like to dedicate this to my parents, Brian and Maureen Hanley, my sister, Meaghan Hanley and my friends. Without their constant support and encouragement, I never would have been able to pursue higher education and a career in ecology and conservation. Also, I would like to dedicate this to Katie Quakenbush, my field research partner and close friend; without her dedication the fieldwork would have been significantly less enjoyable.

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CHAPTER ONE: LITERATURE REVIEW

A central focus of ecological research has been to try to understand the relationship between species and their environment. These relationships are complex, and understanding them has taken on new importance in the wake of climate change. Global climate change is expected to have profound effects on ecosystems around the world. Temperatures are predicted to increase by 2 – 5 °C (IPCC 2014) globally over the next century while rainfall patterns will change in complex ways as well. Species will have to adapt genetically or compensate behaviorally, or shift their distributions in order to survive (Chen *et al.* 2011). Range shifts to higher elevations or latitudes have been well documented in many taxonomic groups (Thomas 2010). However, the mechanisms driving these changes are not well understood due to the complex interactions between climate, habitat, and the species. Additionally, the strength of these mechanisms may vary depending on the spatial and temporal scales at which they are studied. Often, as spatial and temporal scales broadens there is a dampening effect of the magnitude of the responses. This dampening effect can be due to compensatory interactions, feedback loops, buffers and other higher order interactions that may mask strong responses at the local level. Given the significance of spatial scale, geographically extensive research at finer spatial resolution may offer important insights to the effects of climate not caught with lower resolution data (Carter *et al.* 2015, Leuzinger *et al.* 2011). In this thesis, I explore the environmental determinants of American pika distribution and abundance in montane areas of the American West. This work grew out of concern that this species is threatened by global warming.

Ecology of Montane Ecosystems

Anthropomorphic climate change will impact nearly all ecosystems, but montane ecosystems are arguably among the most sensitive to this change. Montane ecosystems have experienced nearly three times the global average temperature increase over the past century (Hall *et al.* 2016). In addition to warming temperatures, mountain habitats are also experiencing dramatic declines in snowpack, which can expose species to greater winter cold stress while reducing critical water sources for ecosystems downstream (Rodhouse *et al*. 2018). Understanding how climate varies with topography, especially in mountainous terrains, is necessary to understand the magnitude of change species are facing (Wang *et al.* 2012). Also, montane species may provide valuable insights to species' responses to climate change because they are often specialized for their extreme environment, making them particularly sensitive to warmer temperatures. In addition, their populations are often geographically isolated, restricting gene flow, and have relatively long generation times, limiting the role of adaptive evolution (Castillo *et al.* 2016). Even if a beneficial mutation were to appear in one of these small, isolated populations, the probability of it spreading to other local populations is unlikely (Robson *et al.* 2015). Instead, the persistence of montane species under stressful or changing climates will be based on more immediate responses such as behavioral plasticity (Hall *et al.* 2016).

Climate can vary substantially over scales as small as a few hundred meters in mountainous regions (Wang *et al.* 2012). It is characterized typically by two main factors, temperature and precipitation, and elevation strongly influences both (Gates 2012). Temperature typically decreases with elevation but the relationship can quite complex. In dry conditions, winds that blow toward mountains are forced to higher elevations, cooling by 10 °C/km increase until the dew point is reached, where the air is saturated with gaseous water vapor. As the air rises and cools further, its ability to contain water vapor continues to decrease, and the vapor condenses to liquid form and yields precipitation at higher elevations. The heat of condensation reduces the cooling rate partially to 6 °C/km of additional elevation increase. As the air descends on the downwind slope, it warms at 10 °C/km, becoming warmer and drier than at the same elevation on the upwind side. The adiabatic cooling rate is lower in more humid conditions, adding complexity to how climate changes with respect to elevation. Large-scale effects across mountain ranges are modified and sometimes reversed by other climate patterns operating at smaller scales. Local slope and aspect influence the amount of solar radiation warming the ground and air, and the topography can have profound influences through the trapping or directing of air masses through phenomena such as rain shadows, inversions, katabatic winds and cold air drainages (Blandford *et al.* 2008, Daly *et al.* 2008).

Because of these climatic effects and the heterogeneous topography, the mountain ranges of western North America including the Greater Yellowstone Ecosystem (GYE) are quite climatically diverse. There are prevailing winds from the west which create consistently cool, moist conditions on the upper western slopes of mountains, and hot, dry conditions on the lower eastern slopes, the rain shadow effect (Daly *et al.* 2002). At a smaller scale, the solar heating of lower air masses can generate uphill winds in the afternoons. At night, these air masses cool, become dense, and flow downhill to lower elevations. Topographic features such as river canyons can funnel these cool air masses to quite low elevations providing local refugia for sensitive species such as pikas. Complex topography of mountainous areas can pose quite a challenge for climate models and for achieving the resolution necessary to investigate the relationship between climate and species' local distributions (Carter *et al.* 2015, Wang *et al.* 2012).

Study Organism

The American pika (*Ochotona princeps*) is a textbook example of a montane species at risk from global warming (NRC 2008). These small alpine lagomorphs are restricted to open talus habitats of western North America, and maintain high resting body temperatures close to their upper lethal temperature suggesting they have little physiological resilience to temperature extremes (Figure 1.1, Mathewson *et al.* 2017). These characteristics makes them susceptible to the predicted 1 – 4 °C temperature increase within the GYE (Chang 2015). The warming temperatures could lead to chronic and acute heat stress in the summer and the loss of insulating snow cover in the winter, threatening both low and high elevation populations though in different ways. In addition, their small size and limited dispersal ability leaves them tied to patches of talus habitat, areas of rock fall and boulders (Figure 1.2), and threatened by genetic isolation and population instability unless these patches are large or connected (Castillo *et al.* 2016). Finally, pikas do not hibernate but instead must survive on plants collected through the summer, so they may be particularly dependent on the quantity and quality of their food plants.

Changes in resource selection may allow individuals to offset climatic stress (Hall & Chalfoun 2018). These three factors are linked since climate varies with elevation, talus may be more common on higher or steeper slopes, and plant communities themselves vary with climate. Therefore, a warming climate may not just push pikas to sites with warmer microclimates but may also change the availability and quality of their habitats (Calkins *et al.* 2012).

Pikas are diurnal, active in open habitats, and use calls to defend their territories and warn of predators, making them easy to detect compared to other mammals of similar size (Beever *et al.* 2011). Their restriction to talus slopes constrains their ability to move to more suitable habitats, which is an issue for many other montane species. They can therefore serve as indicators of change for more elusive plant and animal species that share their remote and often inaccessible habitats (Beever *et al.* 2003).

Pikas' relationship with climate is quite complex. Overall, their sensitivity to heat means they are restricted from talus sites at lower elevations and latitudes (Beever *et al.* 2016, Smith & Nagy 2015). But in some areas, including those that appear inhospitable, pika populations are stable and even predicted to increase over the next century (Millar & Westfall 2010, Schwalm *et al.* 2016). Millar *et al.* (2018) found considerable overlap between the climatic envelopes of signs of long, extirpated and extant pika populations within talus sites in the Great Basin. Pikas may not be limited by climate even though they are physiologically constrained by the summer heat (Millar *et al.* 2018). At local levels, variation in topographical relief and habitat heterogeneity can increase thermal heterogeneity, which pikas can exploit for thermal regulation (Varner & Dearing 2014). This thermal heterogeneity is especially evident in the rough, open lattice of talus that pikas inhabit. For example, cold air can settle deep under the lower margins of talus, keeping it cooler than surface air temperatures throughout the warm season. The cooler interior would allow pikas to accommodate warmer summers by becoming crepuscular, feeding in early morning and late evening, and seeking shelter in the talus during the day (Beever *et al.* 2017). This behavioral adaptation has been observed in low elevation populations such as those found in the Columbia River Gorge (Simpson 2009). However, cool talus microhabitats will not help pikas to disperse throughout the environment in areas and seasons of extreme heat (Millar *et al.* 2016).

Because pikas do not hibernate, but instead remain active through winter by feeding on vegetation cached through the summer, they are at risk of acute hyperthermia from low winter temperatures. Snow pack provides insulation and a buffer against the extreme low temperatures, and greater snow depth has been suggested to allow longer site occupancy at Craters of the Moon National Monument and Preserve in Idaho (Rodhouse *et al.* 2018). For this to hold true, pika populations should decline in periods of snow drought, which was not found in populations in the Sierra Nevada Mountains of California (Smith & Millar 2018). This discrepancy may be due to the uncertainty in downscaling regional climate and snow accumulation records to local levels of individual pika populations in these complex landscapes. The decoupling of large-scale climate with what organisms experience could be catastrophic if local-scale conservation strategies are developed based on responses to broad scale forecasting (Rodhouse *et al.* 2018). Adding to the complexity, deep snow often melts later in the year, delaying spring vegetation growth and potentially restricting accessibility to critical forage. In fact, mortality rates increased with later dates of snow melt in American pikas in the Beartooth Plateau (Kruezer & Huntly 2003) as well as in the related collared pikas *(O. collaris)* in similar habitats in Northern Canada (Morrison & Hik 2007). The variable response to snow pack shows how subpopulations can respond to climate in different ways.

While talus habitat may provide a temperature buffer for pikas, it is naturally patchy in distribution across the landscape and therefore isolates pika populations from one another. These isolated populations have relatively low genetic variation within their populations and may not be able to respond to changing environments (Calkins *et al.* 2012). Pikas are also poor dispersers, making both genetic and demographic renewal of local populations less likely. Juvenile pikas establish their own territories before their first winter, traveling up to 3 km away from their natal territory. This low dispersal rate will most likely be further depressed by raising temperatures, which will both isolate habitable talus sites further and make the intervening matrix more inhospitable (Castillo *et al.* 2016). Population persistence may be enhanced by interconnected patches of talus, providing the animals greater genetic and demographic potential for weathering unusual or changing climates, similar to large talus areas, providing a greater variety of microclimates and resilience (Beever *et al.* 2016).

Because pikas remain active throughout the year, they must collect and cache forage in summer for the winter months and their distributions are linked to quality of forage. Vegetation quality has been an important descriptor American pika populations in the Wind River Range and the Bighorn Range of Wyoming as well as the Southern Rocky Mountains (Erb *et al.* 2014, Yandow *et al.* 2015). Collecting vegetation during the growing season may become more difficult as temperatures warm. Rising temperatures could reduce the amount of time that conditions are suitable for pikas to forage, forcing them to choose between increased risk of heat stress in summer or greater risk of starvation or hyperthermia during winter (Mathewson *et al.* 2017). However, resource selection is a potentially plastic behavior and may be a way for pikas to acclimate to the changing environment. In fact, pikas at lower elevations that are exposed to more extreme daytime temperatures have shown an increased selection for high-nitrogen and low fiber vegetation, supporting this food quality hypothesis (Hall & Chalfoun 2018).

Study Area

I studied the factors influencing the distribution of American pikas in the Beartooth Plateau of south-central Montana and northwestern Wyoming, and in three sites within YNP to the southwest (Figure 1.3). The Beartooth Plateau is the largest, true high-elevation plateau in the United States. The plateau slopes upwards to the east, peaking at 3900 m, and the alpine habitat at the top grades into sagebrush steppe to the west and south, to a rain-shadow desert to the east, and to woodlands to the north, with elevation reaching as low as 1300 m (mean = 2833 m, standard error = 444 m). Deep river canyons dissect the plateau and can funnel cool air from the tops of the plateaus to the valleys. Talus is found along the full elevational gradient and at all aspects. The cooler temperatures and extensive talus at high elevation may provide a critical refuge for pikas in a warming future climate. Extensive high elevation habitat is a different situation than many montane species face, in which shifts to higher elevations may restrict them increasingly to smaller and more isolated habitats. The Beartooth Plateau may provide a unique refuge for pika because the amount of talus may increase to high elevations instead of declining as in typical mountains.

At 3122 m, Mount Washburn is the tallest peak of the Washburn Range in YNP. This mountain differs from the Beartooth Plateau in several ways: it rises to a single peak that is lower in elevation than much of the Beartooth Plateau and therefore has little area at higher elevations, most of the talus is near the top, and there are no major river canyons to funnel cold air downhill. Pika populations on this mountain will have less opportunity to move to higher elevations, or to slopes with northern exposures, if the climate continues to warm, and they are far more isolated from other populations. Population persistence there may require that other factors considered in this research - microclimate, talus area and connectivity, or food plants - are favorable and allow them to persist.

At 2610 m, Bunsen Peak is even lower in elevation than Mount Washburn while still isolated from other potential pika habitats. Therefore, pika populations found near its peak may be at more immediate risk due to a warming climate. Finally, the Hoodoos are even lower in elevation (2100 m) and warmer, and therefore considered to be an unusual location for pikas. The Hoodoos are a boulder field of large, carbonate rocks, formed by a landslide of limestone deposits from an ancient hot spring and creating a low elevation site similar to a talus field. Their complex structure creates pockets of cooler temperatures that pikas can utilize via behavioral thermoregulation.

Hypothesized Determinants of Pika Distribution and Abundance

In this thesis, I examine several potential environmental determinants of pika distribution and abundance: features of climate, habitat, and vegetation (Table 1.1). Climate variables included summer maximum and minimum temperatures, winter maximum and minimum temperatures, summer precipitation, winter precipitation, and number of hours pikas could be active at the surface of the talus during the summer months. Habitat variables included measures of topography, talus site area, and the proportion of area containing talus within a 1 km radius of each sampling site. The proportion of talus within 1 km radius of each sampling site is used as a measure of a site's connectivity to other talus slopes.

Vegetation variables included the maximum Normalized Difference Vegetation Index (NDVI) and time of maximum NDVI and the ratio of forb to graminoid cover and forb species richness. The ratio of forbs to graminoids and forbs species richness were only included in the abundance analysis because these variables were only measured at sites where latrine density was also measured.

To understand how montane species will respond to the changing climate, we must first understand how climate varies locally in the landscape. In this remainder of this chapter, I describe how we determined the extent of pika habitat (talus) in the Beartooth Plateau and three Yellowstone National Park sites and characterized local climates in these regions using both *in situ* measurements and extrapolations from a high-resolution climate data set. In Chapter 2, I describe how we quantified plant diversity and abundance and examined how climate and pika habitats related to pika occupancy and density. This information about current determinants of pika distribution and abundance will be critical to predicting the distribution of pika in a warmer future climate.

Potential Habitat

Pika may be more abundant in areas with more talus. We therefore developed maps of talus within each study area (see Figure 1.4 for descriptive flow chart showing the steps to this process). We first identified areas of talus within each of the study regions using the imagery collected by the USDA National Aerial Imagery Project (USDA 2015). In ArcMap, we then used ISO unsupervised classification to develop a map of the talus within each study area. We used the resulting map of talus to calculate the percent of area containing talus within a 1-km radius of each talus site by extracting the percentage of raster cells that contained talus within this buffer area. Pikas may disperse further than 1 km, but this radius was used successfully to discriminate sites in California where pikas were extant from ones from which they had disappeared in historical times (Stewart *et al.* 2015).

In the Beartooths, the amount of talus appears to increase well into the alpine habitat (up to 3400 m in elevation) and only then starts to decline (Figure 1.5), while talus on Mount Washburn and the Bunsen-Hoodoo study area were found in a shorter range of elevation (Figure 1.6). Mount Washburn talus ranged from elevations of 2300 m to 3100 m with the most talus found around 2800 m. Talus slopes were found at a shortened range of elevation as well as declined quickly with elevation (Figure 1.7). Bunsen-Hoodoo area talus ranged from 1800 m to 2600 m with most of the talus found around 2200 m (Figure 1.8).

General Climate Trends of the Northern Range of the GYE

To understand the general climate found in this region, temperature and precipitation data was extracted from PRISM normal monthly climate model (www.prism.oregonstate.edu). PRISM (Parameter-elevation Regressions on Independent Slope Model, Daly *et al.* 2002) performs well in regions of complex terrain and has a relatively fine spatial resolution of 800 m. I summarized the overall climate for the Beartooth Plateau using the annual temperatures and precipitation from PRISM.

Maximum annual temperature ranged from 0.7°C to 16.1°C, and minimum annual temperature ranged from -11.5°C to 1.2°C. Average annual precipitation ranged from 185.8 mm to 1784.6 mm. Temperatures declined as elevation increased (Figure 1.9). Maximum annual temperatures declined by 6 °C/km but minimum annual temperatures only declined by 4 °C/km. Also, minimum annual temperatures varied more strongly than maximum annual temperatures at mid-elevations (2000 m to 3000 m). Precipitation increased by 412 mm/km and showed more variability after 2,500 m (Figure 1.10).

Thermal Heterogeneity of Talus Slopes

Previous research has shown that the talus interior temperatures can vary from temperatures at the surface (Millar *et al.* 2014). We verified that within our study area using temperature data loggers. In late September 2016, we placed Thermochron iButtons DS1921G data loggers w at 22 of the 49 intensively studied sites in the Beartooths, 2 of the 4 sites at the Hoodoos, and 4 of the 5 sites on Mount Washburn, to record temperatures to +/- 0.5 °C every two hours for a year. At each site, one data logger was placed at a depth of 1 m in the talus and another was placed at the surface. To limit their exposure to direct sunlight, data loggers were placed in chicken wire baskets and placed in full shade; rocks were piled as needed to ensure shading. We used these sensor data to calculate measures of microclimate including duration of snowpack and the difference in surface and interior temperatures. Additionally, we compared them to derived microclimate temperatures.

Maximum winter temperature recorded by the data loggers ranged from -7 °C to 4 °C at the surface of the talus and from -7 °C to -0.2 °C within the talus. Minimum winter temperatures recorded by the data loggers ranged from -29 °C to -0.3 °C at the surface and from -33 °C to -0.3 °C within the talus. Maximum and minimum winter temperatures did not vary significantly between the interior and talus surface (t-test, respectively $t = 1.3$ & 0.06, $p > 0.10$). Minimum winter temperature increased with elevation (Figure 1.11). The number of days with snow pack, measured by days where temperatures varied less than 2 °C, ranged from 167 days to 292 days at the surface and 187 days to 294 days within the interior of the talus. This number increased with elevation, but there was no significant difference between the days of snow pack experienced than did the surface compared to the interior (t test,, $t = 1.3$ $p = 0.26$, Figure 1.12).

Maximum summer temperatures recorded by the data loggers ranged from 4.2 °C to 40.9 °C at the surface and 4.7 °C to 28.2 °C at the interior. Minimum summer temperatures ranged from -2.5 °C to 0.5 °C at the surface and -3.2 °C to 0.5 °C at the interior. There was no difference between minimum summer temperatures at the surface compared to the interior (t test, $t = 0.16$ $p = 0.87$), but the interior experienced significantly cooler maximum summer temperatures compared to the surface (t test, $t = 1.7$, $p = 0.04$, Figure 1.13).

Biophysical Model and Pika Activity on the Talus Surface

In areas of population extripation, warming temperatures have been implicated as the main culprit (Calkins *et al.* 2012). However, it remains unclear how specifically temperatures operate to limit pika distributions. Temperatures may exceed the pikas' thermal limits, directly causing mortality through heat stress, or they may influence distributions more subtly, by changing the vegetation community or reducing snow cover (Moyer-Horner *et al.* 2016). If temperatures limit pikas through heat stress, the animals must balance the need to thermoregulate with the need to graze and collect vegetation for the winter. High sustained temperatures may restrict pikas ability to maintain this balance and restrict their distributions more than outright mortality. This potential mechanism is best studied using biophysical modeling that calculates windows of activity for animals as a function of their biology and local temperatures (Mathewson *et al.* 2017).

Niche Mapper$_{TM}$ is one biophysical model which couples microclimate and an animal heat-mass-balance model to calculate how many hours the animal can remain active at given local temperatures (Porter & Mitchell 2006). Specifically, the program computes hourly values of local microclimate for a month's "average" day from monthly extreme temperatures and topographical features of the location (slope, aspect, elevation). Then the model numerically solves the heat balance equation and calculates whether the organism can remain active, whether for foraging, caching food for the winter, interacting with other individuals or other behaviors without thermal stress (quantified as a multiple of Basal Metabolic Rate, predefined by the researcher (Moyer-Horner *et al.* 2015). In addition, Niche Mapper$_{TM}$ calculates the amount of grams of food necessary to maintain the organism's metabolic rate, dependent on the microclimate experienced. Ultimately Niche Mapper$_{TM}$ predicts the number of hours an individual can be active on the average day for each month, a simple, mechanistic variable that is well-suited to investigating the response of specific organisms to rising temperatures (Mathewson *et al.* 2017) as well as the amount of food necessary to remain active in their environment, potentially a more sensitive mechanistic variable. Niche Mapper$_{TM}$ has been used to predict the metabolic heat production, habitat use, and landscape distribution for a variety of animals, including successful predictions of pika metabolic rates and activity within Glacier National Park. It successfully predicted metabolic rates of pikas measured in situ (Moyer-Horner *et al.* 2015). Surface activity hours derived from Niche Mapper$_{TM}$ successfully predicted the landscape level-distribution for pikas across western North America (Mathewson *et al.* 2017).

We used Niche Mapper$_{TM,}$ to estimate the number of hours that pikas could remain actively foraging and engaging in other similar activities during each of the summer months (June—September).

Monthly minimum and maximum temperatures were extracted from PRISM and ClimateWNA and were used as the input for the microclimate model and previously described physiological traits of pikas were used for the animal model (Moyer-Horner *et al.* 2015).

Niche Mapper$_{TM}$ was relatively accurate at predicting the temperatures recorded at our sites during the summer months, showing similar results to those found by Moyer-Horner *et al.* (2015). Temperatures recorded by the data loggers followed the predicted temperatures from Niche Mapper$_{TM}$ using the PRISM and ClimateWNA climate data (Figure 1.14). Niche Mapper$_{TM}$ was less accurate predicting temperatures during the winter months, predicting colder temperatures than those recorded by the data loggers. These colder temperatures may be due to the fact that the data loggers were covered by snow for most of the winter months, thus not truly recording surface temperatures. The discrepancies between temperatures recorded by the data loggers and the temperatures derived by Niche Mapper$_{TM}$ are most likely due to the fact that Niche Mapper$_{TM}$ only predicts an average day and temperatures are more variable *in situ*.

Surface activity had a strong relationship with elevation but not aspect (Figure 1.15). There was some variability between predicted activity hours derived from PRISM (Figure 1.16) compared to the ClimateWNA (Figure 1.17) but it was not statistically significant. Of the 158 Beartooth sites in the occupancy analysis, 41 sites had the same activity hours from each model, 75 had more activity hours under the WNA model (maximum difference of 92 more hours than predicted by PRISM) and 42 sites had more activity hours under the PRISM model (maximum difference of 61 hours, Figure 1.18). ClimateWNA predicted more variability in surface activity hours at lower and middle elevations, but PRISM predicted more hours at higher elevations (Figure 1.15).

Concluding Remarks

Through these preliminary analyses, the Beartooth Plateau is in the position to be an area of conservation for pikas as the climate warms. It has large tracts of talus found at high elevations that may be cooler and less thermally stressful for pikas. But quantifying the amount of talus within each study area is likely not enough to predict the stability or persistence of pikas in this region. Understanding the relationship between other environmental variables and the presence and density of pikas currently is necessary to make predictions for the future and to identify key habitats for conservation.

Climatic parameters are often used to make predictions to how populations will change as the climate changes in the future, but species experience temperature on a finer scale, not two meters above the surface, where temperature generally is measured. This operative temperature is influenced by the local topography and biophysical models can downscale climate to temperatures experienced at the organismal level (Porter & Mitchell, 2006). Biophiscal models, and the mechanistic parameters derived from them, are a more direct approach to understanding how climate can influence populations. Mechanistic parameters, such as surface activity hours and necessary amounts of food predicted by Niche Mapper, may have a stronger relationship with occupancy and population densities than climate parameters because Niche mapper$_{\text{TM}}$.is able to model the consequences of interactions between a species environment and its characteristics (morphology, physiology and behavior) on the species' activity levels and energetics (Mathewson *et al.* 2017). Recently, mechanistic approaches were successful at modeling species distributions. Specifically, surface activity hours have accurately predicted pika presence across the western United States, and they have accurately described occupancy of talus sites in Glacier National Park (Mathewson *et al.* 2017, Moayer-Horner *et al.* 2016). However, surface activity hours have not been related to measures of population densities. The study I describe in the next chapter is the first to use a high spatial resolution climate model for pikas and to relate surface activity hours with pika abundance.

CHAPTER TWO

INTRODUCTION

Ongoing climate change is expected to have profound effects on ecosystems around the world. Species will either tolerate these changes, adapt to them through behavioral or genetic mechanisms, shift to new regions with more favorable climates, or disappear. Range shifts to higher elevations or latitudes have been well documented across many taxonomic groups (Chen *et al.* 2011, Thomas 2010). However, when the range shift is an elevational shift, potential habitat may become smaller and farther apart, isolating species and increasing the potential for bottleneck effects (Beever *et al.* 2016, Elsen & Tingley 2015). Montane species are especially at risk of isolation through range shifts because their habitat is often already fragmented (Calkins *et al.* 2012). As the climate changes, it is becoming more critical to understand determinants of montane species' distributions in relation to help predict their responses.

The American pika (*Ochotona princeps*) has become a model of a montane species at risk from climate change (*e.g.*, NRC 2008). These small alpine lagomorphs are restricted to open talus habitats of western North America and have little physiological resilience to temperature extremes because of their high basal metabolic rates and low thermal conductance (Moyer-Horner *et al.* 2015). This thermal sensitivity makes pikas susceptible to the changes in climate expected over the next century. The warming temperatures could lead to chronic and acute heat stress in summer while the reduction in snow pack and loss of its insulating cover could lead to pikas freezing (Rodhouse *et al.* 2018) or starving in winter (Bhattacharyya & Ray 2015). In addition, their small size and limited dispersal ability leave them tied to patches of talus habitat, and they may disappear if these patches are not large or connected (Castillo *et al.* 2016). Finally, they do not hibernate but instead must survive on plants collected through the summer, so they may be particularly dependent on the quantity and quality of their food plants, which may also change with climate and range shifts. These three factors of climate, habitat and food are linked because climate varies with elevation, talus may be more common on higher or steeper slopes, and plant communities themselves vary with climate. Therefore, a warming climate may not just push pikas upslope but may also change the availability and quality of their habitats.

American pikas are found at a range of elevations but recently, there have been reports of extirpations of low elevation populations (Beever *et al.* 2003, 2016). However, in other portions of their range, pika populations are stable at low elevations (Simpson 2009). While many believe the warmer climate is the culprit, the dominant mechanism underlying pika range shifts has not been identified (Stewart *et al.* 2015). Particular populations may be buffered from decline by cool microclimates, large metapopulations, high quality forage (Erb *et al.* 2014, Mathewson *et al.* 2017), or a combination of them all. The variety of responses to climate by pika populations across western North America suggests that the future of these populations are context dependent. Here we seek to characterize the distribution of pikas in the Beartooth Plateau northeast of Yellowstone National Park (YNP) and in three sites within YNP in the American West, with the goal of predicting this species' fate under a future warming climate. We compared characteristics of the habitat, climate, and vegetation relationship with site occupancy and pika latrine densities to understand what influences pika populations within this region currently. If similar factors predict occupancy and latrine density, then how these factors will change under future climate scenarios can give us insight on how pika distributions may change in this region.

METHODS

Study Area

We conducted this research in the Beartooth Plateau, northeast of YNP, and in three isolated mountains, Mount Washburn, Bunsen Peak and the Hoodoos, within YNP. The Beartooth Plateau is the largest, true high-elevation plateau in the United States and is bisected by deep river canyons that can funnel cool air to lower elevations. It contains extensive, high elevation talus that may provide critical refuge for pikas as the climate warms. The Beartooth study area (about 4,300 km^2) was constrained to the area east of the Stillwater River, with most of our study locations along the Beartooth Highway (Highway 212), which bisects the plateau from southwest to northeast and provides access to sites at all elevations across this vast area (Map 1A). Mount Washburn (9.5 km^2) and Bunsen study areas (8.2 km^2) were defined by their hydrological boundaries. We constrained the area within the Hoodoos (1.1 km^2) to the area downslope of the travertine cliffs for logistical reasons. Data from Bunsen Peak and the Hoodoos were combined because of their proximity and pikas potential stability to disperse between the two areas.

Classification of Topography and Climate

We described the topographical characteristics of each region using a high resolution (10 m cell width) digital elevation model (DEM). Because pikas may be responding to different topographical characteristics of their habitat, we extracted the slope and aspect of each site using the high resolution DEM. We constructed a measure of solar insolation as a function of slope and aspect with the relation insolation = (sin(slope) * cos(aspect), following Rodhouse *et al.* (2018). Insolation varies on a gradient from steep southern slopes to flat slopes to steep northern slopes. To incorporate aspect as a predictor variable separate from insolation, we linearized it with the equation sin(aspect) + cos(aspect) (Al-Daffaie & Khan 2017). This linearization ranges from -1, facing due south, to 1, facing due north. To measure talus area, we identified the talus sites on Google Earth and measured the area of the polygon outlining each site. To include a measure of habitat connectivity, we calculated the proportion of area covered by talus within 1 km diameter of each site which was identified by a classification process of USDA aerial photos (Chapter 1). Annual climate variables were derived from the PRISM climate dataset (www.prism.oregonstate.edu). Winter and summer climate variables were extracted from both PRISM (800 m resolution) and ClimateWNA datasets (10 m resolution, Wang *et al.* 2012).

Surveys for Pika Presence

Between June-August of 2016, we surveyed 69 talus sites within the Beartooth Plateau for the presence of pikas. These sites were chosen to represent a range of elevations, slopes, and aspects, but were concentrated along Highway 212, which traverses the plateau from southwest to northeast and provides access to an otherwise remote, vast wilderness. Pikas have a high detectability rate, upwards of 90% (Beever *et al*. 2003). At each site, two people walked transects searching for fresh scats, haypiles, and individuals for 30 minutes to determine if pikas were present. We recorded the GPS coordinates of each site, along with slope, aspect, and area. Between June-August of 2017, we resurveyed 67 of these sites, and surveyed an additional 89, 6, 5, and 5 sites in the Beartooth Plateau, Mount Washburn, Bunsen Peak, and the Hoodoos, respectively for a total of 158 sites in the Beartooths and 16 sites within YNP. These sites were chosen based on their aspects and elevation (1900 m to 3500 m) and, in the case of sites within YNP, the Park's approval process.

Estimating Pika Densities

To estimate pika density, we measured the density of pika latrines in 65 of the 158 sites that had been surveyed for pika presence. Because pikas are territorial, they will reuse latrines within their territory, making latrines the most consistent available signs for current densities of pikas (Yandow *et al.* 2015). We examined 49 sites in the Beartooths (31 in 2016 and 18 more in 2017) and all 16 sites in YNP in 2017. Eight of the 31 Beartooth sites surveyed in 2016 were surveyed again in 2017 to determine whether latrine densities change substantially between years. We walked transects parallel to the bottom of the talus site, starting 15 m from the lower edge and at 30 m intervals. On each transect, we counted the number of latrines within 15 m on either side of the transect to avoid double counting (Erb *et al.* 2014).

Characterization of Vegetation

At the 65 sites where pika densities were estimated, we also sampled the vegetation. To measure vegetation on the talus slopes, we used the point-intercept method from Yandow *et al.* (2015). The first 50-m transect was parallel to the bottom of the slope and 10 m from the talus edge. The next transect was 10 m upslope of the first transect, and this was continued up slope for up to 6 transects, depending on the patch size. Along each transect, we recorded the vegetation type at -m intervals, identifying forbs, shrubs and trees species, and recording grasses, rushes and sedges together as graminoids. When present, mosses, lichens, and bryophytes were recorded, but no attempt was made to distinguish species. If no vegetation was present, then bare rock was recorded. All the vegetation surveys were conducted after mid-summer (mid-July), so that the vegetation was identifiable. During the second season, we initially sampled eight of the 30 original intensively studied locations to investigate if there was a change in latrine density or vegetation community before sampling 34 additional sites. Neither latrine density nor the vegetation community varied substantially between the two years. Pika latrine densities ranged from 20 to 297 per ha (mean = 104, SE = 60) and did not differ significantly between the two years.

Characterization of Niche Mapper$_{TM}$ and Derived Mechanistic Variables

We used Niche Mapper$_{TM,}$ a coupled microclimate and a biophysical model of animal heat-and-mass balance (Porter *et al.* 2000, Porter & Mitchell 2006), to estimate the number of hours that pikas could remain actively foraging and engaging in other similar activities during each of the summer months (June—September). Monthly minimum and maximum temperatures were extracted from PRISM (www.prism.oregonstate.edu) and ClimateWNA (Wang *et al.* 2012). These temperatures were used as the input for the microclimate model. Niche Mapper$_{TM}$ uses the input temperatures and location specific topography to calculate the hourly profiles of air temperature, wind speed, relative humidity and thermal radiation that an organism experiences. After calculating the microclimate profile, Niche Mapper$_{TM}$ incorporates information on animal mass, morphology, fur properties, behavior and physiological responses to stress, to predict the number of hours pikas can remain active at two times the basal metabolic rate (Mathewson *et al.* 2017).

Indirect Measures of Vegetation

To include measures of vegetation quality and quantity in the occupancy analysis, we measured the maximum Normalized Difference Vegetation Index (NDVI) and Julian date of maximum NDVI from Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation phenology dataset at 250 m resolution (Zhang *et al.* 2003). MODIS collects daily multi-angle, cloud-free, and atmospherically corrected surface reflectance over 16-day periods. A piecewise logistic function calculates NDVI throughout the season, and then max NDVI and timing of max NDVI are derived. These remotely sensed data provide a simple tool to quantify levels of live green vegetation and time of peak productivity using 36 measured spectral bands between 0.405 and 14.385 μm.

Statistical Analyses

We evaluated models of occupancy and density with respect to predictor variables of topography, climate, habitat, and vegetation. Models were fit in R (R Development Core Team 2012) using function glm.nb from MASS, version 7.3-51.1 for modeling latrine density (Venables & Ripley 2002) and function colext from Unmarked version 0.12-2 for multiple season occupancy modeling of pika presence (Fiske and Chandler 2011). Models were compared using the Akaike Information Criterion corrected for finite sample sizes (AICc). For occupancy, the Mackenzie-Bailey Goodness of Fit was used to determine if there was over dispersion in detection probabilities measured by the $\hat{c}$, a variance inflation factor (MacKenzie *et al.* 2002). We used negative binomial models for latrine density because latrine densities are derived from count data with a variance that exceeds the mean (Zuur *et al.* 2009).

All predictor variables were standardized before analysis by subtracting the mean value of the variable, and dividing by one standard deviation. All main effect variables were examined for collinearity before analysis by calculating their Variance Inflation Factor (VIF) and pairwise correlations. Because surface activity hours was derived from climate data used by Niche Mapper, these variables are not independent and none of the models included variables of climate and mechanistic variables. Also, climate variables and elevation showed signs of colinearity and thus were also separated from each other in the candidate model set. None of the vegetation and topographical variables had a VIF > 3 or pairwise correlation > 0.5 and therefore all were retained for analysis. Beartooth and YNP sites were pooled together because preliminary analyses indicated no effect of site on pika density or occupancy. Additionally, one site was excluded due to its unusually high presence of forbs.

Model coefficients of the suite of candidate models within 4 AICc were averaged using model.avg and coefTable from MuMin package version 1.42.1 (Barton & Barton 2018). We also report the standard error and weight for each parameter.

RESULTS

Detection and Proportion of Sites Occupied

Of our initial 69 surveys, 79.7% of sites were occupied by pika. During the second season, 5.8% of those initial surveys became occupied and 8.7% became unoccupied. Of the total 158 sites (the original 69 surveys and another 89 only surveyed in the second season), 80.4% were occupied. The detection probability was 0.787 during our initial season (95% CI = 0.715 – 0.859) and was higher the second season (detection probability = 0.924, 95% CI = 0.881 – 0.967).

Determinants of Occupancy

We compared multiple season occupancy models with combinations of a variety of variables from the 28 potential variables, including topography, habitat connectivity, vegetation, climate, and summer activity hours (Table 2.1). Mackenzie-Bailey Goodness of Fit tests showed that the models were a good fit for the first season's survey but were not the second season data. The $\hat{c}$ was 1.62, which does not suggest over dispersion. The null model was a good fit for the first season's data ($\lambda = 35.85$, $p = 0.10$) but was not a good fit for the second season's data ($\lambda = 7.38$, $p = 0.045$). The lack of fit to the second season's data may be due to to an unmeasured site characteristic or, potentially, the high detection of pikas because of their high visibility and vocalizations. Because of the high detection probability, we assumed constant detection probability for our occupancy analysis. Out of the 33 potential variables related to occupancy, there were 4 top parameters: Julian day of maximum NDVI, proportion of talus within 1 km, summer precipitation and winter precipitation (Table 2.1). Overall, the probability of occupancy increased with greater habitat connectivity and with primary productivity peaking later in the year. Habitat connectivity, measured by proportion of talus within 1 km of the site, and seasonal precipitation were the most important variables related to pika occupancy. Time of maximum vegetation cover (NDVI) was the strongest predictor of occupancy (weight = 0.98), followed by percentage of talus within the local area (weight = 0.97). Occupancy increased with respect to both (Figures 2.1 and 2.2, respectively). Summer precipitation (WNA, weight = 0.77) and winter precipitation (WNA, weight 0.57) had a positive relationship with occupancy (Figures 2.3 and 2.4). Climatic variables derived by ClimateWNA appeared to be better predictors of site occupancy than PRISM because they had stronger weights, 4 out of 6 times (Table 2.1).

Determinants of Pika Density

Of the 35 potential variables, the best predictors of latrine density included a combination of habitat quantity, topography, climate, and vegetation (Table 2.2). The ratio of forbs to graminoids, degree of slope, area of talus, and maximum NDVI were the strongest parameters. More latrines were found in more open areas with flatter, larger talus fields with higher levels of forbs compared to graminoids (Figure 2.5). Annual climate variables were the weakest predictors of latrine density. Parameters derived from the higher spatial resolution climate model, ClimateWNA, were often stronger predictors of latrine density than those derived from PRISM. The number of activity hours had a negative relationship with latrine density and was a stronger predictor of latrine density than parameters measuring amounts and quality of food (i.e. grams of food derived by Niche Mapper$_{TM}$).

DISCUSSION

Our results yielded unexpected insights on how climate and vegetation govern occupancy and abundance of pikas in an area that could be a refuge for montane species under future climatic scenarios. There appeared to be contradictory relationships between the influencers of occupancy and abundance. Unexpectedly, occupancy declined with increased maximum winter temperatures while pika abundance increased with winter temperatures. Additionally, occupancy increased with energy requirements, measured in grams of food necessary to maintain metabolic activity, whereas density declined with increasing energy requirements. Abundance is considered a noisier indicator of ecological change than occupancy, but it is more sensitive to environmental changes and habitat characteristics than incidence (Noss 1990). This sensitivity and the unexpected relationships may indicate that factors influencing occupancy do not have the same relationship, or strength of relationship, as with abundance. This inconsistency could have large implications for management because many regional monitoring programs use incidence monitoring protocols instead of abundance data. Those protocols may not help managers determine which areas have conditions and resources for populations to be stable.

Pikas are known to be sensitive to both extreme summer and winter temperatures (Moyer-Horner *et al.* 2015, Hall *et al.* 2016). Previous findings have suggested that maximum temperature is important to pika distribution and abundance because a pika's limited ability to dissipate heat makes it prone to death by from heat exposure Beever *et al.* 2003, 2016, Jeffress *et al.* 2013). Surprisingly, maximum summer temperature was not a strong predictor of occupancy or density, suggesting pikas within this region are not limited, currently, by high summer temperatures. Pikas begin to experience thermal stress near 25 °C and only 5 of our surface data loggers recorded maximum temperatures above that threshold. Activity hours were negatively related to pika abundance, which could result from pikas using time they could be collecting forage to defend larger territories. Alternatively, the Beartooths aren't currently experiencing restricting summer temperatures.

Influence of Climate on Pika Occupancy and Abundance

The presence of winter climate variables in the top models suggests that pikas in the Beartooths are more limited by the winter climate. As winter temperature warmed, occupancy declined. Warmer winter temperatures have been related to less snowpack, which is critical insulation for pikas (Morrison & Hik 2007). However, for this to hold true, we would expect occupancy and abundance to increase with winter precipitation, which is not what we found. Microclimate of the talus matrix stabilizes relatively quickly after a certain amount of snowfall (Millar *et al.* 2014, Varner & Dearing 2014). Therefore, there may be a critical amount of snowfall necessary to allow pikas to persist but precipitation past that point would have negative consequences. Areas that experienced later snow melts, such as snowfields, created a population sink and this was found to be true on the Beartooth Plateau (Kruezer & Huntly 2003).

Abundance increased with winter temperatures, suggesting, at the local level, less extreme winter temperatures allow higher population of pikas to persist.

Interestingly, seasonal temperature variables derived by PRISM were stronger predictors of occupancy, but ClimateWNA precipitation variables were stronger predictors than those derived by PRISM. Precipitation can vary more dramatically than temperature across montane ecosystems and thus, higher resolution climate data may be better suited to understand precipitation's role in describing species distributions. Therefore, high resolution climate data should be used when it is available (Wang *et al.* 2012, Schwalm *et al.* 2016).

Influence of Habitat on Pika Occupancy and Abundance

Habitat size and connectivity play an important role in providing ample space for population stability (Castillo *et al.* 2016). The amount of talus in the surrounding habitat, a measure of habitat connectivity, was a strong predictor of pika occupancy and abundance. Pikas are relatively poor dispersers and having more potential habitat within the surrounding area can facilitate movement, maintain genetic diversity and stabilize metapopulations (Kruezer & Huntly 2003, Schwalm *et al.* 2016). Also, large amounts of talus can increase the heterogeneity of the thermal environment and pikas can use the variation in microclimate to behaviorally thermoregulate more effectively while foraging and grazing (Millar *et al.* 2014). It should be noted that area was not a significant influencer of occupancy and had a negative relationship with pika abundance. This result is similar to that found by Erb *et al.* (2014) in the Southern Rocky Mountains and may result from competition for space or edge effects at the rock-meadow interface. Slope of the talus site was another strong predictor of pika abundance in our study but was absent from the top models of occupancy. Flatter slopes may provide more complex microclimates because the internal matrix structure found on these types of talus causes cool air to pool within the talus instead of sinking to lower elevations (Millar *et al.* 2014).

Influence of Vegetation on Pika Occupancy and Abundance

Pikas may be able to mitigate some of the effects of stressful temperatures through their forage selection. Pikas harvest throughout the growing season but sites with peak growth later in the year might be higher quality habitats (Huntly *et al.* 1986). The longer plants have been cut, the less nutritious they may become. Therefore, if the time of peak primary productivity is later in the year, the haypiles may retain more nutrients and provide critical forage during the later months of winter. Caching later in the year may explain why occupancy increased with later timing of peak primary productivity (maximum NDVI).

Vegetation quantity and quality were also strong predictors of latrine density, and presumably pika density. Latrine abundance increased as more forbs were found within the talus slopes and, less strongly, increased with forb richness. Pikas are generalist herbivores but forage selectively to optimize nutritional gains in their winter caches (Bhattacharyya & Ray 2015). Forbs are higher quality forage, and it has been shown that pikas prefer caching forbs to other sources of food, such as graminoids (Huntly *et al.* 1986, Smith & Erb 2013). Their preference for forbs may also explain the positive relationship with forb species richness. The presence of both forage quality metrics in the top models show there are direct effects of forage quality mediating pikas' response (Erb *et al.* 2014). Higher quality forage may be able a useful tool for pikas in a warmer climate (Hall & Chalfoun 2018). If pikas optimize the nutrition and energy they gain from each haying event, they may be able to collect enough nutrients in a shorter amount of time. This hypothesis was supported by Hall & Chalfoun (2018) in the Bridger-Teton National Forest, the southeastern portion of the GYE. In that area, pikas experiencing warmer daytime temperatures were more selective in their foraging, collecting plants with higher nitrogen and lower fiber content, indicating a shift in resource selection. By shifting resource selection, pikas may be able to modulate the negative impacts of warming summer temperatures.

It should also be noted that vegetation communities vary with respect to climate (Johnson & Billings 1962). Alpine plants are often sensitive to microhabitat requirements, including duration of snow cover. Winter precipitation duration and depth can insulate plants from extreme cold stress and influence the beginning of the growing season (.Gasarch & Seastedt 2015) Within the scope of this study, the ratio of forbs to graminoids may be a more comprehensive measure of the local climate than ambient or surface temperatures. This measure may indirectly describe the amount of precipitation and temperature to provide the most suitable habitat for pika.

Relevant Spatial Scale Climate Data

High-resolution climate data are critical for relevant ecological research, especially in areas of heterogeneity such as montane ecosystems. Montane ecosystems can experience changes in climatic conditions in matters of a few hundred meters, which is typically within one grid cell of most climate models (Wang *et al.* 2012). PRISM and ClimateWNA-derived variables showed similar relationships with occupancy and abundance, with the exception of winter precipitation. When modeling occupancy, both model variables were equivalent in model weight (Table 2.3). However, ClimateWNA variables were consistently stronger at predicting abundance. Abundance is more sensitive than occupancy to environmental variability, and obtaining high-resolution climate data may be crucial to studies of why species abundance varies over the landscape. High-resolution climate data will only become more critical as the climate changes and as we attempt to predict how species will respond to these changesclimate. Ultimately, species will not be responding to large-scale climate trends but instead to climate they experience at a local level. Modeling those trends will better predict how species distributions will change and strengthen our abilities to create successful conservation plans (Mathewson *et al.* 2017).

Concluding Remarks

Our investigation of pika distributions within the northern portion of the Greater Yellowstone Ecosystem yielded insights into the controls underlying pika occupancy and abundance in this region. Pikas in this region do not appear to be experiencing limiting summer temperatures but instead appear to be limited by precipitation and winter temperatures. They appear to have ample surface activity hours, emphasized by the unexpected negative relationship we found with latrine density and this variable.

Connectivity, vegetation and timing of vegetation were strongly associated with occupancy and abundance, emphasizing the importance of non-climatic factors in species distributions. In addition, this study highlights how climate data at a fine spatial scale can be more informative than previously described models, with predictors derived by the ClimateWNA often having a stronger relationship with occupancy and latrine density. When possible, higher resolution climate data should be used to better understand how species will respond to climate. Finally, this study identified the Beartooths as an area where pikas are not experiencing thermally stressful conditions. This bodes well for pikas in the region as well as other species such as marmots, alpine forbs and other speices which are also sensitive to warmer temperatures. Due to its topography, the Beartooth Plateau provides a refugia for pikas under the present, and quite possibly the future, climate. It has large portions of talus at high elevations providing ample habitat for pikas. Identifying areas that are similar should be a top conservation priority because of their uniqueness and ability to sustain genetic diversity, especially for montane species that are expected to have dramatic range shifts under future climate scenarios. For pikas, using imagery classification to identify large areas of talus for conservation or identify areas where management could connect talus to foster dispersal could help maintain populations.

Future Research

Pika distress due to summer temperatures have been well documented across their range, but my work emphasizes the importance of winter climate, habitat connectivity, and vegetation quality as factors describing pika distributions. Winter snow pack and temperatures describe pika distributions within this region. It is important to note that there is limited research on pika activities throughout the winter, even though it is one of a select few non-hibernating alpine mammals. Pikas are expected to survive by grazing on the vegetation in their haypiles, but that has not been thoroughly studied. In addition, little is known about the potential thermal benefits of the haypiles, and they may help pikas insulate against cold winter temperatures during years of snow drought. The extreme winter environment and remoteness of the alpine would make it quite difficult to study these aspects, but improvements in cameras, remote sensing and data loggers will make these studies more feasible.

Large amounts of talus and increase connectivity can facilitate dispersal but little is known when pikas disperse, except that time of dispersal is near the end of the growing season and most often done by juveniles (Peacock & Smith 1997). Human-facilitated dispersal, which involves capturing organisms and moving them or by manipulating the habitat to become more connected, might be an effective way to connect suitable talus sites. Gathering more information on dispersal events and juvenile survivorship after dispersing may give us the necessary information to facilitate the movement of pikas among metapopulations. Regardless, habitat will need to remain functionally connected as the climate changes to maintain stable populations.

Vegetation quality was shown to be important through this research, and pikas at lower elevation have been observed shifting their diet where they experience warmer summer temperatures (Hall & Chalfoun 2018). But this research is not extensive, showing only a potential adaptation. More extensive work is necessary to fully understand thermoregulatory risks influencing forage behavior. Resource plasticity will only be successful as long as the higher quality resources are available for exploitation, and the alpine vegetation community is expected to change with the climate. Graminoids may become more prevalent as the climate warms and dries, outcompeting the nitrogen-rich forbs. As climate change continues, efforts to understand the changing animal-habitat relationships will be necessary, especially considering species abilities to modify resource selection. Regardless of future efforts to mitigate climate change, we are experiencing a shift in climatic norms, and montane ecosystems are at the forefront of these changes. Understanding how these changes will impact pika distributions will offer insight on the potential changes montane species will experience as the climate warms. Conservation and management efforts should focus on understanding all potential buffers to these changes.

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Figure 1.1: An American pika. Photo credit: Kaitlyn Hanley.

Figure 1.2: A typical talus slope in the Beartooth Mountains.
Photo credit: Kaitlyn Hanley.

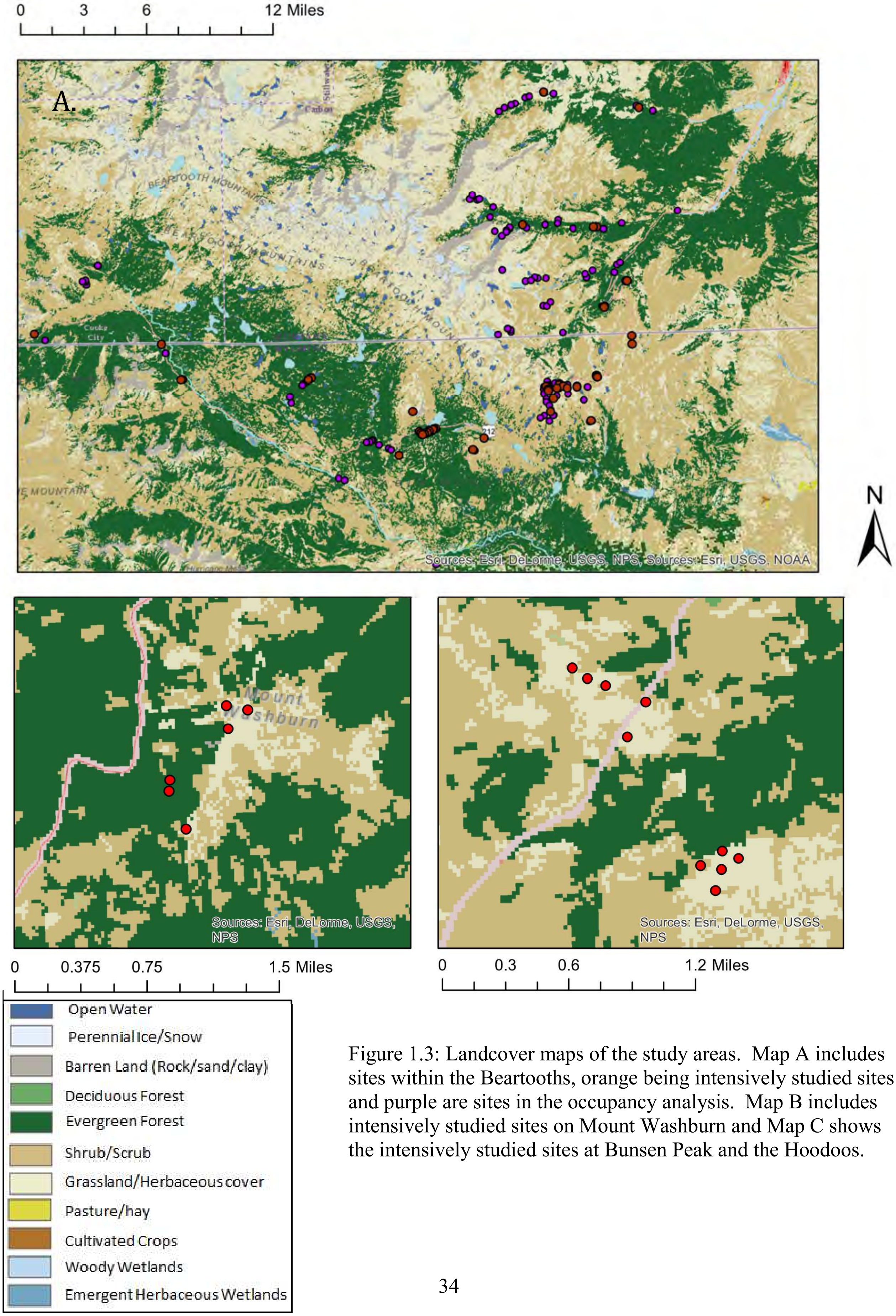

Figure 1.3: Landcover maps of the study areas. Map A includes sites within the Beartooths, orange being intensively studied sites and purple are sites in the occupancy analysis. Map B includes intensively studied sites on Mount Washburn and Map C shows the intensively studied sites at Bunsen Peak and the Hoodoos.

Table 1.1: Description of variables include in occupancy and abundance analysis including a short description of how the data was acquired and predicted relationships.

Parameter	Variable description	Definition of ecological relationship
Topography		
Elevation (m)	Extracted from 10 m resolution DEM	Elevation indexes many key climate metrics, resulting in cooler, more moist sites at higher elevations.
Slope (°)	Extracted from 10 m resolution DEM	Extracted from 10m resolution DEM, steeper slopes may cause cooler air to sink into the talus and provide refuge. Steeper slopes increase talus complexity (Millar et al. 2016).
Sin(aspect) + cos(aspect)	Extracted from 10 m resolution DEM	Aspect was extracted from 10m resolution DEM. This is a linearization of aspect for logistic modeling (Al-Daffaie & Khan. 2017). Northeast aspects are cooler, preferred climate.
Insolation sin(slope)*cos(aspect)	Extracted from 10 m resolution DEM	A measure of topographic position based on slope and aspect (Rodhouse et al. 2017). Varying from -1 to 1, it captures a gradient from steep, south facing slopes to steep, north facing slopes.
Habitat connectivity		
Talus area (ha)	Measured area of a polygon overlaying imagery of site	Increase talus size will provide more area for pika populations (Schwalm et al. 2016).
Percent Talus (%)	Number of pixels classified as talus within circle with a radius of 1 km surrounding each site	Increase in talus in the surrounding area could provide source populations and foster dispersion (Schwalm et al. 2016).
Vegetation		
Total vegetation (%)	Summation of percent covered by vegetation measured within our intensively studied sites	Increase vegetation would increase potential forage and energy for pika, critical for maintaining activity, especially in the winter (Yandow et al. 2015).

Table 1.1 (Continued): Description of variables include in occupancy and abundance analysis including a short description of how the data was acquired and predicted relationships.

Parameter	Variable description	Definition of ecological relationship
Vegetation		
Forbs:grams ratio	Ratio of forbs to graminoids measured at intensively studied sites	A metric of high quality food source (forbs) compared to lower quality food source (graminoids). Pikas are known to be selective when collecting for their haypiles (bias towards forbs, Huntly *et al.* 1986).
Forb Richness	Number of species of forbs identified at intensively studied sites	Provides a variety of highly nutritive forage for pikas (Erb *et al.* 2014).
Max NDVI	Extracted from Moderate Resolution Imaging Spectroradiometer	Quantifies the level of greenness during peak growing season.
Climate		
Time of Max NDVI (Julian day)	Extracted from Moderate Resolution Imaging Spectroradiometer	Peak primary productivity will happen later in the year.
Maximum temperature - PRISM	Maximum annual temperature extracted from PRISM normal data set	Due to sensitivity to heat stress, pikas abundance and occupancy should decline as temperatures warm (Beever *et al.* 2013).
Minimum temperature - PRISM	Minimum annual temperature extracted from PRISM normal dataset.	Pikas are sensitive to colder temperatures (Rodhouse *et al.* 2018).
Precipitation – PRISM (mm)	Annual precipitation extracted from PRISM normal dataset	Precipitation may indicate areas of cooler climates, its direct influence on the vegetation community, specifically its water balance. Increase precipitation may mitigate heat stress.
Winter precipitation – PRISM (mm)	Extracted from the monthly PRISM climate data, adding the months of December, January, February	Increased snowfall creates a buffer against extreme winter temperatures (Millar *et al.* 2016).
Winter precipitation – WNA (mm)	Extracted using a 10 m resolution DEM and ClimateWNA model	Increased snowfall creates a buffer against extreme winter temperatures (Millar *et al.* 2016).

Table 1.1 (Continued): Description of variables include in occupancy and abundance analysis including a short description of how the data was acquired and predicted relationships.

Parameter	Variable description	Definition of ecological relationship
Climate		
Summer precipitation – PRISM (mm)	Extracted from the monthly PRISM climate data, adding the months of June, July, August	Increased precipitation may indicate areas of cooler climates, its direct influence on the vegetation community, specifically its water balance. Increase precipitation may mitigate heat stress.
Summer precipitation – WNA (mm)	Extracted using a 10 m resolution DEM and ClimateWNA model	Increased precipitation may indicate areas of cooler climates, its direct influence on the vegetation community, specifically its water balance. Increase precipitation may mitigate heat stress.
Summer minimum and maximum temperature – PRISM	Average maximum/minimum temperature for the months of June, July and August (summer)	Acute and chronic heat stress would cause pikas to decline as summer temperatures warmed (Beever *et al.* 2013).
Summer maximum and minimum temperature – WNA (°C)	Extracted using a 10 m resolution DEM and the ClimateWNA model	Acute and chronic heat stress would cause pikas to decline as summer temperatures warmed (Beever *et al.* 2013).
Winter maximum and minimum temperature – PRISM	Average maximum/minimum temperature for the months of December, January, February	Extreme winter temperatures can exacerbate cold stress (Rodhouse *et al.* 2018).
Winter maximum and minimum temperature – WNA (°C)	Extracted using a 10 m resolution DEM and ClimateWNA model	Extreme winter temperatures can exacerbate cold stress (Rodhouse *et al.* 2018).

Table 1.1 (Continued): Description of variables include in occupancy and abundance analysis including a short description of how the data was acquired and predicted relationships.

Parameter	Variable description	Definition of ecological relationship
Energy requirement		
Winter + Summer + Annual Amount of food – PRISM (hrs)	Using monthly minimums and maximums from PRISM and the topography of each site, Niche MapperTM calculated the amount of food in grams pikas would maintain activity based on their metabolic rates on an average day for each month.	Regardless of season, increased number of food would increase the demand for grazing and haying on pikas.
Winter + Summer + Annual Amount of food – WNA (hrs)	Using monthly minimums and maximums from PRISM and the topography of each site, Niche MapperTM calculated the amount of food in grams pikas would maintain activity based on their metabolic rates on an average day for each month .	Regardless of season, increased number of food would increase the demand for grazing and haying on pikas.
Behavioral response		
Activity hours - PRISM	Using monthly minimums and maximums from PRISM and the topography of each site, Niche MapperTM calculated the number of hours pikas would maintain activity on the surface on an average day for each month.	Increased number of activity hours provides pikas more opportunities to collect vegetation for sustaining their metabolic rates during the winter (Mathewson *et al.* 2017).
Activity hours – WNA	Using monthly minimums and maximums from PRISM and the topography of each site, Niche MapperTM calculated the number of hours pikas would maintain activity on the surface on an average day for each month.	Increased number of activity hours provides pikas more opportunities to collect vegetation for sustaining their metabolic rates during the winter (Mathewson *et al.* 2017).

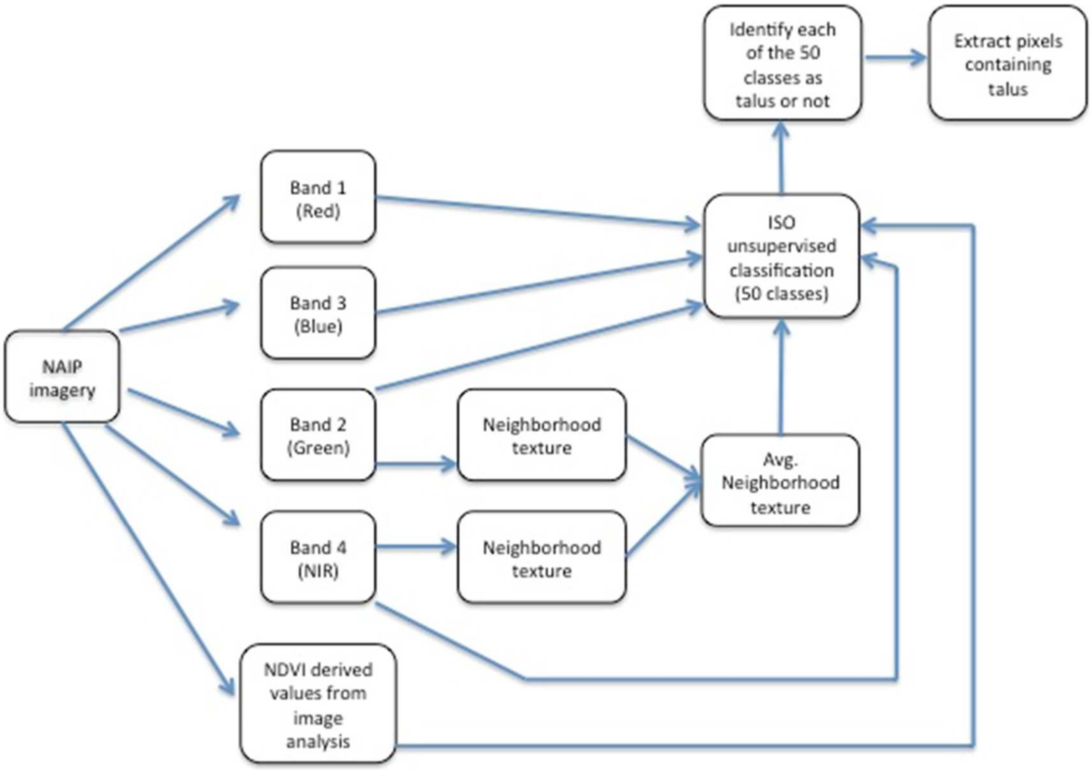

Figure 1.4: A flow chart describing the methods used to classify the talus within each of the study regions. Neighborhood texture analyzed the variation between the pixels of the green and NIR bands to help clarify how the landscape's "roughness" changes. After the 50 classes were created, I identified each class as either as talus or not, for simplicity.

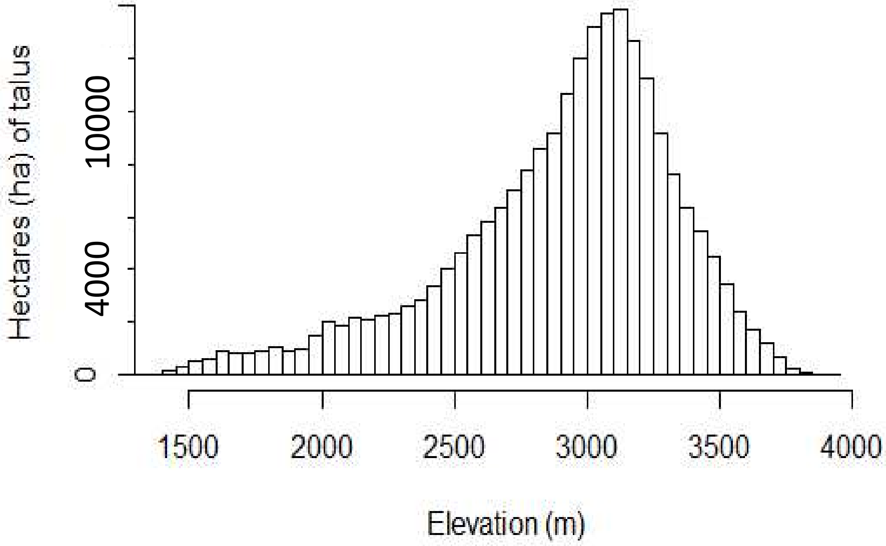

Figure 1.5: Distribution of talus across elevation on the Beartooth Plateau.

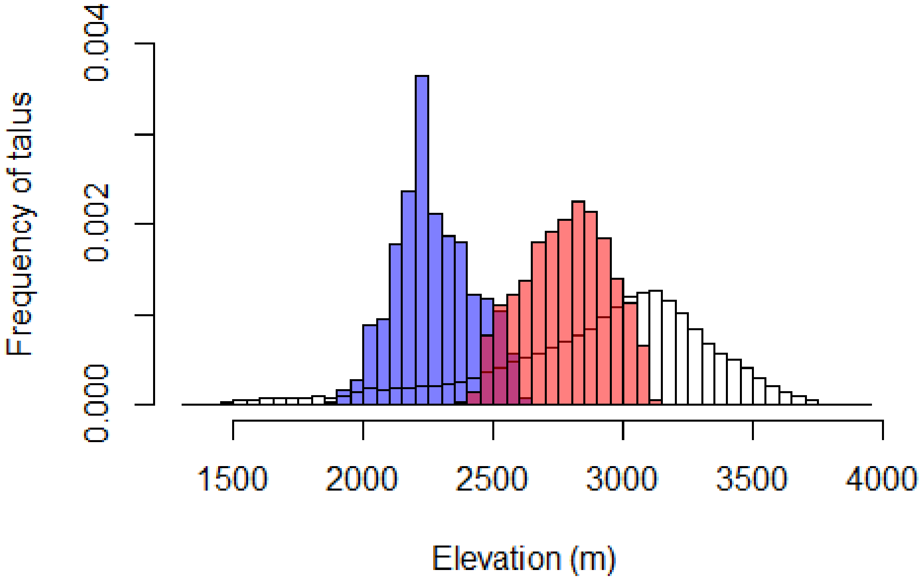

Figure 1.6: The frequency distribution of talus elevation in the different study areas. The transparent histogram represents the talus within the Beartooths; the red histogram represents the talus within Mount Washburn study area; and the blue histogram represents the Bunsen-Hoodoo study area.

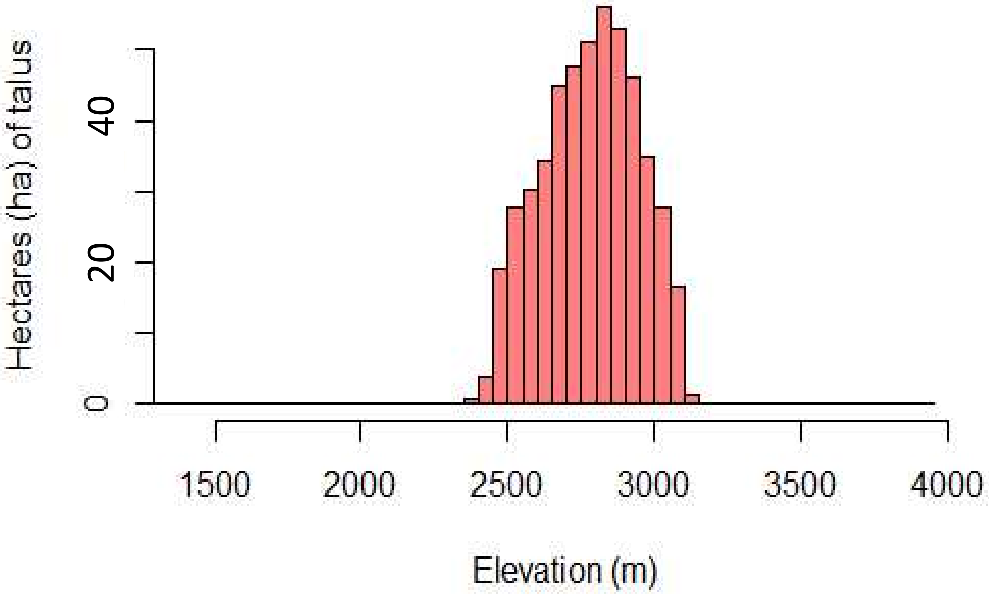

Figure 1.7: Distribution of talus across elevation on Mount Washburn of Yellowstone National Park.

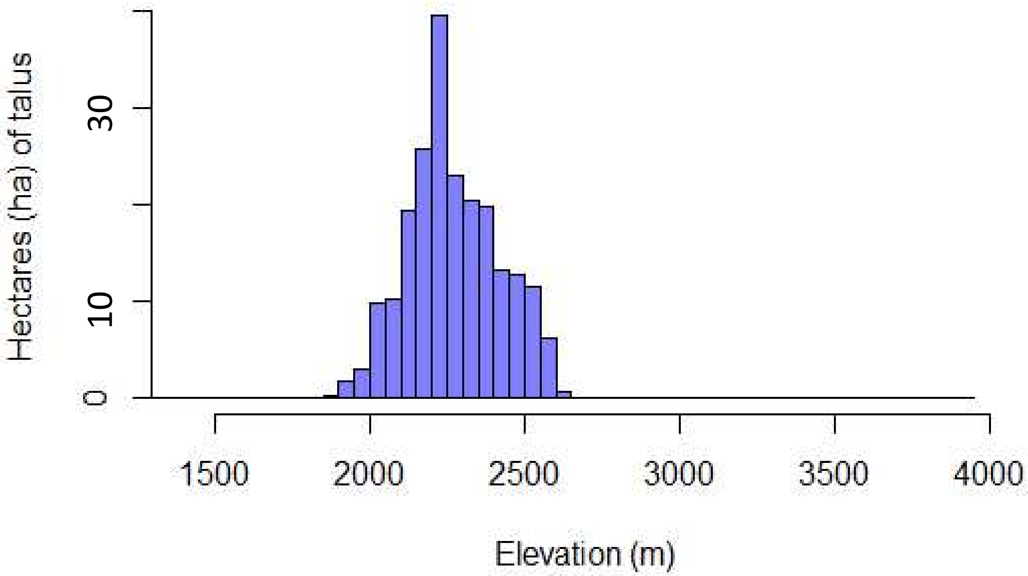

Figure 1.8: Distribution of talus across elevational within the Bunsen Peak – Hoodoo Region of Yellowstone National Park. Due to proximity of the Hoodoos to Bunsen Peak, they were combined to one study area.

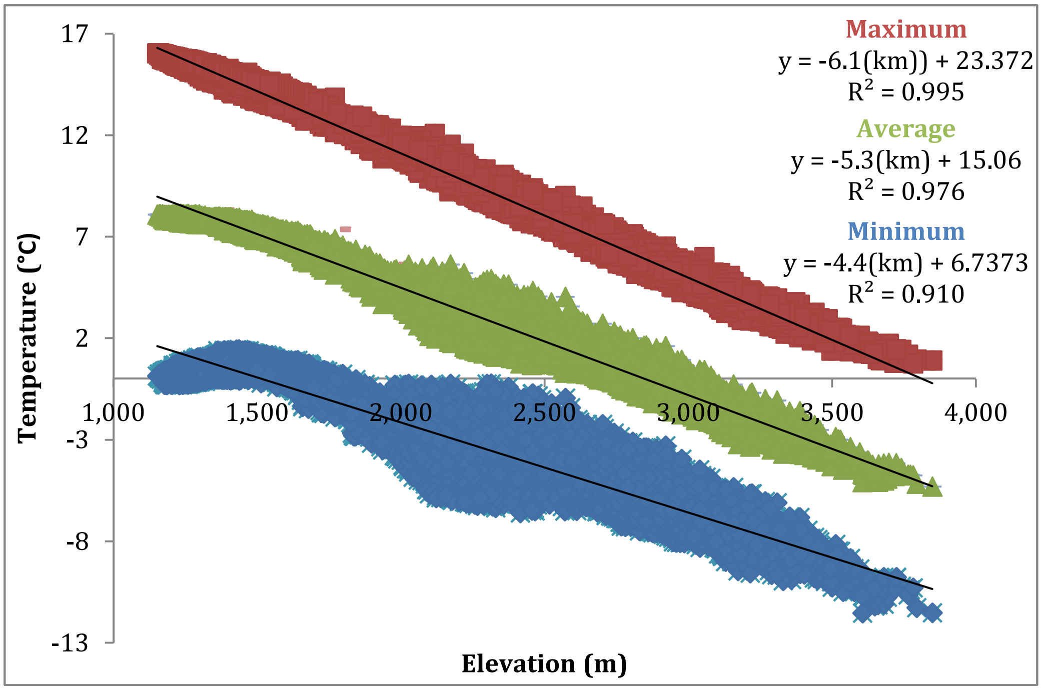

Figure 1.9: Scatter plot of average minimum, mean and maximum temperatures, extracted from the PRISM normal climate data seta at 800 m resolution, across the Beartooth Plateau, plotted against elevation.

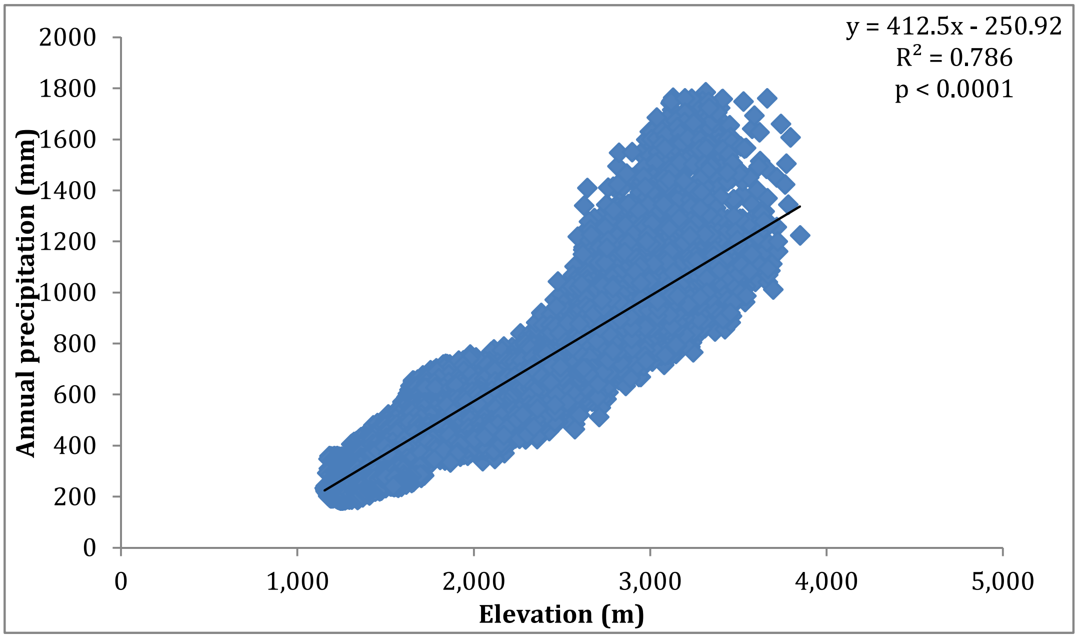

Figure 1.10: Scatterplot of the annual precipitation, extracted from the PRISM normal climate data seta at 800 m resolution, across the Beartooth Plateau, plotted against elevation.

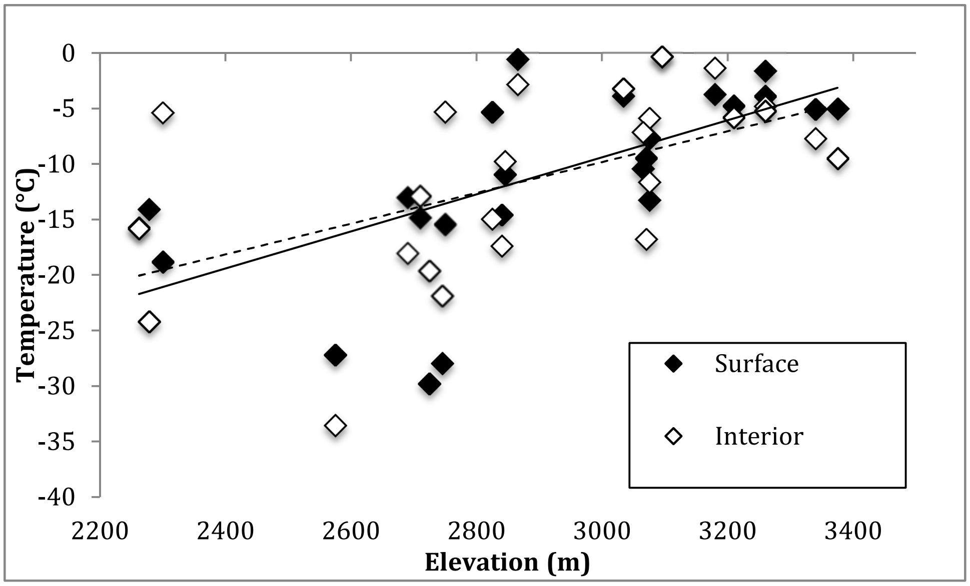

Figure 1.11: Scatter plot showing the general increase in minimum winter temperature with increase in elevation. There is no significant difference (two sample t- test, $p > 0.10$) between the minimum temperature experienced at the surface of the talus compared to the

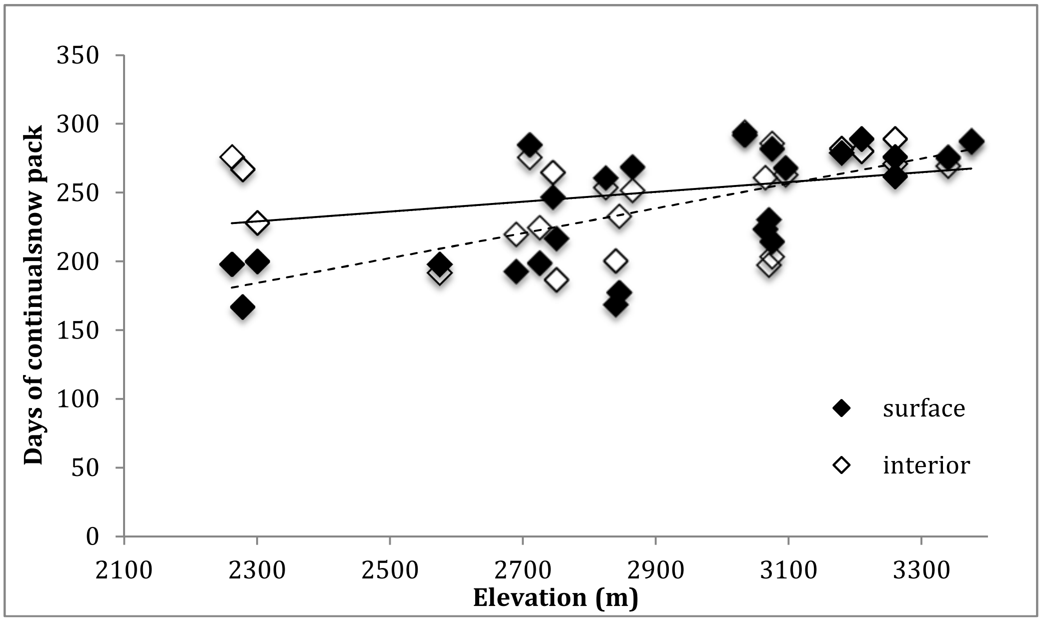

Figure 1.12: Scatter plot showing the general increase winter snow pack with increase in elevation. There is no significant difference (two sample t- test, $p > 0.10$) between at the surface of the talus compared to the interior of the talus.

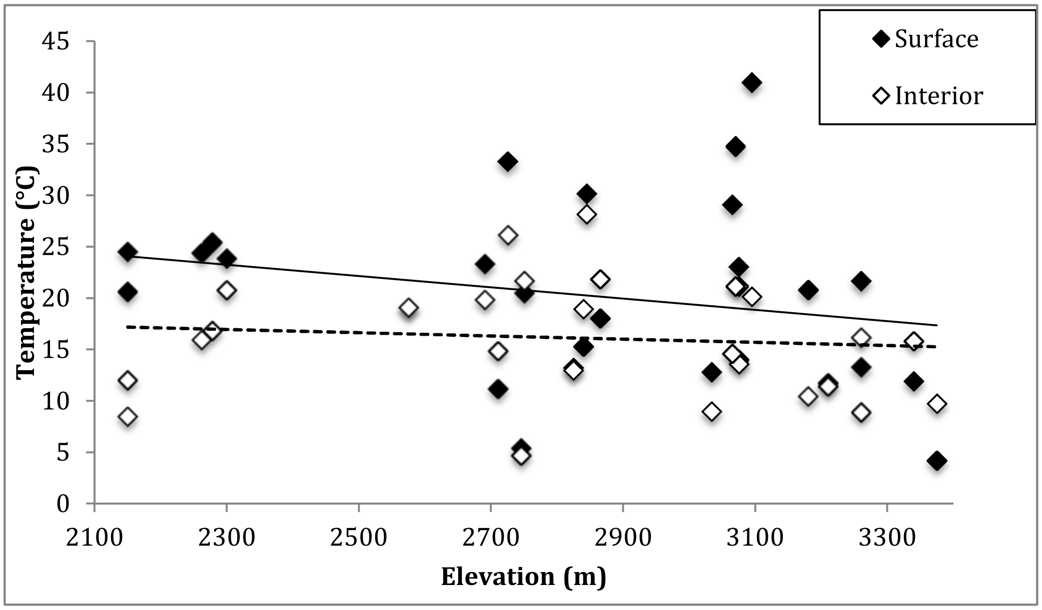

Figure 1.13: Scatter plot showing the significant difference between the maximum summer temperatures recorded at the surface and interior, independent from elevation ($p < 0.05$). Both, maximum surface temperature and maximum interior temperatures increased with elevation ($p < 0.01$).

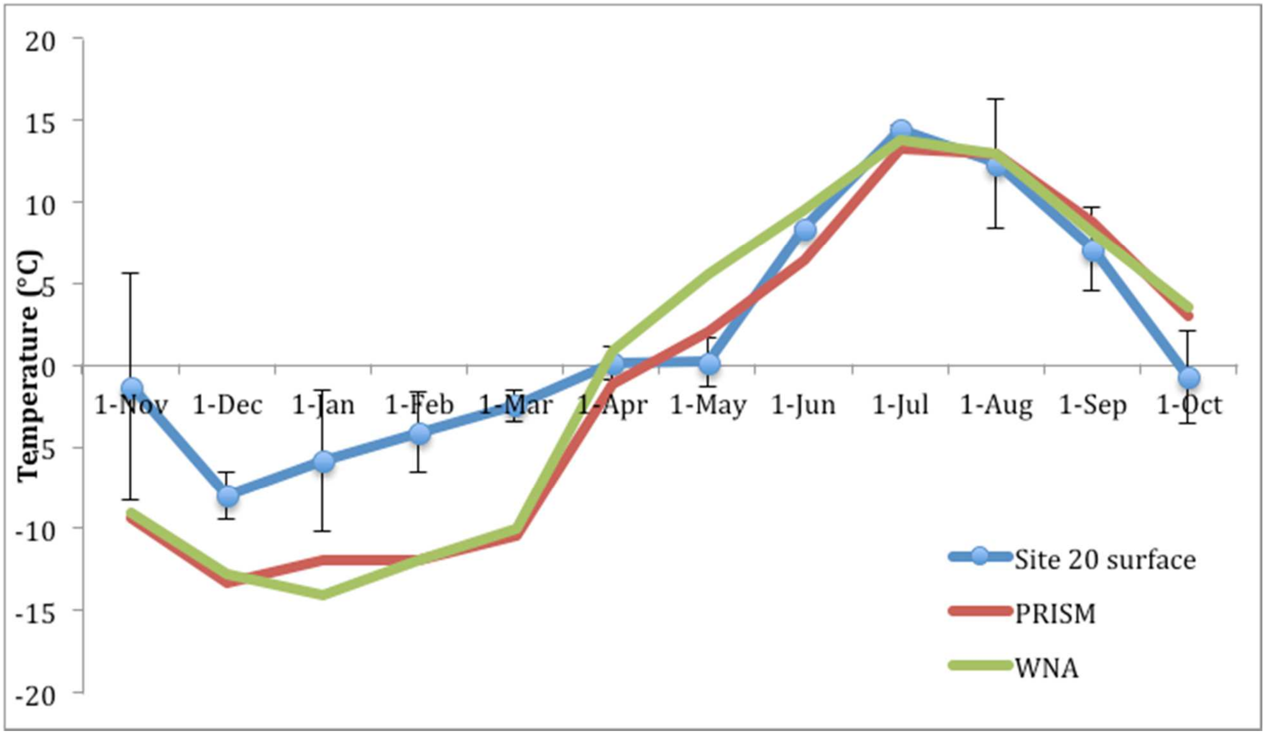

Figure 1.14: Graph showing the microclimate predicted by Niche Mapper$_{TM}$ using PRISM and ClimateWNA and temperatures recorded by the data loggers. Under predictions in the winter is most likely due to insulating snow experienced by the data logger, also shown through low standard errors during months of snow cover.

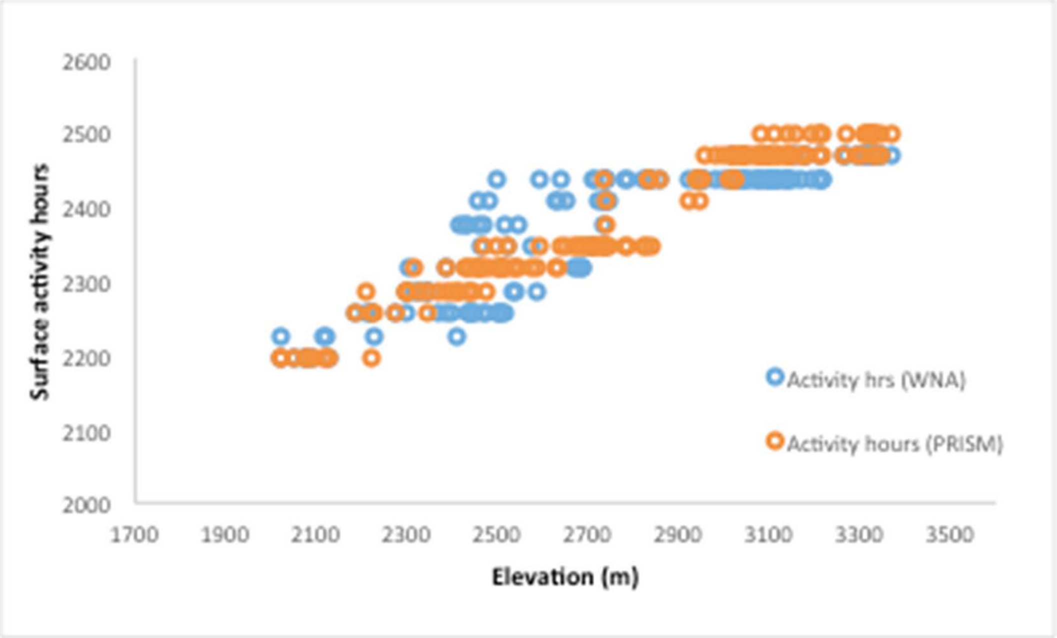

Figure 1.15: Scatterplot showing the variation in surface activity hours calculated using the PRISM climate data and the ClimateWNA climate data.

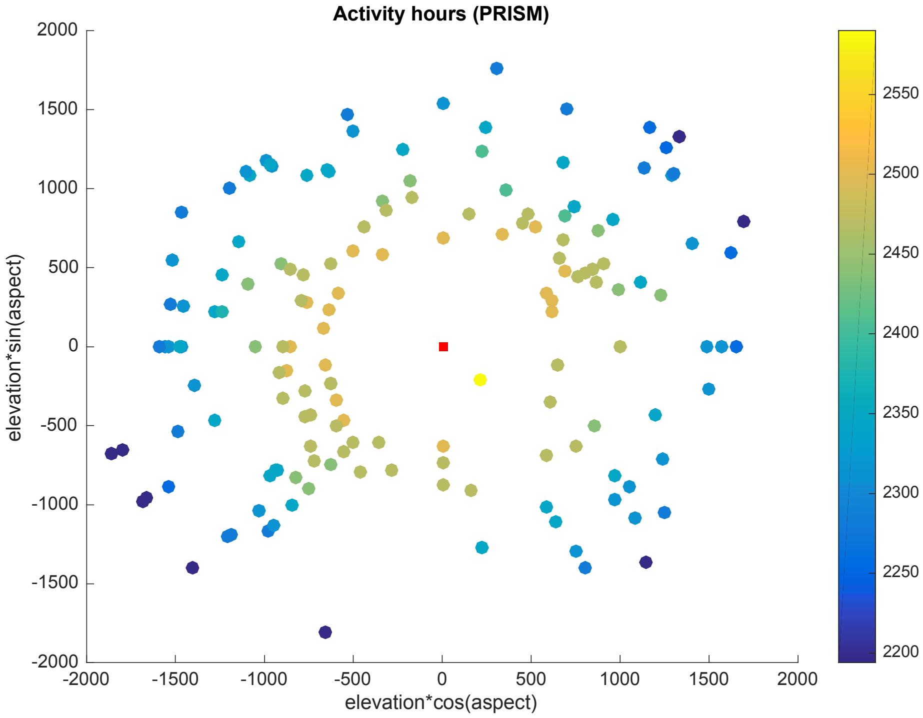

Figure 1.16: Polar graph showing the variation in surface activity hours (PRISM), indicated by color, with respect to elevation and aspect. Red square is a flat site at 4000 m. Moving left to right on the x axis moves from west facing slopes at low elevation to east facing slopes at low elevations. Moving along the y-axis, you move from low elevation south facing slopes to north facing slopes. The center of the graph is a flat slope at high elevation, 4000 m.

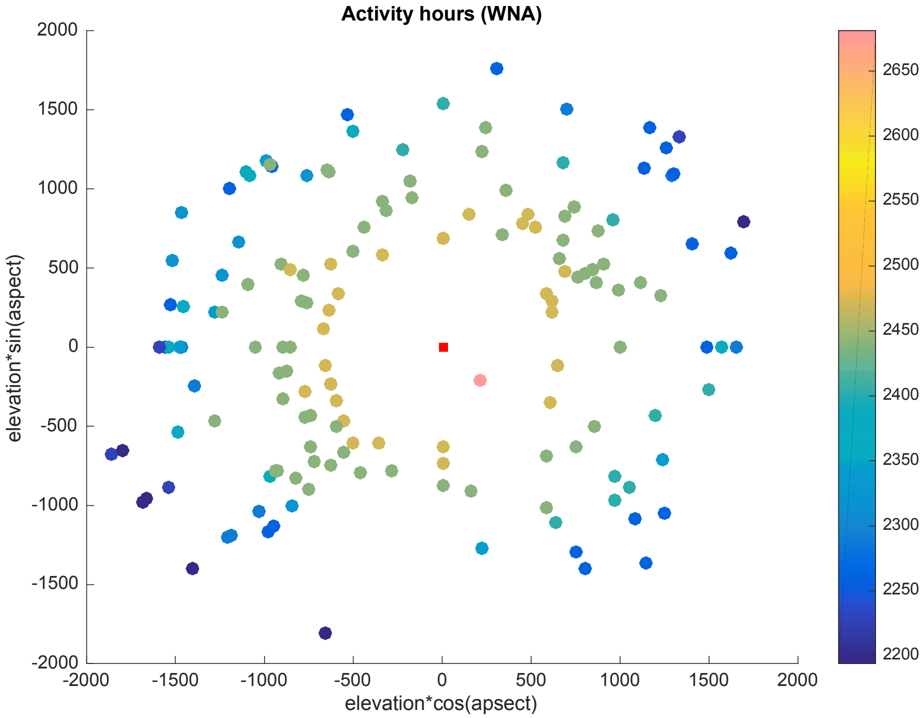

Figure 1.17: Polar graph showing the variation in surface activity hours (WNA), indicated by color, with respect to elevation and aspect. Red square is a flat site at 4000 m. Moving left to right on the x axis moves from west facing slopes at low elevation to east facing slopes at low elevations. Moving along the y-axis, you move from low elevation south facing slopes to north facing slopes. The center of the graph is a flat slope at high elevation, 4000 m.

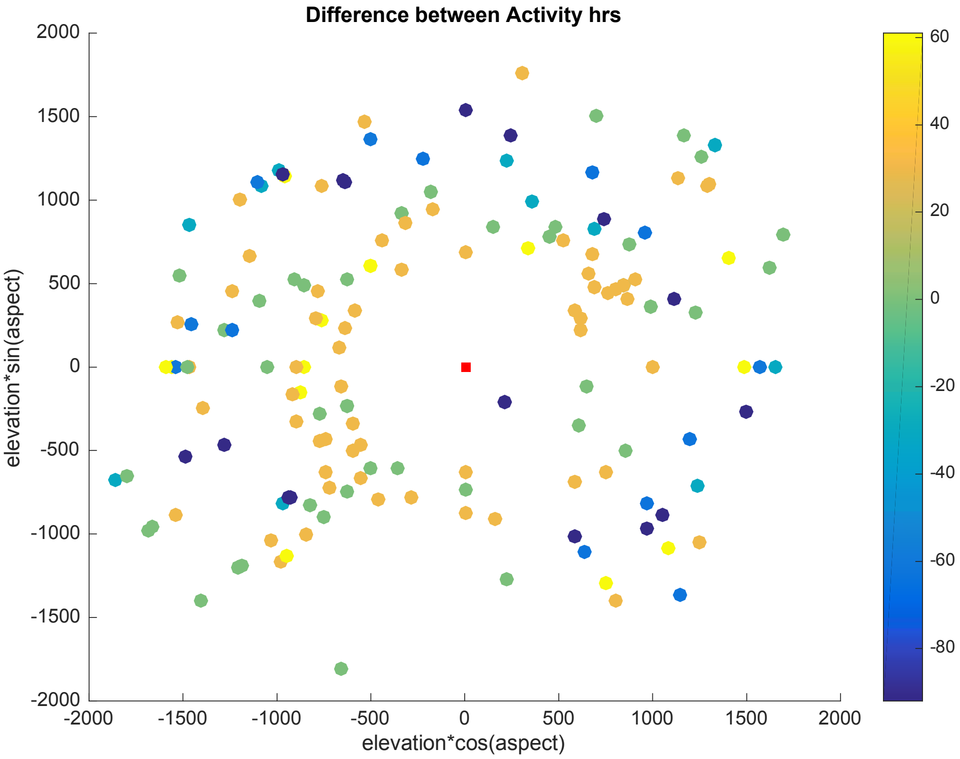

Figure 1.18: Scatterplot showing the difference in activity hours derived by Niche Mapper$_{TM}$ using PRISM and WNA (difference = PRISM – WNA) with respect to elevation and aspect in the form of a polar graph. Red square is a flat site at 4000 m. Positive values are where PRISM predicted more activity hours and negative values is where WNA predicted more activity hours. Moving left to right on the x axis moves from west facing slopes at low elevation to east facing slopes at low elevations. Moving along the y-axis, you move from low elevation south facing slopes to north facing slopes. The center of the graph is a flat slope at high elevation, 4000 m.

Table 2.1: Model averages of the occupancy covariates, summed Akaike weights of each model where the parameter was present, average coefficient and standard error.

Parameter	Weight	Coefficient	Std. Error
Time of max NDVI	0.98	2.98	1.84
Proportion of talus within 1 km	0.97	3.55	2.41
Summer precipitation (WNA)	0.77	2.26	1.92
Winter precipitation (WNA)	0.57	1.98	2.34
Slope	0.39	0.87	1.50
Area of talus site	0.33	3.12	3.80
Insolation	0.29	0.28	2.27
Perimeter of talus area	0.27	-1.42	2.91
Max. winter temperature (WNA)	0.20	-2.06	0.73
cos(aspect)	0.13	-0.35	1.67
sin(aspect)	0.13	-0.35	1.58
Min. winter temperature (WNA)	0.13	0.90	1.70
Min. summer temperature (WNA)	0.11	-0.07	3.50
Activity hours (WNA)	0.09	0.51	1.11
Min. winter temperature (PRISM)	0.07	0.05	0.95
Elevation	0.03	1.62	0.67
Max. winter temperature (PRISM)	0.02	-2.31	0.86
Summer precipitation (PRISM)	0.02	0.53	1.49
Winter food amount (WNA)	0.02	1.48	0.70
Annual food amount (WNA)	0.02	1.42	0.66
Summer food amount (WNA)	0.02	1.41	0.66
Annual precipitation (PRISM)	0.01	1.36	0.73
Max summer temperature (WNA)	0.01	-1.40	0.68
Max annual temperature (PRISM)	0.01	-1.50	0.98
Max summer temperature (PRISM)	0.01	-1.61	0.54
Winter food amount (PRISM)	0.01	2.90	33.89
Winter precipitation (PRISM)	0.01	1.54	3.11
Max NDVI	0.00	0.93	18.28
Annual food amount (PRISM)	0.00	1.77	3.32
Summer food amount (PRISM)	0.00	1.64	3.71
Annual min. temperature (PRISM)	0.00	-0.61	0.89
Min summer temperature (PRISM)	0.00	-0.45	9.44
Activity hours (PRISM)	0.00	1.43	0.59

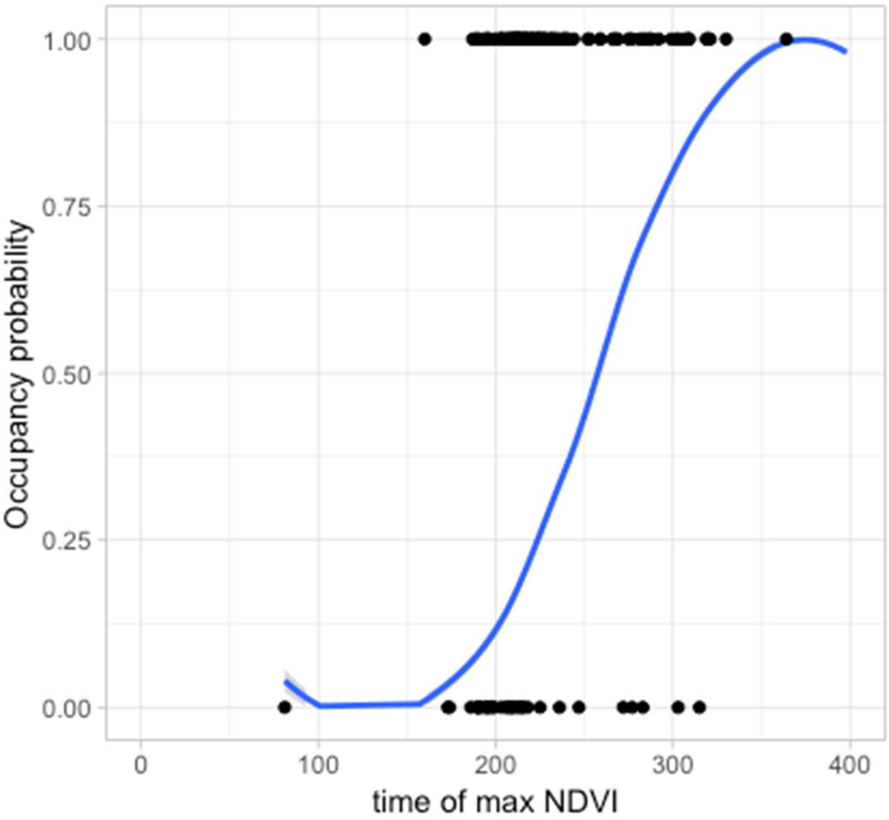

Figure 2.1: Probability of occupancy with relation to Julian day of maximum NDVI (standard error = 1.84). Black dots represent whether a site was occupied the second sampling year. The blue line indicates the predicted relationship between time of max NDVI and occupancy probability predicted by the occupancy model averaging.

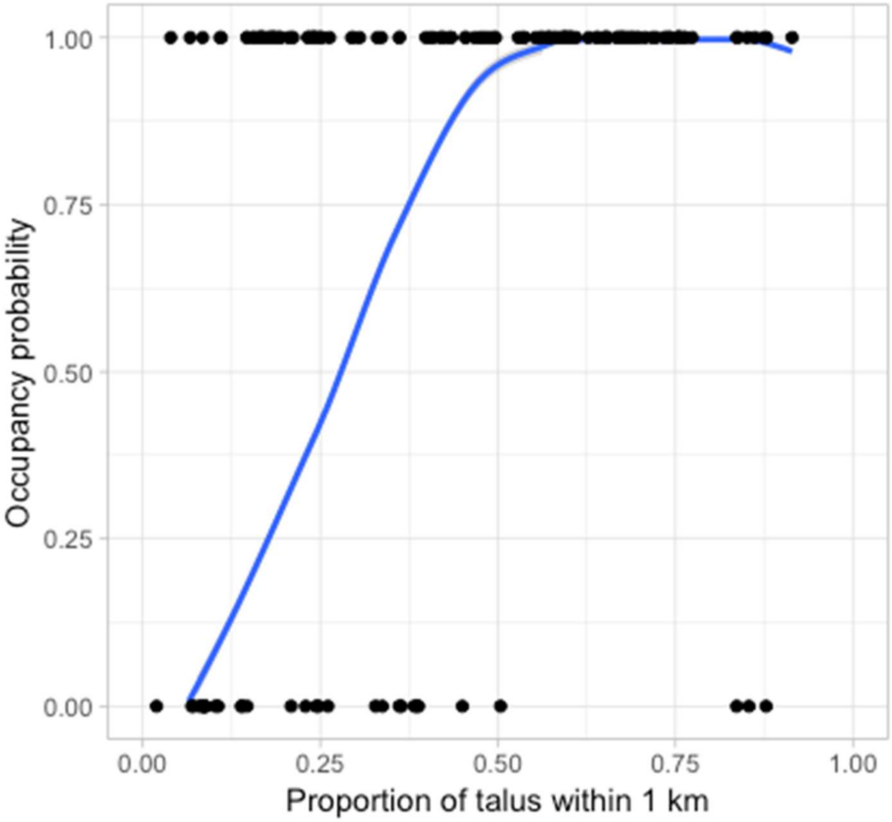

Figure 2.2: Probability of occupancy with relation to proportion of talus within 1 km of site (standard error = 2.41). Black dots represent whether a site was occupied the second sampling year. The blue line indicates the predicted relationship between proportion of talus within 1 km and occupancy probability predicted by the occupancy model averaging.

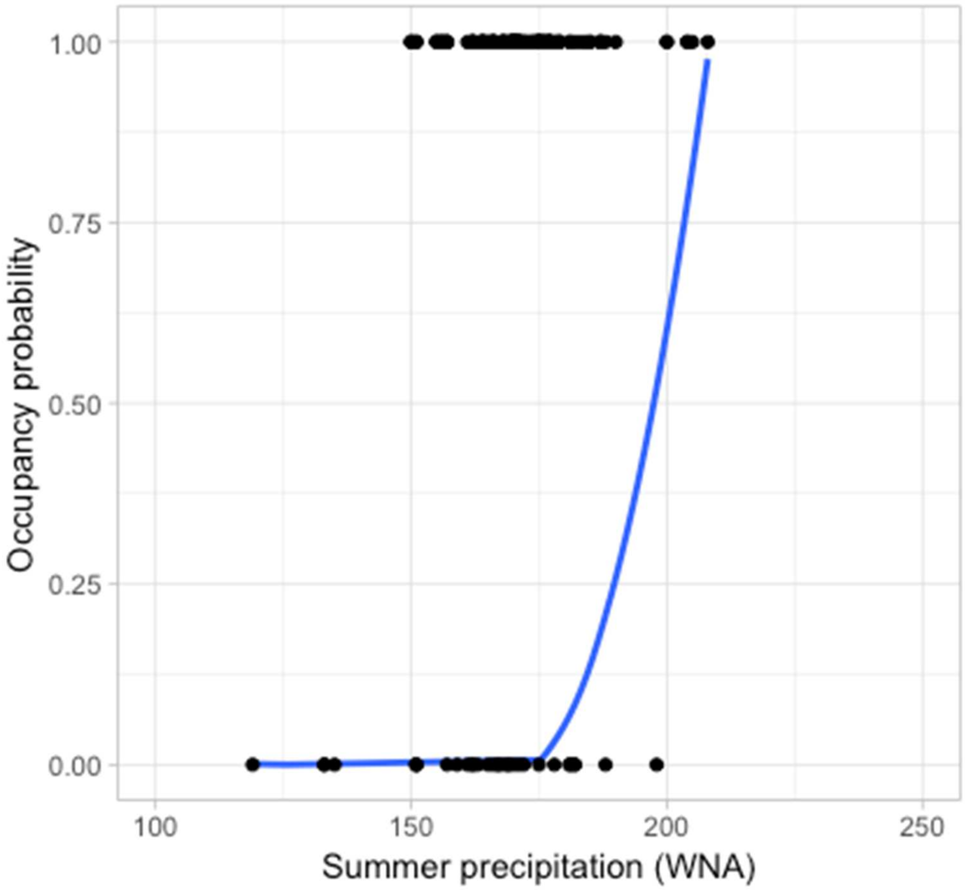

Figure 2.3: Probability of occupancy with relation to summer precipitation (WNA, standard error = 1.92). Black dots represent whether a site was occupied the second sampling year. The blue line indicates the predicted relationship between summer precipitation and occupancy probability predicted by the occupancy model averaging.

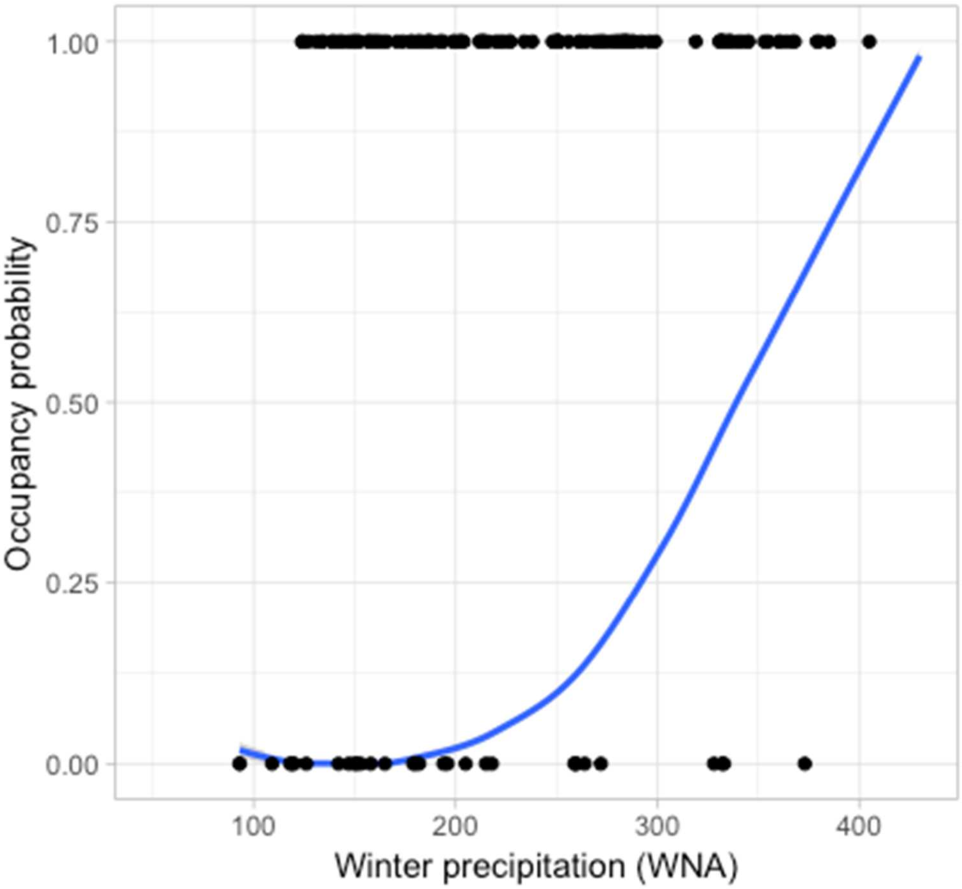

Figure 2.4: Probability of occupancy with relation to winter precipitation (WNA, standard error = 2.34). Black dots represent whether a site was occupied the second sampling year. The blue line indicates the predicted relationship between winter precipitation and occupancy probability predicted by the occupancy model averaging.

Table 2.2: Model averages of the occupancy covariates, summed Akaike weights of models where the parameter was present, average coefficient and standard error.

Parameter	Weights	Coefficient	Std. Error
Forbs to graminoids ratio	0.95	0.21	0.07
Slope	0.82	-0.16	0.07
Area of talus site	0.75	-0.17	0.07
Max NDVI	0.56	-0.15	0.08
Proportion of talus within 1 km	0.44	0.12	0.09
Forb richness	0.28	0.06	0.08
cos(aspect)	0.24	0.04	0.07
Time of max NDVI	0.24	-0.03	0.08
Total vegetation	0.23	-0.02	0.07
Insolation	0.21	0.00	0.07
Activity hours (WNA)	0.12	-0.15	0.08
Summer precipitation (WNA)	0.10	0.04	0.11
Summer precipitation (PRISM)	0.10	0.02	0.09
Summer food amount (WNA)	0.06	-0.12	0.09
Perimeter of talus site	0.06	-0.03	0.07
Max winter temperature (PRISM)	0.06	0.12	0.09
Annual food amount (WNA)	0.06	-0.12	0.09
Min winter temperature (WNA)	0.05	0.12	0.10
Max winter temperature (WNA)	0.05	0.12	0.10
Activity hours (PRISM)	0.05	-0.11	0.09
Winter food amount (WNA)	0.05	-0.10	0.09
Max summer temperature (PRISM)	0.04	0.10	0.10
Min summer temperature (WNA)	0.04	0.11	0.09
Summer food amount (PRISM)	0.04	-0.09	0.08
Winter precipitation (WNA)	0.04	-0.09	0.09
Annual food amount (PRISM)	0.04	-0.08	0.08
Winter food amount (PRISM)	0.03	-0.08	0.08
Winter precipitation (PRISM)	0.03	-0.07	0.08
Min summer temperature (PRISM)	0.03	0.06	0.08
Max summer temperature (WNA)	0.03	0.10	0.10
Elevation	0.03	-0.10	0.10
Min winter temperature (PRISM)	0.03	0.06	0.07
Annual max temperature (PRISM)	0.03	0.10	0.10
Annual min temperature (PRISM)	0.03	0.08	0.08
Annual precipitation (PRISM)	0.02	-0.07	0.09

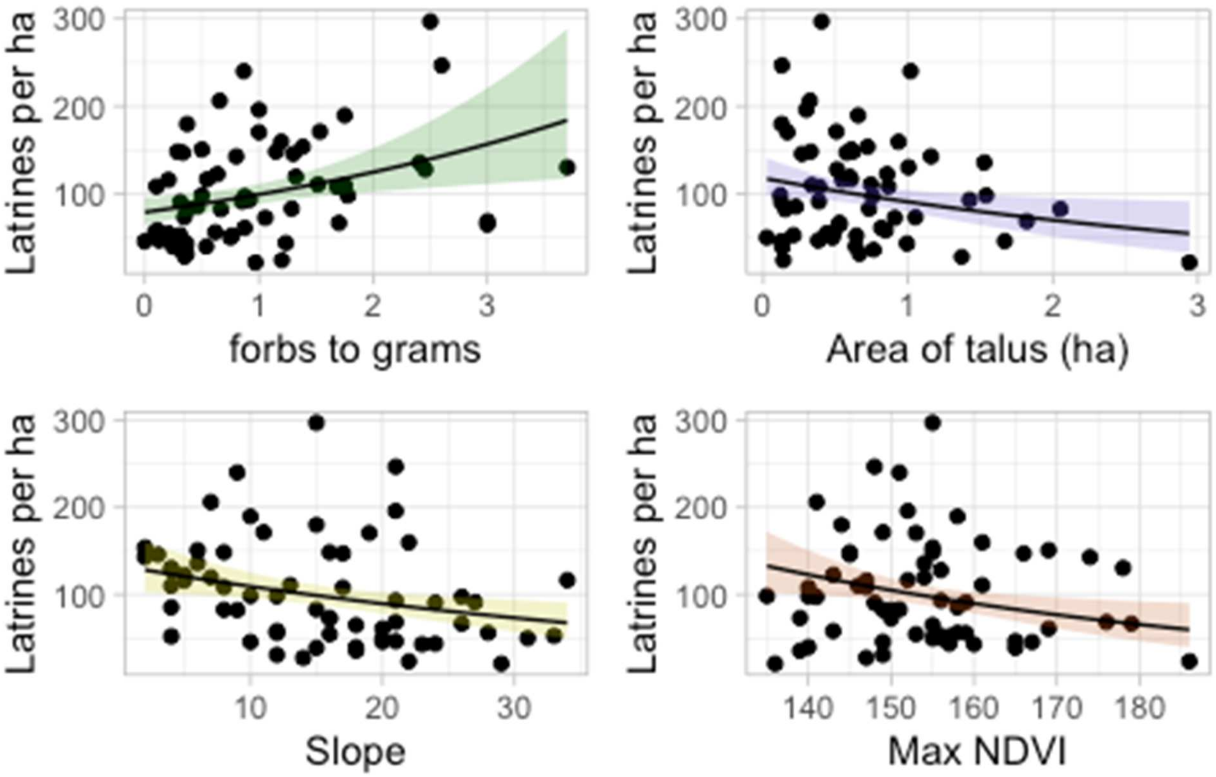

Figure 2.5: Pika latrine density plotted against the top predictors of latrine density. Shaded regions represent the confidence intervals.