Microtopoclimatic effects on a climate-sensitive habitat specialist, the American pika (*Ochotona princeps*)

by

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The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline.

ABSTRACT

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Microtopoclimatic effects on a climate-sensitive habitat specialist, the American pika (*Ochotona princeps*)

Thesis directed by Professor Katherine N. Suding

There has been increasing acknowledgement that refugia at different scales facilitate the long-term survival of species and populations through climate oscillations. Species distributions and persistence are already affected by current climate change, and many taxa will become more spatially limited and less connected under further warming scenarios. Identifying likely microrefugia will improve our predictions of how species, communities, and ecosystems are likely to respond to climate change by providing a clearer understanding of likely demographic processes and connectivity. In this thesis, I considered suitable microhabitat in the face of current changing climates in the context of the persistence or development of microrefugia. The processes that drive microhabitat use by individuals likely also scale up to impact broader scale occupancy and connectivity patterns. Describing those fine-scale processes may therefore better predict how species will react to environmental change. To address these issues, we studied the ways in which fine-scale features of the terrain drive microhabitat use for the American pika *(Ochotona princeps*), a small lagomorph of western North America that has been cited as a likely climate and ecosystem change indicator species. The microtopoclimatic effect on habitat may drive patterns at the scales of individual habitat use, territory occupancy, patch occupancy, and regional population health. Though many studies have addressed some of the macroclimatic drivers of occupancy, we addressed fine scale processes and variation that likely interact with those broader factors. In the first chapter, we used radio telemetry to track pikas October-July in the Niwot Ridge Long Term Ecological Research site (NWT LTER) in Colorado's Roosevelt National Forest and compared those data to records of summertime trapping success in the same area from 2008-2015. We used logistic regressions to test how terrain drives habitat use and how those effects vary seasonally. In the second chapter, we made predictions about suitable habitat across NWT using probability surfaces from Chapter 1 and supervised models made using remotely sensed data. We compared these predictions and discussed the importance of relevant habitat parameters and data at the appropriate scale to detect processes impacting species distribution models and larger predictions.

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CONTENTS

CHAPTER

TABLES

FIGURES

INTRODUCTION

There has been increasing acknowledgement that refugia facilitate the long-term survival of species and populations through climate oscillations (Shimokawabe et al. 2015). Rull et al. (1988) introduced the term "microrefugium" as a *small area with local favorable environmental features, in which small populations can survive outside their main distribution area (the macrorefugium), protected from the unfavorable regional environmental conditions.* Species distributions and persistence are already affected by current climate change (Chen et al. 2011), and many taxa will become more spatially limited and less connected under further warming scenarios (Parmesan et al. 2003, Rull 2009, Mosblech et al. 2011). Patches of suitable habitat in which microclimatic conditions are decoupled from the surrounding climatic conditions may therefore provide essential relief for affected taxa and slow extinctions in the face of climate change (Pearson 2006). Similarly, climate microrefugia during the last glacial maximum (LGM) facilitated faster range shifts in response to early Holocene warming than can be explained by long distance dispersal models, as pockets of habitat that survived regionally unsuitable conditions began to expand (Clark et al. 1998, Mosblech et al. 2011).

Identifying likely microrefugia will improve our predictions of how species, communities, and ecosystems are likely to respond to climate change by providing a clearer understanding of likely demographic processes and connectivity (Gillingham et al. 2012). For example, many mammals in the Great Basin that prefer cool, mesic climates had abundant habitat during the LGM, including in the modern Mojave Desert, but have since been extirpated or forced mostly into isolated patches in disparate mountain ranges (Brown 1971, Grayson 2005, 2006). In this thesis, I consider suitable microhabitat in the face of current changing climates in the context of the persistence or development of microrefugia. Here, microhabitat is small spaces of refuge at the scale exploitable by individuals within their territory, while microrefugia are larger, relevant more to populations than individuals.

It is widely accepted that mountains represent a refuge of relatively mesic climate for many alpine species, relicts of the Pleistocene or early Holocene epochs (Hafner 1993, Schönswetter et al. 2002, Grayson 2006, Millar and Westfall 2010). Recent work has suggested mountain environments will likely provide crucial shelter under new and variable climate scenarios (Schönswetter et al. 2002, Dobrowski 2011, Ashcroft 2010). For plants, Gottfried et al. (2012) observed a significantly higher abundance of thermophilic species in the mountain summits of Europe over the last decade. In addition, recent projections of high mountain species habitat shifts that result from temperature increases indicate that there will be a decline of cold habitats by the end of twenty-first century (Thuiller et al. 2005, Dullinger et al. 2012, Pauli et al. 2012). A similar trend is likely for animals, constrained by both climate directly and by diminished dispersal and connectivity potential because of habitat loss due to climate change (Grayson 2006, Anderson et al. 2009, Galbreath et al. 2009). Mountainous areas are therefore a good model system, as they are likely indicative of what changes may come elsewhere.

Topographical heterogeneity can cause considerable local climate variation (Scherrer and Körner 2011), potentially decoupling local and regional climate. This decoupling is key to developing microrefugia (Dobrowski 2011, Ashcroft and Gollan 2012). There are likely shortcomings in our understandings of species topoclimatic habitat requirements—especially for taxa potentially threatened by climate change (Dobrowski 2011, Sandel et al. 2011). Despite the increased attention to macroclimatic interactions with local climate, there has been little work addressing how terrain heterogeneity may foster suitable of microhabitat in topographically-complex landscapes at scales small relevant to individual habitat patches. The processes that drive microhabitat use by individuals likely also scale up to impact broader scale occupancy and connectivity patterns. Describing those fine-scale processes may therefore better predict how species will react to environmental change.

My thesis will address this knowledge gap by addressing the role of landscape topography at different scales in determining microrefugia and suitable microhabitats. I will particularly focus on populations of American pika (*Ochotona princeps*), a small lagomorph of western North America that is sensitive to both warm and cold temperature extremes (Jeffress et al. 2013, Yandow et al. 2015).

To address these issues, we will study the ways in which fine-scale features of the terrain drive microhabitat use. This microtopoclimatic effect on habitat may drive patterns at the scale of individual habitat use, territory occupancy, patch occupancy, and regional population health. Though many studies have addressed some of the macroclimatic drivers of occupancy, we are addressing fine scale processes and variation that likely interact with those broader factors. For pikas, this means looking at the scale of even a few meters. They do not hibernate, do not disperse far, have small territories, and their habitat can vary significantly at that fine a scale (Smith and Ivins 1984, Smith and Weston 1990, Varner and Dearing 2014).

In the first chapter, we used radio telemetry to track pikas October-July in the Niwot Ridge Long Term Ecological Research site (NWT LTER) in Colorado’s Roosevelt National Forest and compared those data to records of summertime trapping success in the same area from 2008-2015. We used high resolution color imagery and a Digital Elevation Model (DEM) to derive habitat and terrain parameters. We performed a series of logistic regressions with the telemetry and trapping data to test how metrics of the terrain predict habitat use and how those effects vary seasonally.

In the second chapter, we used knowledge gained from Chapter 1 and prior work to make predictions about suitable habitat across NWT. Based on the best fit mixed logistic regression models for winter, summer, and the whole study period, we created probability surfaces by a logit transformation to represent habitat suitability across NWT. This was one method of suitability prediction. Separately, we created supervised models of suitable habitat by maximum likelihood based on landscape variables and expert opinion inputs from field experience and prior studies. We used linear regressions to relate each of those supervised models to the modeled probabilities of habitat suitability based on the probability surfaces. Included among those models was one derived at a coarser scale more commonly used in SDMs for pikas in order to compare the high resolution, fine scale metrics to those more commonly used.

CHAPTER 1

Title: Seasonality in the use of heterogeneous terrain by a territorial habitat specialist, the American pika (*Ochotona princeps*)

Introduction

Climate is one of the main drivers of species distributions (Pintor et al. 2015). As a response to ongoing climate change, many species have started to shift their ranges poleward and toward higher elevations (Walther et al. 2002, Chen et al. 2011, but see Crimmins et al. 2011, Dobrowski 2011). Alpine environments are particularly vulnerable, and predicted to experience especially rapid climatic changes (IPCC 2013). Modeling studies have consistently predicted a greater risk of habitat loss and local extinctions for species at high elevations compared to species at lower elevations (Engler et al. 2011, Bellard et al. 2012). However, species sensitivity to rapid climate change may be modulated, by factors such as terrain heterogeneity that can decouple local microclimate from atmospheric lapse rate, and alpine and montane areas are not often studied at topographic and climatic scales appropriate to the species at risk there (Parmesan et al. 2003, Root et al. 2003, Ashcroft 2010, Dobrowski 2011, Ford et al. 2013, Varner and Dearing 2014). Heterogeneous terrain plays a key role in whether climate change in high-elevation systems will increase the isolation of populations (likely resulting in local extinction) or create high-elevation microclimatic refugia, complicating predictions of both local and regional climate change effects and associated species responses (Anderson et al. 2009, Ashcroft et al. 2012, Hannah et al. 2014).

Considerable seasonal variation in the mountains is another level of heterogeneity that may complicate suitability predictions, and some have argued that seasonal variation in habitat quality should play a role in predicting habitat extent (Ashcroft et al. 2009). Yet our understanding of habitat suitability for many species, especially those in high alpine environments, is typically based on occupancy surveys performed during summer, when the work is most tractable (Van Horne 1983). If wildlife use different habitat in winter, when many taxa and their resources are likely to be more spatially limited (e.g. wolves [Fortin et al. 2005, Bergman et al. 2006, McPhee et al. 2012]), we risk overestimating the extent of habitat available throughout the year, and the number of individuals it can support (Van Horne 1983). Some summer habitat may become entirely inhospitable in winter (Costello et al. 2006) and individuals without both types of habitat may not survive the whole year (Wallmo et al. 1977). For example, changes in the food resources in summer habitat for mule deer makes that same habitat untenable as winter forage, and herds have to move to slightly better areas (Wallmo et al. 1977). Accounting for spatial and climatic variation will therefore more thoroughly show the true extent of suitable habitat (Pintor et al. 2015).

Several studies have shown that topographic heterogeneity likely plays a role in facilitating pockets of habitat for many taxa (Luoto and Heikkinen 2008, Ashcroft 2010, Dobrowski 2011, Ford et al. 2013). Terrain features can create habitat sheltered from wind, sun, or other limiting climatic factors. Topographic features at various scales, even at 10m or less, can influence microclimate shelter exploited by individuals, including wind exposure, snow accumulation, and surface temperatures (Anderton et al. 2002, Winstral et al. 2002). A heterogeneous terrain slows wind and is more likely to accumulate wind-carried snow than a flat landscape with no features to reduce flow, and high points are particularly exposed to high wind effects (Ruel et al. 1998). Prior studies have also shown that terrain heterogeneity can influence snow accumulation and the downstream hydrologic and ecologic effects such as the distribution of alpine meadows (Bell and Bliss 1979, Winstral et al. 2002, Déry et al. 2004, Millar et al. 2014). Adequate snow cover can provide insulation from extreme cold, and has been tied to thermal buffering for species seeking suitable microhabitat (Walter and Broome 1998, Shi et al. 2015). Topographic heterogeneity therefore can structure communities at a fine scale and affect individuals. Considering the impacts of both spatial and temporal heterogeneity, it may be important to evaluate the fine-scale drivers of habitat use throughout the year, which could help to more thoroughly explain the way in which terrain can foster suitable microhabitat.

Heterogeneity in climate, topography, and habitat play a large role in species distributions and interactions (Kubota et al. 2004, Kumar et al. 2006, Mosser et al. 2015). For example, heterogeneity in food resources (i.e. moose habitat vs edible berry patches) is critical for bears preparing for winter (Nielsen et al. 2010). Similarly, carrying capacity and demography for North American *Odocoileus* deer species are driven by the seasonal variation in available range (Wallmo et al. 1977). In those examples, including only one habitat parameter for species that require many would likely lead to overestimating the extent of suitable habitat, as a truly hospitable area would require many different kinds of habitat (Figure 1.1). Therefore, efforts to model and predict habitat use and extent should account for how habitat heterogeneity drives its presence (Luoto and Heikkinen 2008).

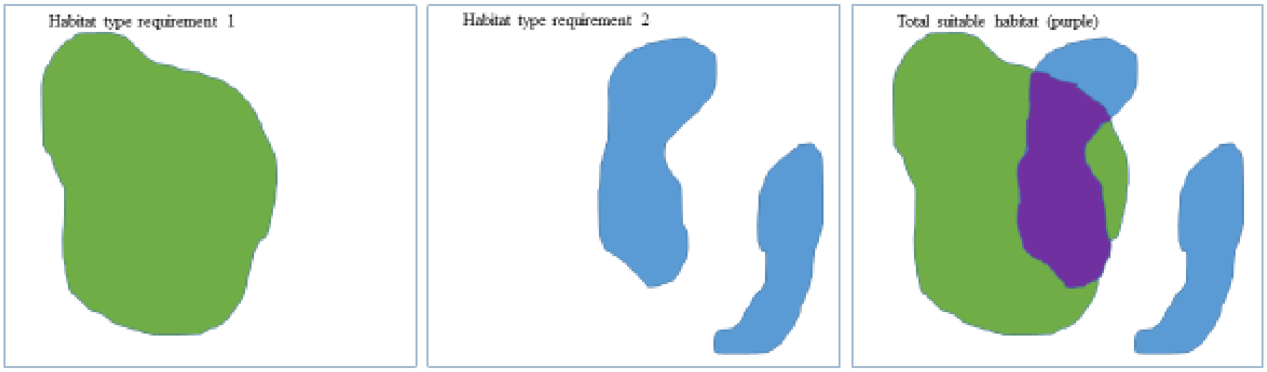


Figure 1.1. Conceptual figure showing how an organism may use different types of habitat within the same area. If both habitat types are required, occupancy projections based on either of the two habitat requirements individually would overestimate the extent of suitable habitat, which is in fact only the purple area that contains both habitat requirements. The scale of this process depends on the species. For more sessile species, this might function within a very small area. For mobile or seasonally migratory species, this could function over a larger extent or only during one season (e.g. mating season).

Among the potentially threatened habitat specialists is the American pika (*Ochotona princeps*), which may already be experiencing climate-driven extirpations (Wilkening et al. 2011, Calkins et al. 2012, Erb et al. 2014, Millar et al. 2014). Pikas are considered good indicators of late Holocene climate change effects (Hafner 1993, Galbreath et al. 2009). Topographic heterogeneity and seasonal variation are likely important for pikas at a very fine scale because pikas are territorial, have fairly small territories, and exploit suitable microhabitat to survive extreme weather (Hafner 1993, Beever et al. 2003, Rodhouse et al. 2010, Millar et al. 2014). Several studies have already suggested important roles for habitat heterogeneity in pika distribution, especially in areas that might otherwise be inhospitable (e.g. Rodhouse et al. 2010, Jeffress et al. 2013). Sub-surface conditions within the pika's preferred microhabitat (talus or boulder fields) can vary greatly within a single pika's territory; by examining habitat use at a very fine scale relevant to the movements and shelter habitat of individual animals, we could study direct effects of heterogeneity at biologically relevant scales (Varner and Dearing 2014).

Because of this affiliation with heterogeneity and climate vulnerability, pikas are therefore a likely model species for studying the interactive effects of topography and climate on species.

Though pikas do not hibernate and remain active through winter and summer, they are sensitive to both high and low temperature extremes (e.g. Ray and Beever 2012, Yandow et al. 2015). Individuals also do not usually disperse great distances and have relatively small territories (14m-50m), giving them a small area in which to find and exploit suitable microclimate (Smith 1974, Smith and Ivins 1984, Smith and Weston 1990). Pikas are considered sentinels, indicators of environmental change in the ecosystems they inhabit. Changes in their distribution speak to changes in availability of resources they require and shifts in the environment. Research suggests pikas are less stressed where sub-surface ice features persist and act as a temperature buffer and potentially a water source (Hafner 1993, Millar and Westfall 2010, Wilkening et al. 2015). Those sub-surface ice features are critical in water cycling and long-term water storage and have strong effects on downstream hydrological and ecological processes (Molotch et al. 2008, Leopold et al. 2015). Given their association with sub-surface ice, an important source of groundwater (Molotch et al. 2008, Millar and Westfall 2010), pikas are an indicator of change to resources in both the alpine and potentially all downstream ecosystems. Understanding how this species responds to climate change therefore provides a model to inform landscape level conservation and management decisions.

During summer months, pikas are vulnerable to heat exposure and have been extirpated from some areas with warming summers (Smith 1974, Beever et al. 2003, 2010, Wilkening et al. 2011). Yet pikas also have been shown to disappear from locations exposed to extremely low temperatures by a lack of snow cover (Beever et al. 2011), and they do not migrate seasonally to find winter shelter beyond their own small territory (Smith and Ivins 1984). Even cold-adapted animals can succumb to extreme cold (Walter and Broome 1998), and pikas rely on snowpack for winter insulation (Krear 1965, Smith 1978). Despite overall climate warming, acute periods of extreme cold will occur, and the predicted decline in snow cover in western North America (IPCC 2013) means that pika habitat may be more exposed to that cold. However, most studies to date have focused on the heat sensitivity of pikas when projecting pika futures (e.g. Calkins et al. 2012, Stewart et al. 2015). Variable terrain is more likely to accumulate snow (Ruel et al. 1998), yet there is an incomplete understanding of how variable mountain terrain impacts pika habitat use, and no published study has addressed habitat use during severe winter conditions.

By evaluating seasonal variation in habitat use, we seek to strengthen predictive models of pika habitat and to demonstrate how this sort of work can provide insight toward a greater understanding of the role that habitat heterogeneity (spatial and temporal) play for this and other species potentially threatened by climate change. For pikas, habitat heterogeneity means a mix of both talus for shelter and nearby vegetation for food (Millar and Zwickel 1972, MacArthur and Wang 1974, Smith and Weston 1990, Erb et al. 2014). Pikas have occasionally been described as an alpine obligate species (Howell 1924, Brown and Knowles 2012), but many observers note that they are in fact more broadly distributed, occurring as low as 300 meters above sea level in mild temperate (Grinnell 1917, Beever et al. 2008, Simpson 2009) or xeric environments (Simpson 2009). In this study we therefore evaluate the effects of topographic and habitat heterogeneity, which could more effectively describe the pika's habitat and suggest a means to do the same for other species with variable habitat requirements. We hypothesized that microhabitat use is driven by fine-scale terrain heterogeneity that buffers both extreme winter cold and summer heat. Pikas are constrained by different factors in summer than in winter, so we predicted that pikas use different types of terrain in winter compared to summer. Because more heterogeneous terrain is more likely to accumulate pockets of snow, we predicted that areas of more heterogeneous terrain would be more suitable for pikas in winter.

Methods

Summary

We used radio telemetry to track pikas October-July in the Niwot Ridge Long Term Ecological Research site (NWT) in Colorado’s Roosevelt National Forest and compared those data to records of summertime trapping success in the same area from 2008-2015. We used high resolution three band color imagery (RGB) and Digital Elevation Models (DEMs) to derive habitat and terrain parameters, including measures of terrain position (prominence) and heterogeneity. We performed a series of logistic regressions with the telemetry and trapping data to test how metrics of the terrain predict habitat use and how those effects vary seasonally.

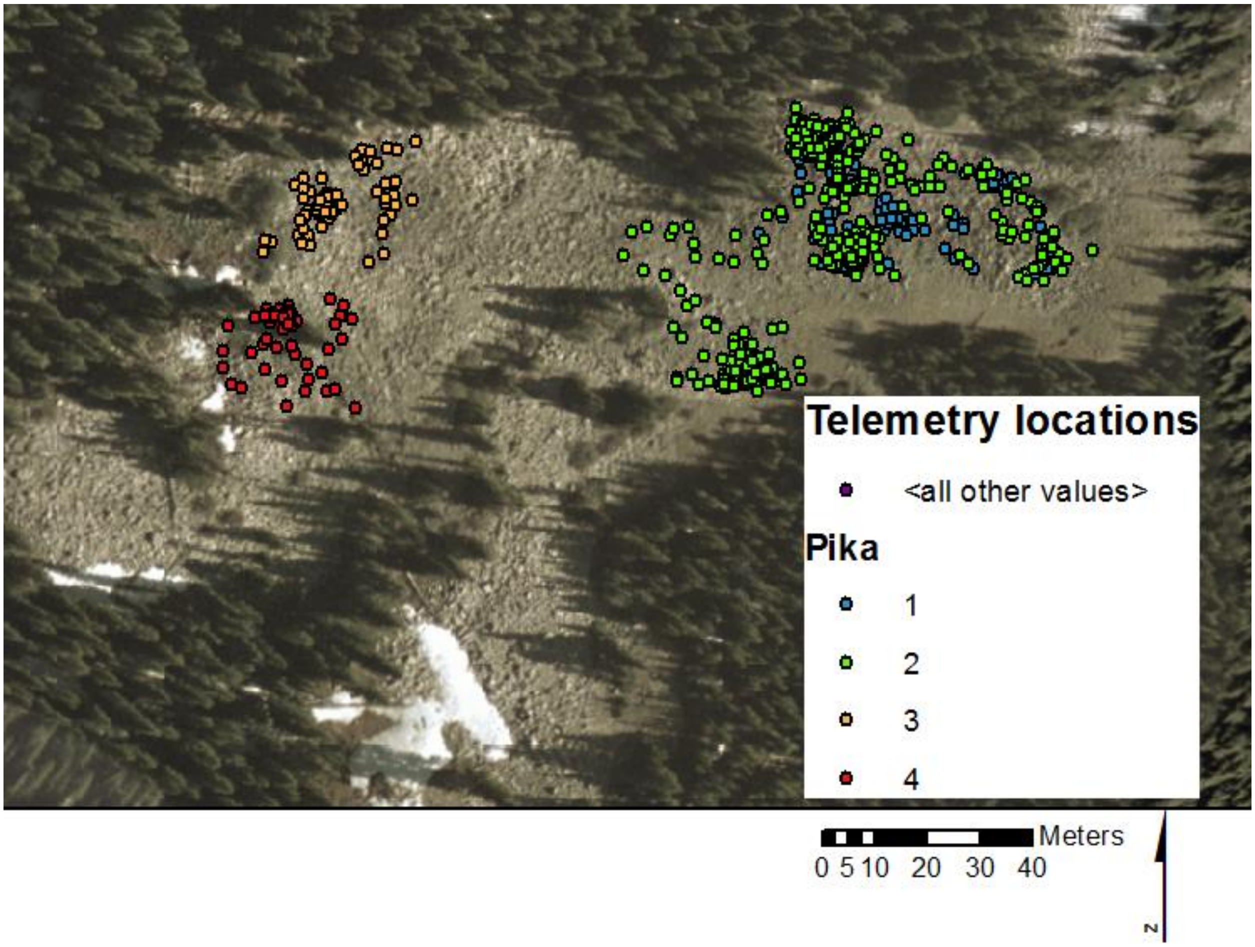
Data collection

There were two lidar-derived DEMs, filtered (vegetation removed) and unfiltered. We used the filtered DEM to derive all terrain metrics. We first performed a 1m resolution land cover classification in ENVI 5.2 (Exelis 2014) using the RGB, measures of topographic heterogeneity and position, and vegetation height, the difference between the filtered and unfiltered DEMs. Also based on this land cover classification we created a metric of distance within talus to the nearest area of meadow (MeadowDist). We created all the terrain metrics using ArcMap 10.3 (ESRI 2014).

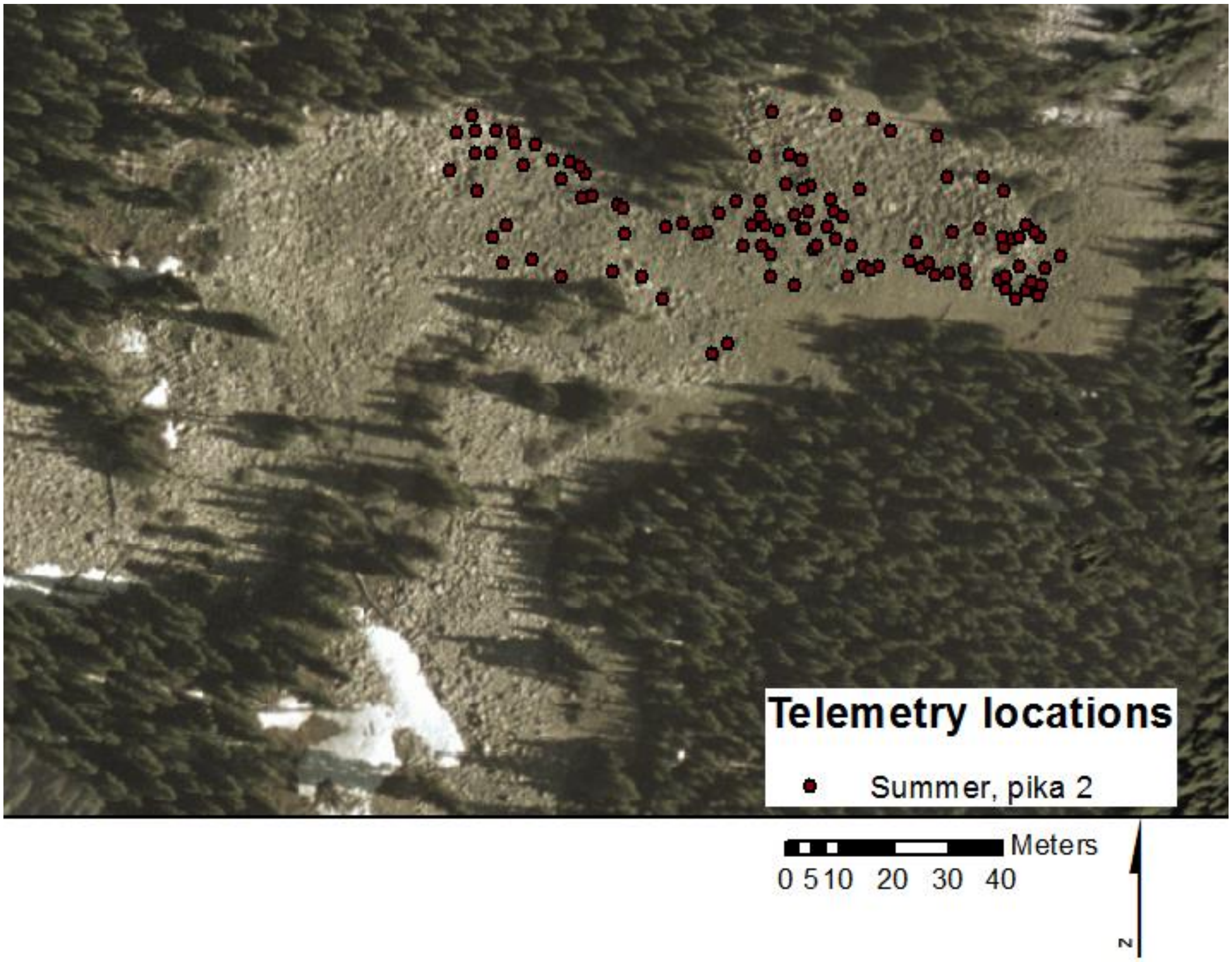
To address our hypothesis, we used radio telemetry to track radio-collared pikas through the year (collars from Telonics, Inc. Mesa, Arizona). The collars were custom fit for each of the four pikas collared. During each visit to the field site, we triangulated each pika's position within the talus every five minutes for one hour, except when extreme cold made data collection untenable. From early October to mid-July we visited the site 44 times, returning every 2-7 days, recording a total of 693 observation points among four pikas (Figure 1.2). The majority of field visits were conducted when snow cover was present at the study site. We defined the period when snow covered much of the study site and likely influenced microhabitat as Winter (October-May) and the period without snow as Summer (June-July). During or immediately following snowfall, most of the rocks (and the spaces between them) were covered with snow. NWT is often windy, and snow is quickly redistributed by wind after a storm. We collected data at different points throughout the day and in conditions ranging from sunny and above 0°C (and above 15°C in summer) to below -20°C with winds in excess of 65 km/h. Through the winter three of the pikas died, dispersed, or dropped their collars. This study was primarily focused on previously unstudied winter habitat use. For that reason and because of unfavorable trapping conditions, we did not re-collar pikas.

For each pika, we first found the minimum bounding extent of true presence points (detections by telemetry). We then created an absence point to correspond to each of those presence points, randomly placed on the landscape within the same bounding extent and restricted to talus (Figure 1.4). These absence points represent the overall landscape within that extent—if the presence and absence points vary significantly in their spatial characteristics, then pikas are likely preferentially selecting microsites with topographic characteristics disproportionate to their availability within the pika's territory.

As a second measure of pika summer habitat use, we used records of pika trapping success at NWT during 2008-2015. Most trapping occurred during July of each year. This amounts to hundreds of attempts and 170 successful traps. However, only the location of successful traps was recorded, so failure locations were drawn from randomly selected points to represent a sample of the characteristics of area where we made attempts. The timing of telemetry and trapping efforts is shown in Figure 1.3. Similar to the randomly selected points for telemetry, we selected random points to represent available trapping area within the same spatial extent, yet restricted to talus. Further, most trapping attempts were made close to talus edge where they are most often observed, so we restricted these random points to within 5m of talus edge and no closer than 5m to a successful trapping location.



A.



B.

Figure 1.2. All radio telemetry locations for radio-collared pikas in winter (October-May) and summer (June-July). Winter was defined as time where snow covered most of the talus in the study area.

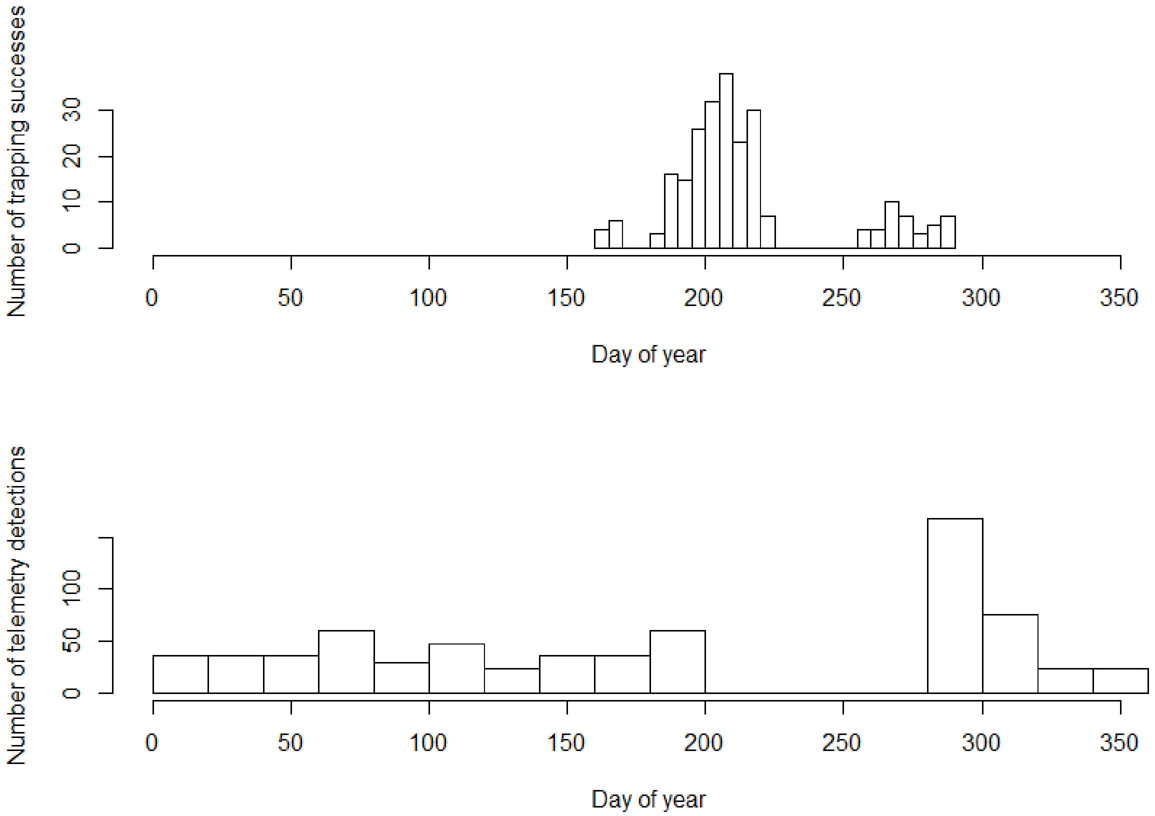


Figure 1.3. Comparison of the timing for radio telemetry efforts (October 2013-July 2014) and trapping success (2008-2015).

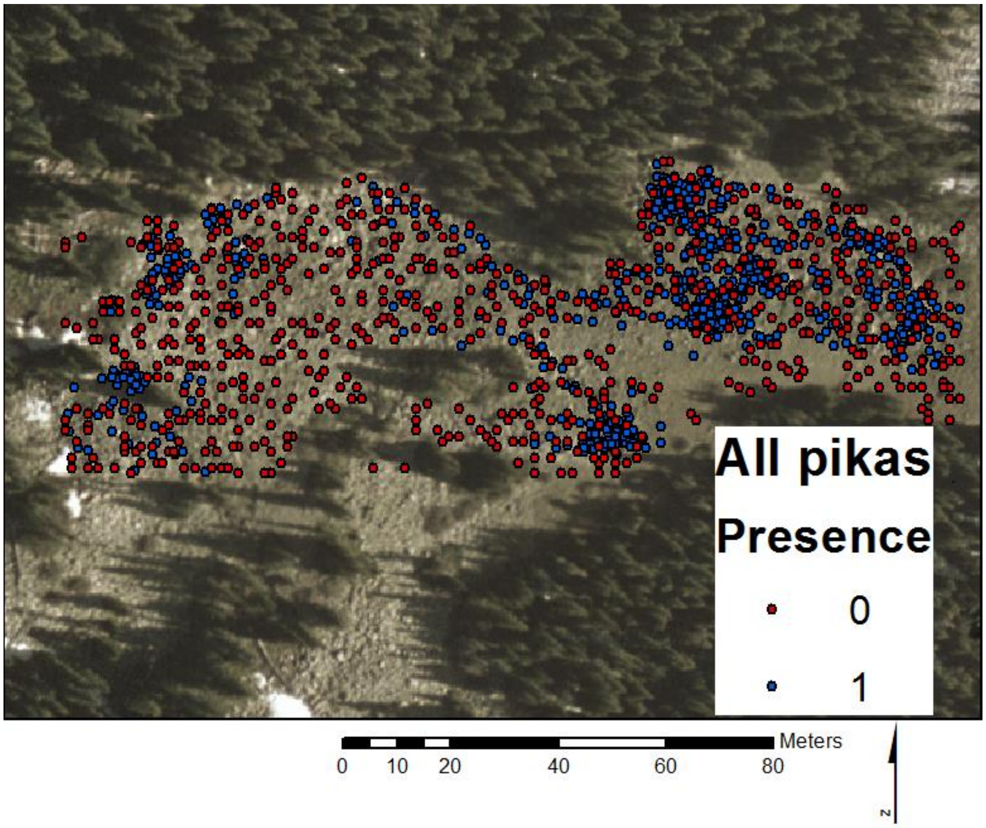


Figure 1.4. All 1386 points used in logistic regressions, colored by presence (1, blue) and pseudo absence (0, red).

Terrain metrics

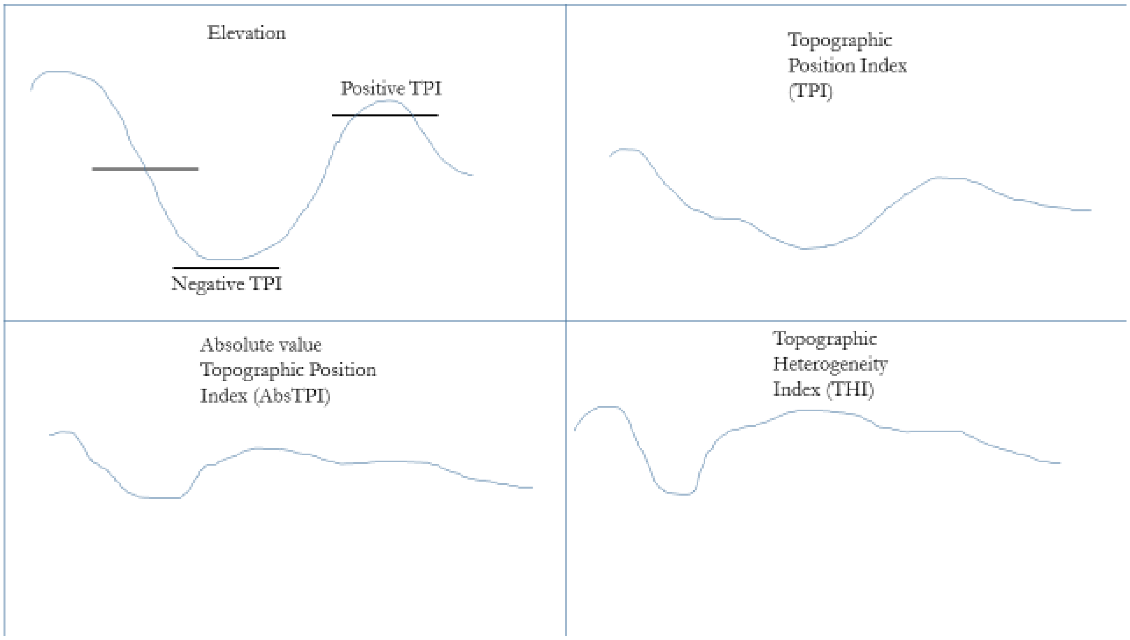
Varner and Dearing (2014) showed that talus subsurface temperatures can vary widely in pika habitat at the scale of a few meters, so studies that involve their habitat use should measure terrain at a fine scale. We therefore used Topographic Position Index (TPI), a measure of a cell's elevation compared to the cells around it within a given radius. We also used the absolute value of the TPI (AbsTPI) to show how extreme a cell's elevation is within that window and created a metric, Terrain Heterogeneity Index (THI), which estimates the total heterogeneity in an area by defining each cell by the summed AbsTPI within the same window size. We calculated each of these metrics at scales of 3m, 5m, and 10m. We show the visual representation of this process in Figure 1.5. We selected these three scales because they may describe different effects of terrain.

THI at a 3m scale (sum of AbsTPI within a 3m radius) is the effect of rocks in the immediate vicinity of any place a pika may take shelter—deeper snow may be just downwind of the largest rocks rather than on them. We called this metric PointRoughness. A 5m radius would capture similar terrain as PointRoughness and some of the same rock effects, but would weight those effects less and begin to capture the larger scale heterogeneity. We called that 5m heterogeneity LocalRoughness. Similarly, heterogeneity within a 10m radius does not give great weight to individual rocks, but does account for land surface topographic features that a small radius does not. This 10m heterogeneity we called PatchRoughness. For example, a pika territory could be close to a cliff wall and sheltered from wind in that direction, but have nearly no large rocks or variation in rock size. Using each of these scales allows us to measure the effect of different terrain-microclimate interactions.

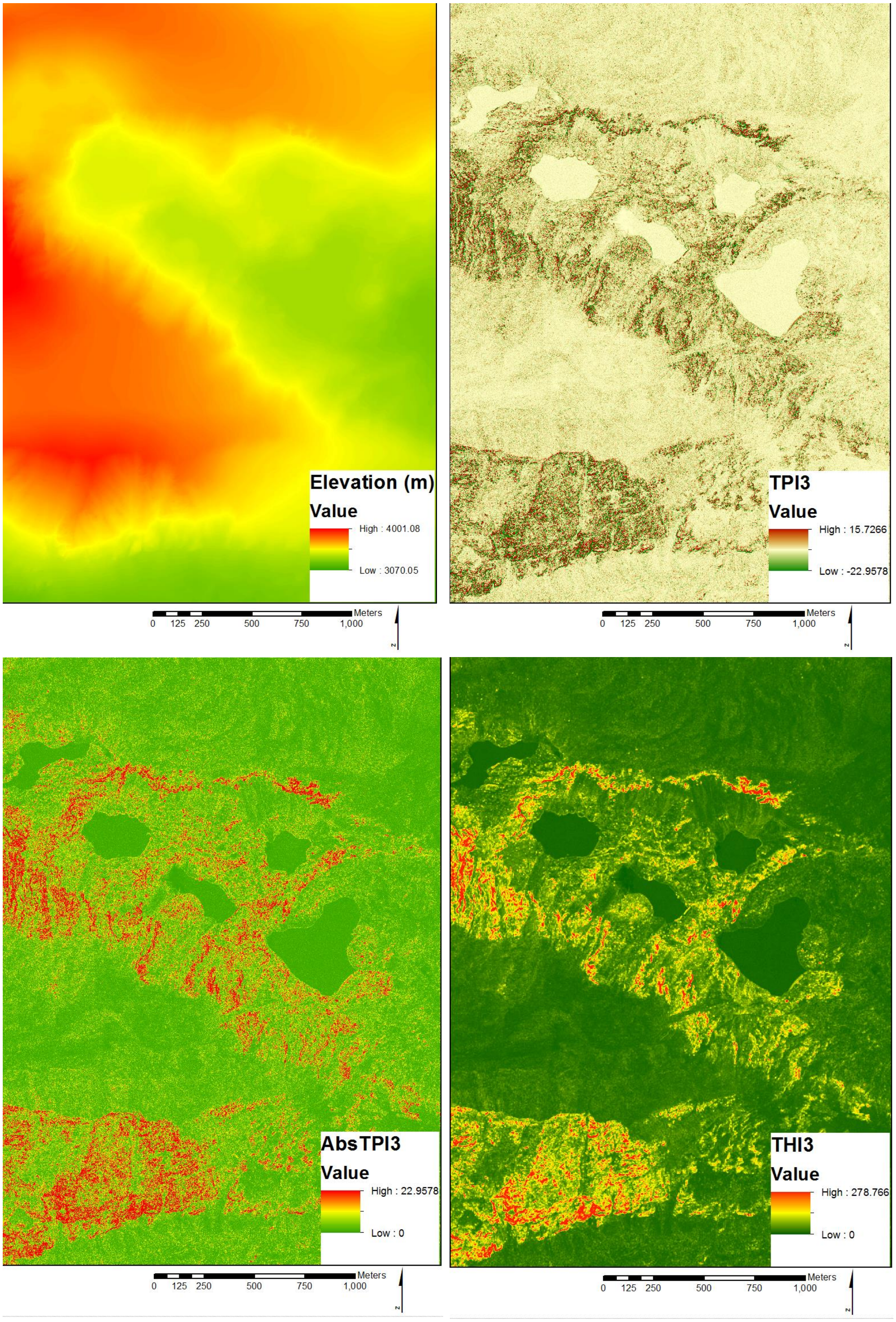
We created a flow accumulation surface (FlowAcc), which uses elevation at each cell to show low points which would attract the flow or pooling of hypothetical fluid; e.g., where cool air might pool in the summer or where snow could accumulate in winter. FlowAcc effectively shows low channels parallel to the landscape's slope. The final predictor rasters were plan curvature (PlanCurv), profile curvature (ProfCurv), total curvature (TotCurv), and slope. Surface curvature is the derivative of the slope, or the second derivative of the surface. PlanCurv is that derivative perpendicular to the slope of the surface, ProfCurv is parallel to the slope of the surface, and TotCurv. Each of the terrain metrics described above could affect microclimate, especially in how they affect snow accumulation, exposure to wind, and subsurface air pooling.

Table 1.1. All possible predictor variables used in detecting terrain effects on habitat use and range of possible values for each.

Predictor variable	Value range	Units
MeadowDist	0-383.85	Meters
Slope	0-87.57	Degrees
Cos(Aspect)	-1.00-1.00	Cosine(degrees)
TPI3	-22.96-15.77	Meters
AbsTPI3	0-22.96	Meters
PointRoughness (THI3)	0-278.77	Meters
TPI5	-29.11-18.78	Meters
AbsTPI5	0-29.11	Meters
LocalRoughness (THI5)	826.07	Meters
TPI10	-54.91-22.10	Meters
AbsTPI10	0-54.91	Meters
PatchRoughness (PATCHROUGHNESS)	0-1149.94	Meters
FlowAcc	0-506673.00	Cubic meters
PlanCurv	-4573.98-4809.50	d(ΔMeters)
ProfCurv	-3696.71- 3832.17	d(ΔMeters)
TotCurv	-6336.94- 6851.78	d(ΔMeters)



A.


Elevation (m)
Value
High : 4001.08
Low : 3070.05
TPI3
Value
High : 15.7266
Low : -22.9578
AbsTPI3
Value
High : 22.9578
Low : 0
THI3
Value
High : 278.766
Low : 0
0 125 250 500 750 1,000
Meters
N

B.

Figure 1.5. A conceptual figure and a subset of the NWT area, each showing how elevation is processed to Topographic Heterogeneity Index (THI). TPI is a measure of a point's prominence, AbsTPI is the absolute value of TPI, and THI is the summed AbsTPI within a user-defined window.

Data analysis

We performed all statistical analyses using R 3.1.2 (R Core Team 2014). We used a series of logistic regressions with the telemetry and trapping data to test how metrics of the terrain predict habitat use in single-predictor models. We also used AIC to find the best multiple-predictor logistic model within each of the three datasets (winter telemetry, summer telemetry, and summer trapping), both by manually comparing progressively simpler models and by the R package *bestglm* (McLeod and Xu 2014). We excluded any models with correlation coefficient between two predictor variables >0.5, and of the two correlated variables we dropped the one with the highest average correlation across all variables. We observed that pika locations were autocorrelated at a temporal scale of five minutes. Therefore, we used mixed effects models, with Date (of visit) as a random effect using the R package *lme4* (Bates et al. 2012). Because we observed any single pika for an hour but never more than once in a day, there are not multiple time sequences for any pika within the grouping variable Date. We tested individual pikas as both random and fixed effects to test individual variation in habitat use.

Winter telemetry presence ~ Terrain metrics + Random effects: Date, Pika

Example equation:

WinterPresence~MeadowDist + PointRoughness + FlowAcc + (1|Date) + (1|Pika)

To analyze the records of successful trap locations, we randomly selected failure points in the same way as the absence points describe the overall territory available for the radio telemetry models. We used all of the same terrain metrics as used for the telemetry models except for MeadowDist as a possible predictor in the summer trapping models, because trap locations and randomly selected points were all within 5m of talus edge

To compare terrain effects across seasons, beyond simply noting different important predictors, we used the parameters and coefficients from the best multiple-predictor model for winter telemetry to perform a logit transformation and make a raster grid of probability of pika presence within the study landscape. We then used logistic regression models to test the ability of those probability surfaces to predict the location of summer telemetry points and summer trapping successes compared to the absence points.

Results

Several terrain metrics were predictive of pika habitat use in single-predictor logistic regressions and the significant predictors were different across seasons (winter telemetry, summer telemetry, summer trapping) (Table 1.2*)*. Of particular note, PointRoughness (Figure 1.6) was positively associated with pika presence in winter ($p<<0.0001$) while it had a negative association with trapping success in summer ($p=0.003$) and no significant association with summer telemetry presence. Similarly, pika presence was positively associated with MeadowDist (Figure 1.7) in winter ($p<<0.0001$) but negatively (though insignificantly) associated with presence and trapping success in the two summer datasets. For every dataset, the null model was a significantly poorer predictor than the best model (Table 1.3).

Both methods of best fit model selection—*bestglm* and manual comparison—arrived at the same best model for each dataset. We tested Pika as a random effect and as a fixed effect. As a fixed effect it did not appear in any of the best models. For no model did its inclusion as a random effect change the p-value or coefficient by more than 0.00001 compared to its absence from the model.

We used the best fit model for each response variable to create three probability rasters by a logit transformation where every cell is the predicted probability of pika presence at that point as a measure of predicted habitat use. Summer trapping was able to predict summer telemetry (p=0.007) and summer habitat use detected by telemetry predicted summer trapping success (0.048). However, neither measure of summer habitat use significantly predicted winter habitat use and winter habitat use did not significantly predict either summer habitat use measure (Table 1.4).

Table 1.2. Effect and significance of all predictor variables in single logistic regressions in each of the datasets, ranked by their explanatory power (AIC).

Dataset	Individual Predictor	p-value	AIC	ΔAIC	Coefficient
Summer telemetry	slope	0.001	294.041	0.000	0.087
Summer telemetry	MeadowDist	0.085	302.407	8.366	-0.052
Summer telemetry	null	1	303.496	9.455	0
Summer telemetry	LocalRoughness	0.183	303.644	9.604	-0.054
Summer telemetry	PointRoughness	0.213	303.876	9.836	-0.241
Summer telemetry	AbsTPI5	0.378	304.657	10.616	-1.195
Summer telemetry	AbsTPI10	0.378	304.879	10.839	-1.195
Summer telemetry	PatchRoughness	0.465	304.903	10.863	-0.025
Summer telemetry	AbsTPI3	0.543	305.068	11.028	-1.343
Summer telemetry	TPI3	0.592	305.152	11.111	-0.732
Summer telemetry	FlowAcc	0.750	305.333	11.293	0.000
Summer telemetry	TPI10	0.754	305.342	11.301	0.129
Summer telemetry	profile curvature	0.767	305.352	11.311	0.004
Summer telemetry	TPI5	0.895	305.422	11.382	-0.105
Summer telemetry	plan curvature	0.911	305.427	11.387	0.002
Summer telemetry	total curvature	0.916	305.428	11.388	-0.001
Summer Trapping	PointRoughness	0.004	319.395	0.000	-0.496
Summer Trapping	AbsTPI10	0.004	319.575	0.180	-2.240
Summer Trapping	PatchRoughness	0.008	320.802	1.407	-0.099
Summer Trapping	AbsTPI5	0.008	321.262	1.867	-3.320
Summer Trapping	LocalRoughness	0.013	321.818	2.423	-0.113

Summer Trapping	slope	0.038	324.2	4.805	-0.046
Summer Trapping	AbsTPI3	0.064	325.108	5.712	-3.424
Summer Trapping	null	1	326.622	7.227	0
Summer Trapping	TPI10	0.208	327.027	7.631	0.552
Summer Trapping	TPI5	0.315	327.603	8.208	0.749
Summer Trapping	TPI3	0.557	328.274	8.878	0.691
Summer Trapping	FlowAcc	0.669	328.443	9.048	0.000
Summer Trapping	plan curvature	0.760	328.528	9.133	0.004
Summer Trapping	total curvature	0.907	328.609	9.214	0.001
Summer Trapping	profile curvature	0.932	328.615	9.220	0.001
Winter telemetry	PointRoughness	<0.0001	1582.29	0.000	0.471
Winter telemetry	AbsTPI3	<0.0001	1586.89	4.604	4.890
Winter telemetry	AbsTPI5	<0.0001	1590.68	8.397	2.710
Winter telemetry	TPI5	<0.0001	1592.86	10.572	1.622
Winter telemetry	TPI3	<0.0001	1595.28	12.994	2.718
Winter telemetry	TPI10	<0.0001	1604.62	22.329	0.819
Winter telemetry	total curvature	<0.0001	1608.5	26.214	0.014
Winter telemetry	plan curvature	<0.0001	1611.29	29.005	0.023
Winter telemetry	meadow distance	<0.0001	1612.51	30.222	0.054
Winter telemetry	profile curvature	<0.001	1614.51	32.220	-0.019
Winter telemetry	LocalRoughness	<0.001	1615.33	33.045	0.060
Winter telemetry	FlowAcc	0.013	1620.92	38.630	0.000
Winter telemetry	PatchRoughness	0.115	1627.47	45.187	-0.021
Winter telemetry	null	1	1627.96	45.677	0
Winter telemetry	AbsTPI10	0.001	1629.3	47.011	-1.213
Winter telemetry	slope	0.464	1629.43	47.141	0.007

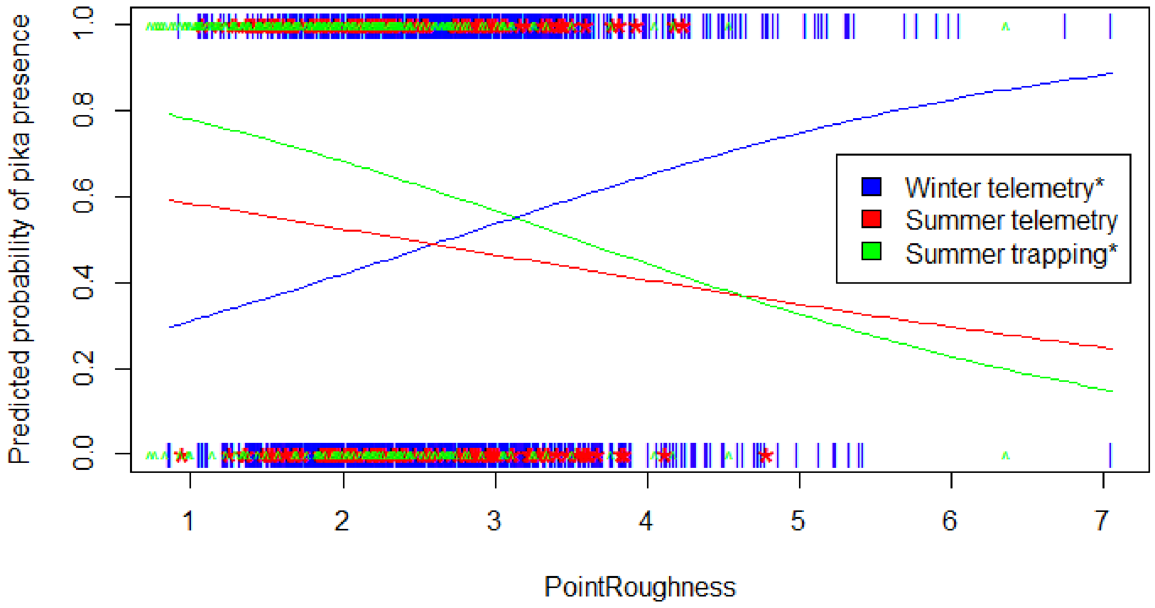


Figure 1.6. Effect of PointRoughness (THI3) on the predicted probability of pika presence or trapping success in each of the three datasets analyzed. *p<0.05. Presence and absence points for each dataset are overlaid.

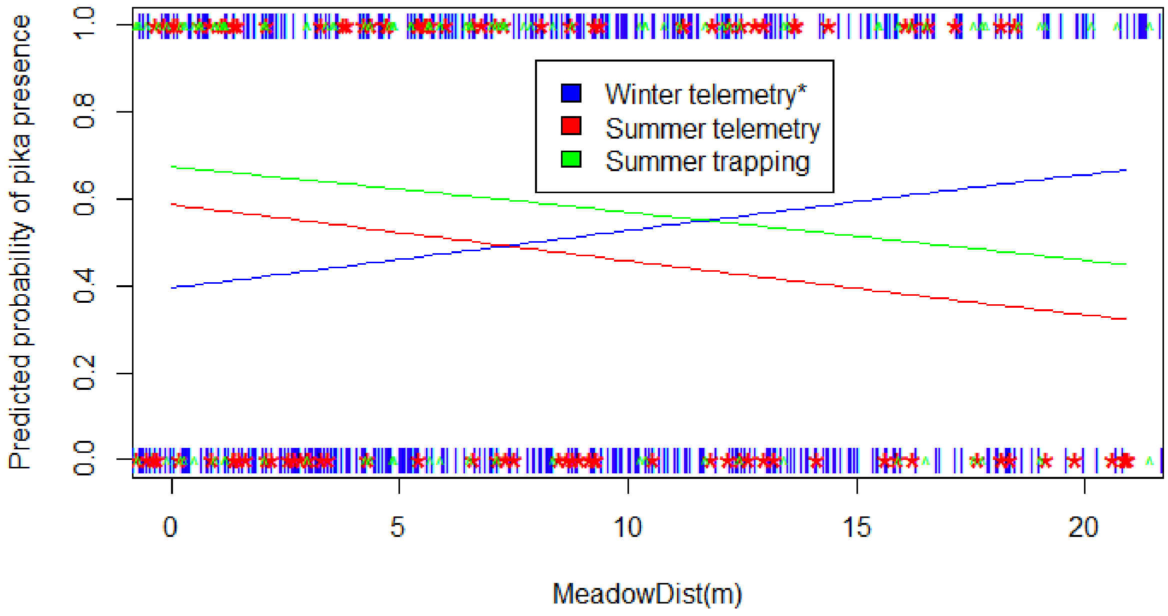


Figure 1.7. Effect of distance to the talus-meadow interface on the predicted probability of pika presence or trapping success in each of the three datasets analyzed. *p<0.05. Presence and absence points for each dataset are overlaid.

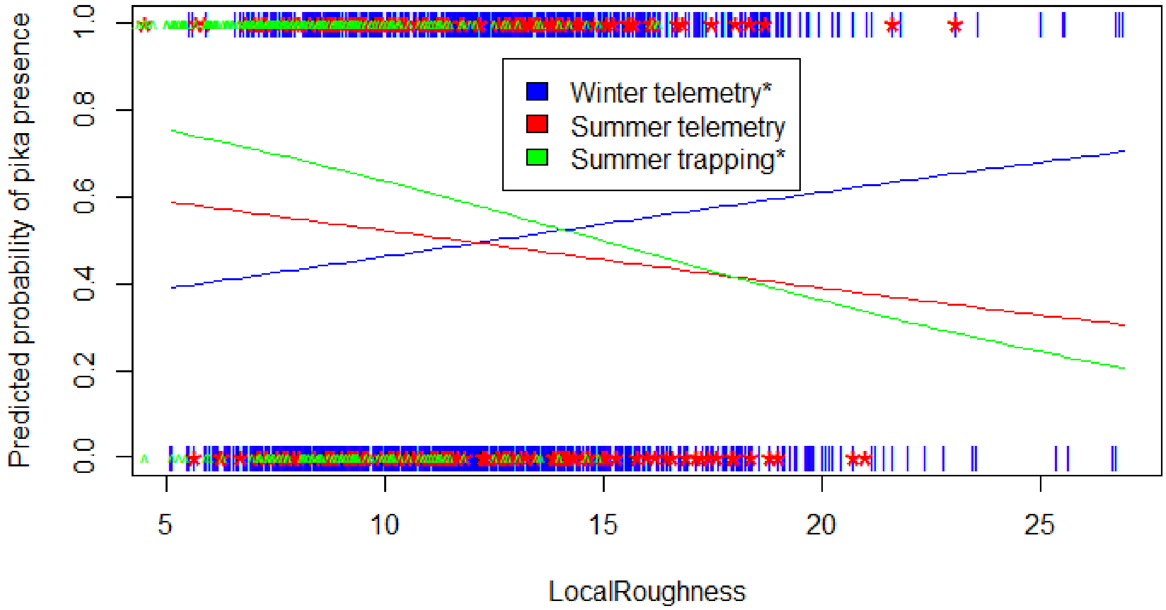


Figure 1.8. Effect LocalRoughness (THI5) on the predicted probability of pika presence or trapping success in each of the three datasets analyzed. *p<0.05. Presence and absence points for each dataset are overlaid.

Table 1.3. Summary of the best model for each of the three measures of pika habitat use. For all models, Pika is a fixed effect, Date is a random effect.

Dataset	Best model (coefficient +/-)	Model AIC	ΔAIC	Rank
Winter telemetry	MeadowDist(+) + PointRoughness(+) + TPI5(+) + AbsTPI5 (+) + PatchRoughness(-)	1478.555	0	1
Winter telemetry	MeadowDist(+) + PointRoughness(+) + TPI5(+) + AbsTPI5 (+) + PatchRoughness(-) + FlowAcc (-)	1478.808	0.253	2
Winter telemetry	PointRoughness (+) + TPI3(+) + LocalRoughness(+) + AbsTPI5(+) + PatchRoughness (-)	1480.609	2.054	3
Winter telemetry	PointRoughness (+) + TPI3(+) + LocalRoughness (+) + AbsTPI5(+) + PatchRoughness (-) + slope(+)	1483.529	4.974	4
Winter telemetry	null	1627.964	149.409	null
Summer telemetry	MeadowDist(-) + Slope(+)	292.2563	0	1
Summer telemetry	MeadowDist(-) + slope(+) + TPI3(-)	293.939	1.6827	2
Summer telemetry	MeadowDist(-) + slope(+) + TPI3(-) + TPI5(+)	294.9087	2.6524	3
Summer telemetry	null	303.4396	11.1833	null
Summer telemetry	MeadowDist(-) + AbsTPI5(-)	304.0442	11.7879	4
Summer trapping	Slope (-) + AbsoluteTPI10(-)	315.822	0	1
Summer trapping	Slope(-) + AbsTPI10(-) + PointRoughness (-)	316.7686	0.9466	2
Summer trapping	Slope(-) + AbsTPI10(-) + PointRoughness (-) + LocalRoughness (+)	318.2587	2.4367	3
Summer trapping	Slope(-) + AbsTPI10(-) + PointRoughness (-) + LocalRoughness (+) + aspect(+)	320.0374	4.2154	4
Summer trapping	null	326.6222	10.8002	null

Table 1.4. Summary of models comparing different datasets. The predictive models are the probability surfaces generated by a logit transformation of the best fit logistic regression model for each dataset (Table 1.3), and the predicted response is the different datasets of observed habitat use.

Predicted response	Predictive model	p-value	AIC
Summer trapping	Winter telemetry	0.426	327.99
Summer trapping	Summer telemetry	0.048	327.25
Summer telemetry	Winter telemetry	0.192	300.15
Summer telemetry	Summer trapping	0.007	295.79
Winter telemetry	Summer telemetry	0.144	1587.6
Winter telemetry	Summer trapping	0.613	1593.4

Discussion

Our results showed significant impacts of terrain on microhabitat use by pikas throughout the year. This was especially notable in how pikas preferentially used more heterogeneous terrain in the winter. Both the individual logistic regressions and the best fit multiple logistic models suggest that topographic heterogeneity played a significant role in fostering suitable winter microhabitat. This could be due to greater snow accumulation in heterogeneous terrain, which provides insulation from the extreme cold that likely affects pika overwinter survival (Winstral et al. 2002, Beever et al. 2010, Jeffress et al. 2013). Even when wind had scoured snow from most of the study area, we observed deep snow drifts (in some places >3m) and usually found pikas under those drifts when the rest of the talus was exposed.

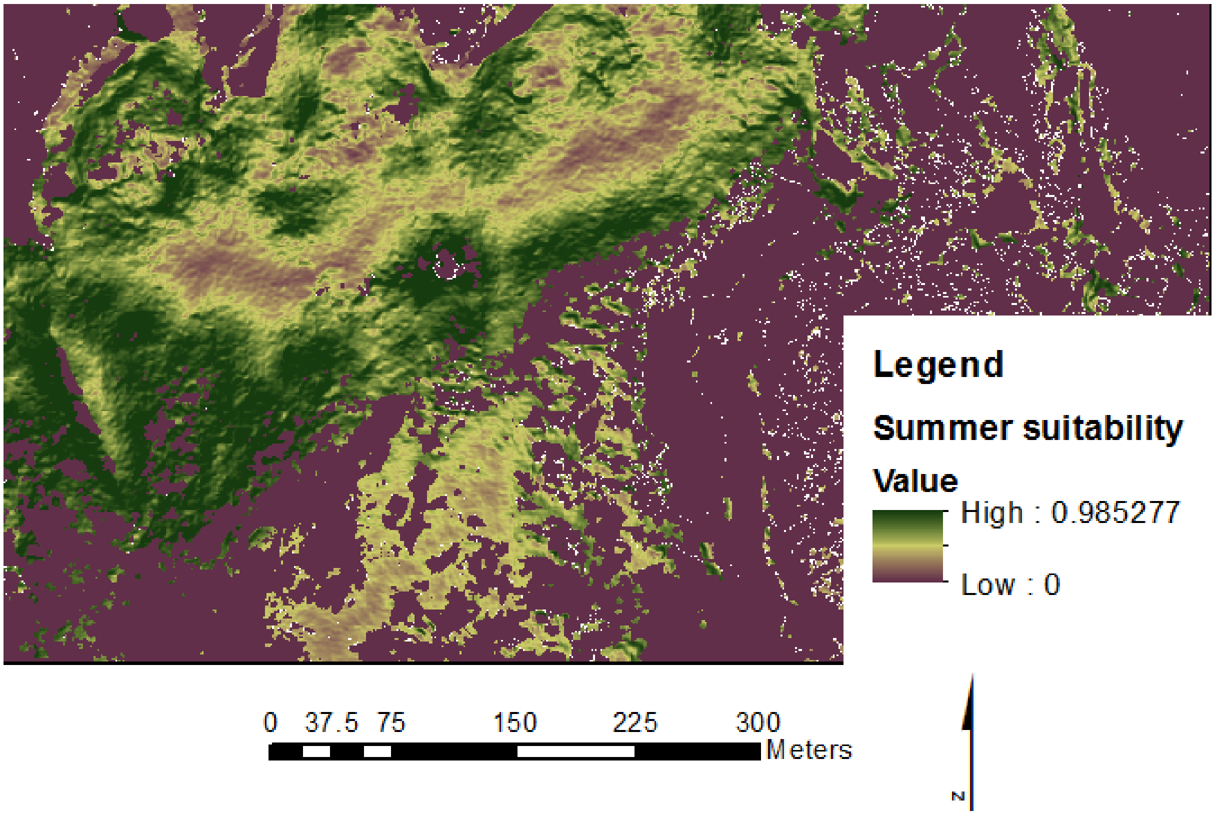
In winter, snow tended to accumulate in some areas more than others, as expected. Most of the meadow area was bare except for during active snowfall, while the talus of higher surface roughness retained snow. In fact, most of the pika presence points were in areas that held snow through the whole winter, including one area where the snow was more than 2-3m deep from January to April. Qualitatively, the pikas seemed far more likely to use other areas of talus during or immediately following snowfall, before wind redistributed it. In Figure 1.9, the two pictures were taken only three days apart. The first was during a heavy snowfall, and all rocks and meadow were covered with even, deep snow, and we detected the pikas across their territory, not constrained to the deepest snow or their haypile. The following few days were windy, and the snow was scoured from much of the talus, leaving it only on the leeward side of the largest rocks and in the most heterogeneous areas.

Figure 1.9. Photos taken days apart from the same point at the study site. Left: January 4. Right: January 8.

It is also notable that pika presence in winter was significantly associated with greater TPI, a measure of a point's prominence, at 3m, 5m, and 10m scales ($p<0.0001$), suggesting that pikas preferentially use points higher on the landscape. This would seem to contradict our explanation for the mechanism driving heterogeneity's role, as higher points at a fine scale are more exposed to wind and accumulate less snow (Ruel et al. 1998). However, pikas were rarely observed at the surface of the talus during the winter. One possibility, then, is that that higher points at this fine scale correspond to larger rocks, which would accumulate more snow than smaller rocks.

The fact that Pika was not a significant fixed effect and had no significant impact on models when included as a random effect suggests that our results are more likely to be generalizable. We found the same impacts of terrain on habitat use for each pika—though there may be some impact of this study site in itself, we expect that these trends will likely translate well to other pika-occupied talus with similar macroclimatic controls.

It is especially important to note the strong seasonal component in these terrain effects. While terrain heterogeneity is important in winter, it had an insignificant or negative effect in summer. This seasonality is also apparent in that pikas were more likely to be found close to meadow edge in summer than in winter. This is possibly because in summer, pikas are more actively gathering food than in winter and spend a great deal of their time foraging and collecting hay from adjacent meadows. On the other hand, in winter they appear to huddle in talus sheltered from the extreme cold; that sheltered, heterogeneous terrain was, at this study site and across the NWT area, also further from the edge (for PointRoughness~MeadowDist, $r=0.37$, $p<0.001$). Similarly, none of the probability surfaces generated from the best fit models for any of the datasets could be used to predict presence and absence in the other datasets. This speaks to pikas' need for habitat heterogeneity. An individual territory with only suitable summer habitat may be one near to meadow edges, while one with only suitable winter habitat is likely to be very sheltered but farther from suitable vegetation. Winter is a large source of mortality for pikas (Kreuzer and Huntly 2003, Beever et al. 2010), and our results demonstrate further why winter may be limiting and suggest the importance of considering the seasonality of pika habitat requirements (Figure 1.10*)*.


Legend
Summer suitability
Value
High : 0.985277
Low : 0
0
37.5
75
150
225
300
Meters
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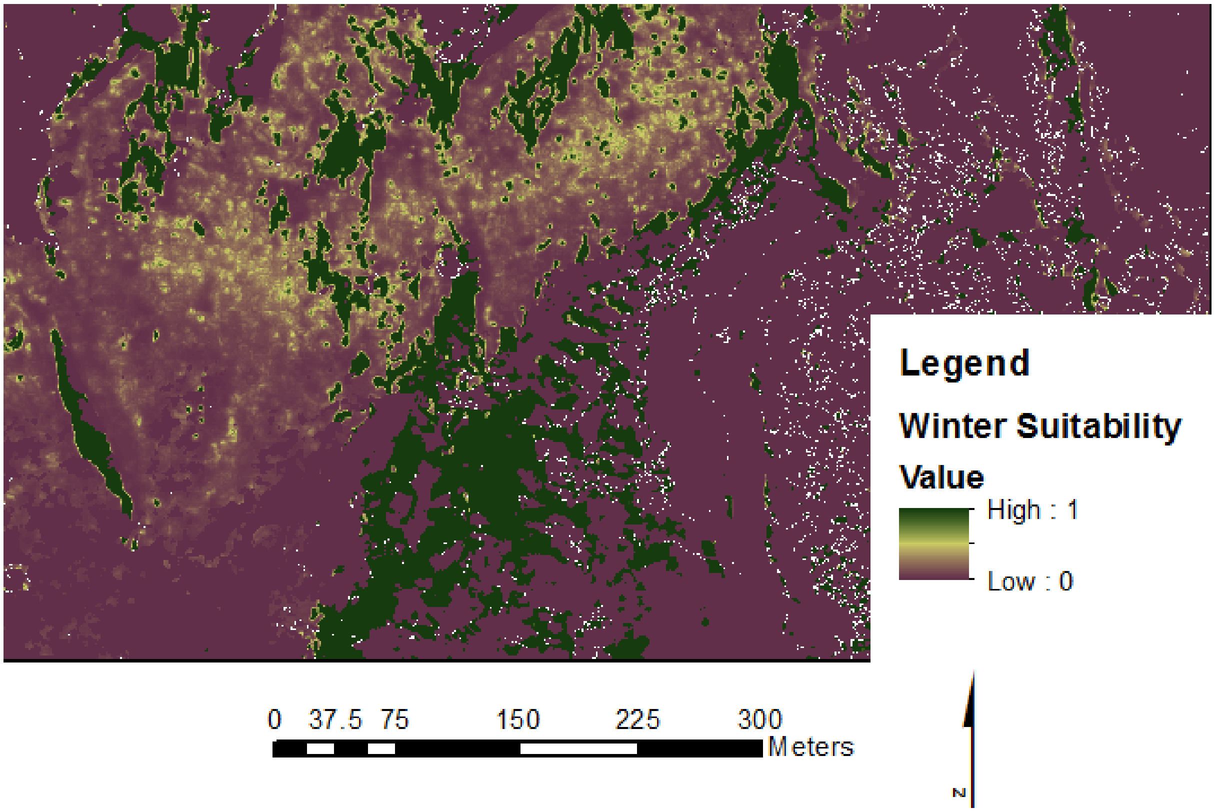
A.


Legend
Winter Suitability
Value
High : 1
Low : 0
0
37.5
75
150
225
300
Meters
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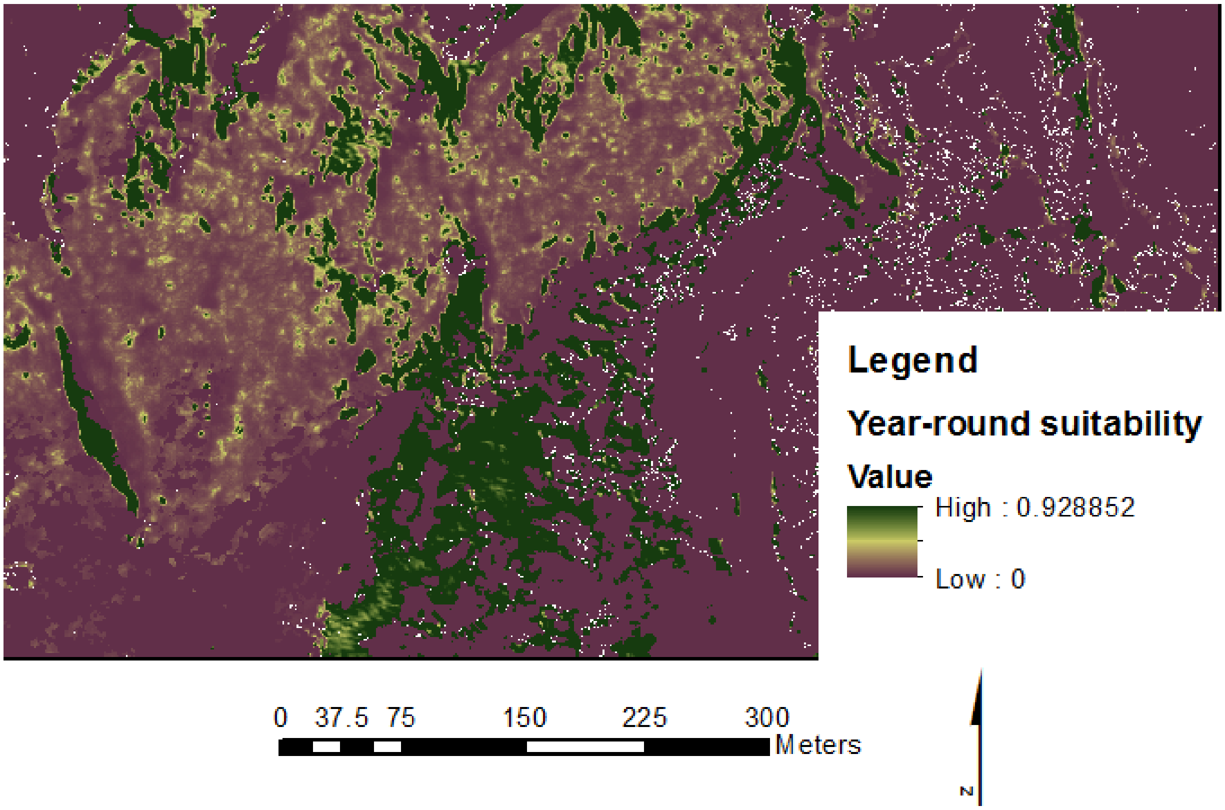
B.



C.

Figure 1.10. The predicted habitat suitability in a subset of the NWT area using a logit transformation of the best fit models of habitat use from A) Summer telemetry, B) Winter telemetry, and C) Summer and winter telemetry multiplied to show the overall suitability.

Most models of pika habitat are based on occupancy surveys conducted in summer (Rodhouse et al. 2010, Erb et al. 2011, Jeffress et al. 2013, Stewart et al. 2015, Schwalm et al. 2016). The seasonality in habitat requirements that we observed suggests that these models may overestimate the extent of suitable habitat, as they do not account for winter habitat requirements. Further, the fact that we found significant effects of topographic heterogeneity at three different spatial scales suggests that the processes that create refugia and microrefugia likely function at multiple spatial scales. Though species distribution models (SDMs) can be powerful tools for estimating habitat suitability and population connectivity, many do not use high resolution data to address relevant habitat requirements (Gillingham et al. 2012). It is therefore problematic to rely on regional climate projections and SDMs when both conservation decisions and habitat heterogeneity occur at mostly finer scales (Dobrowski 2011, Ashcroft et al. 2012). Instead, models should be based on data scaled to account for both spatial and temporal heterogeneity in the habitat used by individuals to best quantify occupancy (Quintero and Wiens 2013, Valladares et al. 2014, Schwalm et al. 2016) (Quintero and Wiens 2013, Valladares et al. 2014, Schwalm et al. 2015).

Our results continue to build support for the role of various sorts of heterogeneity at different scales in driving species occupancy and habitat use. These processes may be especially important to understand in ecosystems such as alpine and montane environments that are more threatened by climate change. If those environments are to serve as refuge for climate-sensitive species, then they must do so at scales relevant to each species. Our results emphasize the need for models of occupancy and connectivity at biologically relevant scales that account for both spatial and temporal heterogeneity to better understand how climate change is likely to affect threatened species, the resources they require, and downstream ecosystems.

CHAPTER 2

Title: Predicting habitat suitability for a habitat specialist, the American pika (*Ochotona princeps*) using high resolution remotely sensed data

Introduction

Topographic and climatic heterogeneity create ‘microrefugia’—patches of suitable habitat within regionally unfavorable conditions (Rull 2009, 2010). Their distribution and responses to climate are important for understanding ecosystem responses to climate change in both historical and contemporary contexts (Pearson 2006, Keppel et al. 2012). Because climate change is likely to have the strongest effects on alpine ecosystems (Hughes 2000, Parmesan 2006), it will become ever more important to identify refuge habitat within those sky islands that will remain suitable for vulnerable species despite an increasingly hostile matrix (Thomas et al. 2004, Hannah et al. 2014). Despite an overall warming climate, the mountains will likely still provide needed refuge habitat for cold adapted species from unfavorable climate (Holderegger and Thiel-Egenter 2009, Rull 2009, Dobrowski 2011, Hannah et al. 2014). However, even these patches of relative shelter vary in their suitability, and some may offer only a temporary reprieve from climate effects. It is important to detect microrefugia and quantify their relative quality to predict the role they may play in species persistence (Keppel et al. 2012, Hannah et al. 2014). Understanding that role and predicting suitable habitat patches at scales relevant individual movements and survival could have a great impact on conservation decisions (Ashcroft et al. 2012, Hannah et al. 2014).

By the same mechanism that allows microrefugia to persist in hostile landscapes, the suitability of habitat patches will vary, especially in mountainous terrain where climate varies dramatically over short distances (Whiteman et al. 2004, Pepin and Lundquist 2008). In some cases, mountain ridges can actually be less hospitable to mesic species than the adjacent valleys;

site climate on the ridge is more closely coupled with broader atmospheric conditions and likely to experience large temperature swings, while a valley is more stable (Dobrowski 2011). Because of this, some plants may actually move *downhill* in response to regional warming, as cold-air pooling makes the valleys more hospitable than the temperature swings on high slopes (Lundquist et al. 2008, Dobrowski 2011). Habitat models that do not account for more fine-scale topoclimatic phenomena may fail to predict these trends (Thornthwaite 1953, Lundquist et al. 2008, Dobrowski 2011, Hannah et al. 2014). Predictions based only on coarse-scale metrics and surveys are likely to overestimate occupancy where pockets of unsuitable habitat exist. With a strong influence of topography on microclimate, there are likely patches of occupied habitat that will become less suitable with any advance of climate change (Ashcroft 2010, Dobrowski 2011, Hannah et al. 2014).

Among those potentially threatened habitat specialists is the American pika (*Ochotona princeps*), which may already be experiencing climate-driven extirpations (Wilkening et al. 2011, Calkins et al. 2012, Erb et al. 2014, Millar et al. 2014). The climatic effects of topographic heterogeneity are likely important for pikas at a very fine scale because pikas are territorial, have fairly small territories, and exploit suitable microhabitat to survive extreme weather (Hafner 1993, Beever et al. 2003, Rodhouse et al. 2010, Millar et al. 2014). Several studies have already suggested important roles for habitat heterogeneity in pika distribution, especially in areas that might otherwise be inhospitable as their overall range retracts, and they likely currently occupy patches within inhospitable landscapes that could function as microrefugia (Simpson 2009, Millar and Westfall 2010, Rodhouse et al. 2010, Henry et al. 2012, Jeffress et al. 2013, Varner and Dearing 2014). Pikas are likely a biogeographic indicator species of late Holocene climate change, already occupying refugia and a likely model species for studying the interactive effects of topography and climate on species (Hafner 1993, Beever et al. 2003, Grayson 2005). Sub-surface conditions within the pika's preferred microhabitat (talus or boulderfields) can vary greatly within a single pika's territory; by examining habitat use at a very fine scale, we could study direct effects of heterogeneity at biologically relevant scales (Varner and Dearing 2014).

Pikas are considered sentinels, indicators of environmental change in the ecosystems they inhabit (Hafner 1993, Jeffress et al. 2013). Changes in their distribution suggest changes in availability of resources they require and shifts in the environment. Research suggests pika presence in many places is closely tied to sub-surface ice features that act as a temperature buffer and perhaps as a water source (Hafner 1993, Millar and Westfall 2010, Wilkening et al. 2015). Those sub-surface ice features are critical in water cycling and long-term water storage and have strong effects on downstream hydrological and ecological processes (Molotch et al. 2008, Leopold et al. 2015). Understanding how pikas respond to climate change therefore may provide a model to inform landscape level conservation and management decisions.

In describing limitations to pika habitat in the cooler, wetter past, Hafner (1993) emphasized that pikas could persist in a region that was not entirely cool and mesic, as long as there were patches of suitable rocky microhabitat. To better understand the response to climate change of these microclimate-constrained specialists, it is necessary to identify the landscape features that create these local anomalies and microhabitat at a relevant scale. Many prior studies identifying suitable habitat for other species have used terrain data at "high" resolutions, though that resolution ranges from 1m-250m, and most commonly is between 25m and 50m (e.g. Lassueur et al. 2006, Copeland and Harrison 2015). However, using even higher resolution terrain data improves species distribution predictions (Lassueur et al. 2006, Nagendra et al. 2013). In this study, we used 1m resolution imagery and elevation models to predict the extent of suitable pika habitat in an alpine environment and compared our predictions with predictions made based on direct observations of habitat use. Our approach allowed predictions of habitat suitability at scales relevant to the daily movements and shelter habitats of individual animals (Varner and Dearing 2014), i.e. scales not commonly used in species distribution models (SDMs).

Though SDMs can be powerful tools for estimating habitat suitability and population connectivity, many do not use high resolution data to address relevant habitat heterogeneity, and many fail to address habitat variables important to a species' niche (Gillingham et al. 2012). It is therefore problematic to rely on regional climate projections and SDMs when both conservation decisions and the phenomenon of habitat heterogeneity occur at mostly finer scales (Dobrowski 2011, Ashcroft et al. 2012). Instead, the set of candidate models for projecting range dynamics should include models based on fine-scale, place-based metrics (Quintero and Wiens 2013, Valladares et al. 2014, Schwalm et al. 2016). In the case of pikas, this means modeling habitat at scales less than 10m and at high resolution, as microclimate in their habitat can vary greatly across even a few meters and their territories are usually less than 25m in diameter (Smith and Ivins 1984, Varner and Dearing 2014). This approach in itself is not novel for wildlife conservation, yet it is a necessary step for understanding pika range dynamics at appropriate scales and for applying that understanding to predict greater landscape change.

I hypothesized that habitat models using remotely sensed data would yield results similar to those derived from direct observation, identifying similar areas on the landscape. Such results would support the importance of considering fine-scale habitat metrics and using remote sensing when projecting range dynamics over a large area without extensive direct observation.

Methods

Summary

In the previous chapter of this thesis, we used radio telemetry to track the movements of radio-collared pikas in the Niwot Ridge LTER area (NWT). To test the effect of terrain on the habitat use we detected, we selected random points to represent the available landscape, constrained by the extent of talus and minimum bounding extent of true presence points. Based on the best fit mixed logistic regression models for winter, summer, and the whole study period, we created probability surfaces by a logit transformation to represent habitat suitability across NWT. Separately, we created supervised models of suitable habitat by maximum likelihood based on landscape variables and expert opinion inputs from field experience and prior studies. We used linear regressions to relate each of those maximum likelihood models to the modeled probabilities of habitat suitability. Included among those models was one using coarser scale predictor variables more commonly used in SDMs for pikas in order to compare the high resolution, fine scale metrics to those more commonly used.

Spatial and spectral data

To derive predictor terrain metrics we used lidar-derived 1m resolution digital elevation models (DEMs), both filtered and unfiltered. We used the difference between the two DEMs to calculate vegetation height and used that in a land cover classification described in Chapter 1. We used the filtered (bare ground) DEM to derive the terrain metrics described in Chapter 1. In this study we again used Topographic Position Index (TPI), the absolute value TPI (AbsTPI), and Topographic Heterogeneity Index (THI) within 3m, 5m, and 10m windows

(PointRoughness, LocalRoughness, and PatchRoughness, respectively). In the land cover model we also used three band color imagery (RGB), which is fine enough to visually pick out individual trees, shrubs, and rocks. This data is at 30cm resolution, though we coarsened it to 1m for these analyses to match the DEMs. We downloaded all data from the NWT LTER project (NWT LTER, http://niwot.colorado.edu).

To compare this high resolution data to that more commonly used in occupancy models for pikas, we also coarsened the predictor variables most commonly used (aspect, slope, elevation) to 10m resolution to match what is often the highest resolution available for large-scale SDMs.

Probability surfaces

In Chapter 1, we collected data on pika habitat use throughout the year using radio telemetry on radio-collared pikas, noting an individual pika's position (presence) within the talus every five minutes. For a comparison to those true presence points, we sampled the terrain characteristics of each cell (1m^2) within the study extent to represent all possible habitat (3717 points). Differences between the detected presences and the total available landscape suggest pikas making choices about terrain disproportionate to its presence on the landscape. We created three probability surfaces based on the best fit (lowest AIC) logistic regression models, excluding models with correlated predictor variables (Table 2.1).

We also created a response surface based on the overlap of summer and winter habitat by multiplying the summer and winter probability surfaces (Year-round). Because habitat use varies through the year (see Chapter 1), this is likely a better indicator of overall habitat suitability than the single-season models. We also created a probability surface using all of the telemetry data combined (Whole year), rather than calculating each season separately and multiplying them.

Table 2.1. Summary of the best fit logistic regression models based on radio telemetry performed in Chapter 1. These models inform the models used for comparing habitat model methods in this chapter.

Dataset	**Best model parameters (coefficient +/-)**	**Null model AIC**	**Best model AIC**	**Null model ΔAIC**
Summer	MeadowDist (-) + Cos(Aspect) (+)	661.348	657.793	3.55
Winter	MeadowDist (+) + Slope (-) + PointRoughness (+) + PatchRoughness (-) + TPI10 (+) + AbsTPI5 (+) + Cos(Aspect) (-)	3402.398	3068.130	334.268
Year-round	Cos(Aspect) (-) + MeadowDist (+) + Slope (-) + PointRoughness (+) + PatchRoughness (-) + TPI10 (+) + AbsTPI5 (+)	3837.832	3583.365	254.467

Supervised habitat suitability models

In ArcGIS 10.3 (ESRI 2014), we stacked rasters of each predictor variable (bands) into one file, then created supervised (user defined) suitability models in the program ENVI 5.2 (Exelis 2014). They are supervised models, meaning they are all expert opinion models that assign each cell in the study area to one of the categories of habitat quality defined by the user. We created five classes of habitat quality: Good, Moderate, Marginal, Bad, and Untenable. Based on our own expert opinion of NWT and pika habitat, we drew polygons on the landscape as training data for each of those classes such that each class had at least 10 polygons and 10,000 input training pixels. It is important that none of the polygons we drew overlapped spatially with any of the observations used to find the best fit models of habitat use and create the probability rasters, so the coefficients for the two kinds of models are derived independently. We selected maximum likelihood as the classification method. In this method, the program creates a probability distribution in multispectral space (across each user-selected predictor band) for each of the five classes based on the characteristics of the pixels we selected as training data. The program then classifies each pixel in the study area based on which of those probability distributions it falls closest to in multispectral space.

Each of the models we created were based a different set of predictor variables, so for each there were slightly different probability distributions to describe each possible habitat category. The same training pixels were used in all supervised models. Because all of the predictor variables were measured at 1m resolution, each model has 1m^2 pixels.

Models 1 included the predictor variables found in the best fit logistic regression models summarized in Table 2.1 as a direct comparison of the two methods. Model 2 included the same variables as Model 1 with color imagery (RGB) added as a way to distinguish further from cover types other than talus. Model 3 included just measures of topographic position and heterogeneity, selected to capture three scales. Models 4 and 5 were based on understanding prior studies—these were meant to mimic what any pika expert might choose as important landscape variables, not necessarily one with empirical data on habitat use and terrain. Model 4, similar to Model 2, included RGB and vegetation height to distinguish further from other cover types or talus interspersed with vegetation. Model 5 includes measures of topographic position and heterogeneity and two predictors that could influence both small and larger scale processes. Aspect may interact with the prevailing wind direction to impact snow accumulation, and MeadowDist may be important in both winter and summer (Smith and Weston 1990, Erb et al. 2014, Chapter 1).

Table 2.2. Summary of all sets of predictors used in supervised maximum likelihood models.

Model	# of bands	Predictor bands
1	7	MeadowDist, Slope, PointRoughness, PatchRoughness, TPI10, AbsTPI5, Cos(Aspect)
2	10	Red, Green, Blue, MeadowDist, Slope, PointRoughness, PatchRoughness, TPI10, AbsTPI5, Cos(Aspect)
3	5	PointRoughness, TPI3, LocalRoughness, AbsTPI5, PatchRoughness
4	10	Red, Green, Blue, Cos(Aspect), PointRoughness, LocalRoughness, TPI10, PatchRoughness, MeadowDist, vegetation height
5	9	Cos(Aspect), TPI3, PointRoughness, AbsTPI5, LocalRoughness, TPI10, AbsTPI10, PatchRoughness, MeadowDist
10m	6	Red, Green, Blue, Elevation, Slope, Cos(Aspect)

In order to test the spatial extent at which habitat suitability can be predicted, for each model, we created four more outputs. We made moving search windows of 1m, 3m, 5m, and 10m radii such that each cell is assigned a 1 if the maximum likelihood model predicted Good habitat within that radius. We then clipped the output of each of these models so that a 1 could only be found on talus, as that is a basic requirement for even marginal pika habitat.

We also performed the same sort of supervised habitat model by maximum likelihood using predictors coarsened to 10m resolution, a more widely available resolution for most North America than 1m and the resolution at which many prior pika habitat models have been made. While many models with large spatial extent include climate variables, the climate does not vary enough across NWT to avoid singularity errors in maximum likelihood estimation. Instead, we used RGB, elevation, slope, and aspect. By including these variables most commonly used for predicting habitat, we can compare this more common method’s similarity to predictions based on radio telemetry and how it performs compared to high resolution models.

Sampling points

At 1m resolution, the total extent of the NWT study area is 22,633,590 pixels. We selected 50,000 randomly distributed points in ArcGIS as a way to sample the area for the predicted suitable habitat of both the probability surfaces and the supervised habitat suitability models. We selected those points in two ways, by 1) randomly selecting them from the entire landscape and 2) by randomly selecting them only from talus-covered portions of the landscape. One of our supervised models uses data at 10m resolution. To avoid pseudoreplication by having more than one sampling point possible in any one pixel, we made a minimum distance of 10m between any of these randomly selected points. Even in that 10m resolution version of NWT, there are 226,149 total pixels and 55,951 pixels classified as talus, meaning there will be no pixels double-sampled, whether or not the selected points are restricted to talus.

Data analysis

In addition to creating expert opinion models of potentially suitable habitat, as many previous studies have done, we compared those predictions to the predictions we made with probability rasters derived from radio telemetry observations. We compared these different predictions by linear regression models, where the predictor variable was the predicted habitat suitability based on the supervised classifications and each probability surface (e.g. Winter) was a response variable. For each of the four probability surfaces, each sampled at the two sets of 50,000 random points, we compared models by AIC to find the best scale at which to identify suitable habitat, including models based on data at10m resolution and at 1m resolution using search windows of 1, 3, 5, and 10 meters. For each comparison to a response variable, we also use the lowest AIC model using more than one search window size. For each possible predictor in the linear regressions (e.g. Model 2), we excluded all multiple-window models but the one with the lowest AIC.

Probability surface ~ Supervised habitat suitability prediction

Example equation:

Predicted winter pika presence ~ Model 2 supervised habitat prediction

MeadowDist + Slope + PointRoughness + PatchRoughness + TPI10 + AbsTPI5 ~ Red + Green + Blue + MeadowDist + Slope + PointRoughness + PatchRoughness + TPI10 + AbsTPI5 + Cos(Aspect)

There is an important distinction between the two kinds of models we compared. They use many of the same metrics of terrain to make predictions about the NWT area. However, the predictor and response variables in these linear models are not based on the same data. The probability surfaces (response variable) were created based on a precise intercept and coefficients for each predictor in the model, giving each cell across the landscape a continuous value between 0 and 1. Those coefficients are not present in the supervised models. The coefficients to define the probability distribution for each level of habitat quality are defined by maximum likelihood and the input training pixels, not any of the data that was used to build the response variables, the probability rasters.

The best of these linear models should reveal the scale of analysis at which this remote sensing-based method is most similar to the probability surfaces. In these analyses, the supervised models were based on expert opinion, a common approach when predicting suitable habitat. We compared these models with probability surfaces, habitat predictions based on empirically derived from field observations. This is therefore not a direct test of either method using other observations of pika presence, but rather we are comparing two different kinds of prediction of habitat suitability. If the supervised models can significantly predict the same suitable habitat as the models based on direct observation, then the supervised models may be useful in other, unsurveyed areas that would otherwise take great effort to survey. While we could also use the probability surfaces based on observation to predict habitat suitability in unsurveyed areas, that method does not allow us to incorporate other predictors that could be more important and comes with previously defined coefficients. For example, a pika expert in the Columbia River Gorge may choose to exclude distance to meadow, as they know that many occupied sites are surrounded by dense forest instead of meadow (Simpson 2009, Varner and Dearing 2014), but include instead the lithology, which could impact fracture size and the amount of subsurface microclimate.

We created a total of 170 candidate models (excluding null models for each response variable). For each probability surface we compared up to 25 competing models. For any response variable (probability surface), there were models of different scales from each of Models 1-5. For the sets of predictor variables (supervised models), Models 1-5, there were at least four candidate models that could predict the probability surface. We created search windows of 1m, 3m, 5m, and 10m. Further, for each of the supervised models, we also included the best fit model that used multiple window sizes. For each response variable we also included the supervised model using 10m resolution data to compare with the other supervised models.

Finally, we performed a series of t-tests to demonstrate how terrain characteristics vary with land cover and the importance of talus to pika habitat.

Results

The supervised models we created consistently predicted suitable habitat in the same places predicted by the probability rasters for each dataset. Of the 170 models, only six were not significant at an alpha level of 0.05. All probability surfaces, regardless of whether the randomly sampled points were restricted to talus, were best predicted by one of the variants of Models 1, 2, or 3.

For all response variables except summer habitat with sample points not restricted to talus, the top five best models had a positive and significant slope, with all p-values<0.0001. For all comparisons, the top model was the best fit by >90 AIC. It is especially important that while Models 1-3 used the predictor terrain metrics from the best fit winter habitat model, they were the best at predicting both winter and summer habitat, as well as the Year-round model of aggregate habitat suitability in both seasons. For both models using only points on talus and those including points off talus predicting Year-round, the best model was that which included all four possible search window sizes (null ΔAIC=1419 for talus only, null ΔAIC=6627 not restricted to talus).

There was a clear difference between the models restricted to talus versus unrestricted models mimicking inputs without adequate land cover data. While these were entirely different datasets and could not be compared directly, for each probability surface the R^2 and null model ΔAIC were notably higher when points could occur outside of talus. When predicting Winter habitat, the top five models with points restricted to talus explained less variation (mean AIC=2750<null AIC, mean R^2=0.054) than the top five models where points were not restricted to talus (mean AIC=42146<null AIC, mean R^2=0.566).

We excluded from comparison all multiple-window models except the best fit one. In some cases this meant that we excluded multiple-window models that used all four window sizes, and had a greater R^2 than the model we included but AIC <2 AIC units lower (Arnold 2010). For each probability surface and in both talus-restricted and unrestricted datasets, the best model (lowest AIC of those included) was one that used more than one size of search window.

For the summer on-talus probability surface, a multiple-window model was the best by AIC=94. In all other cases, a multiple-window model was the best by AIC>195. There was further distinction in the results between those points on talus and those not restricted to talus. Though the best models for each include multiple sizes of window, the next best models when restricted to talus tend to have small search window while the window was more often 10m when the points are not restricted. Among the models with points restricted to talus, a window size of 1m or 3m was among the top 3 models in all cases, while a 10m model was never in the top 8 for that dataset. On the other hand, when points were not restricted to talus, a model with a 10m search window was always the second best in that dataset.

For all probability surfaces, the models using 10m resolution data were among the poorest performers (Figures 2.1, 2.2). In 3 of the comparisons (Winter not talus-restricted, Year-round not talus-restricted, and Whole-year not talus-restricted), the 10m model was the worst, though in all comparisons it was a better fit than a null model by AIC>2. Overall, 123 models had a lower AIC than the 10m model for the same probability surface. Of those 41 that did not, 7 were the 10m resolution models and 14 were predicting summer habitat where all input points were restricted to talus. In building the probability surfaces, the model for summer habitat was the closest to the null (ΔAIC=3.55) and had a lower R^2 (0.01) than the best fit models of winter or year-round habitat use.

Of the 22,627,360 pixels in the study area, our land cover classification detect 24.1% of the landscape was talus or other rock. The supervised suitability models predicted Good habitat would cover between 1.7%-24.7% of the landscape (Table 2.3).

Table 2.3. Percent of the NWT area predicted by each supervised habitat model. The supervised land cover model predicted 24.1% of NWT was talus or other rock.

Predictor variable	% of landscape predicted Good habitat	% of talus predicted Good habitat
Model 1	2.88	11.91
Model 2	3.36	13.91
Model 3	10.54	43.65
Model 4	1.72	7.13
Model 5	2.65	10.97
10m resolution	24.74	102.44

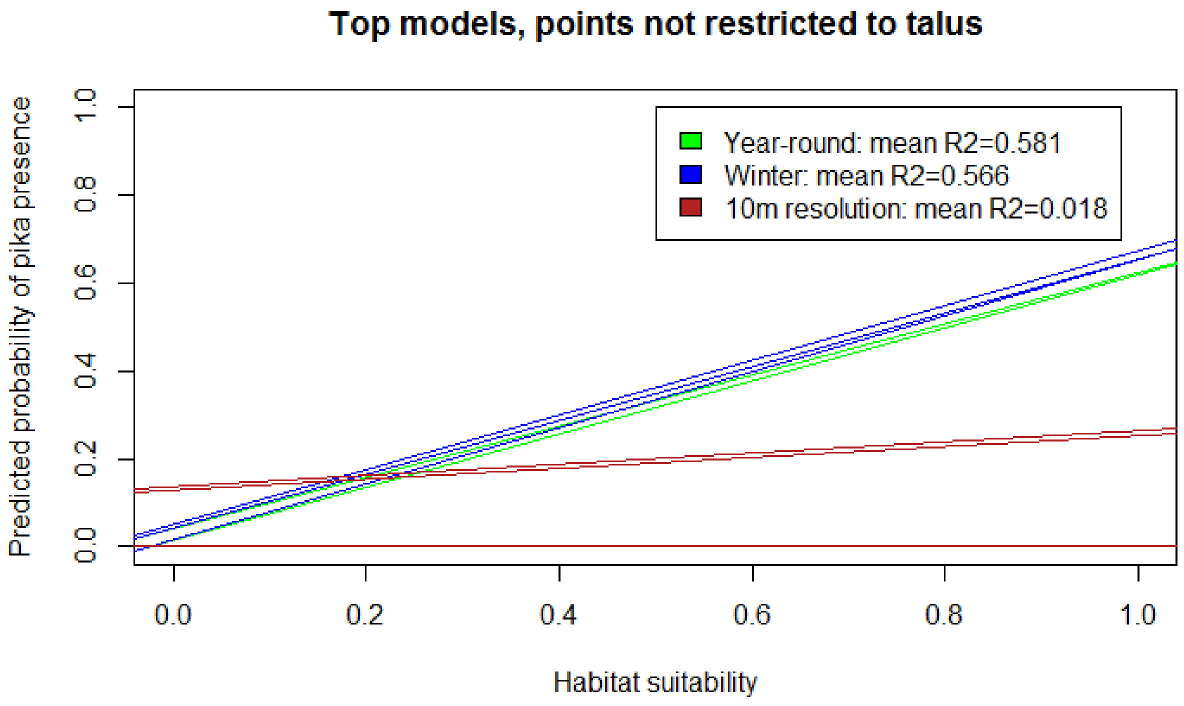


Figure 2.1. Relationship between predicted habitat suitability and predicted winter (blue) or year-round (green) pika presence using supervised models based on high resolution and lower-resolution topographic data (red). In this example, both model predictions were sampled from both talus and non-talus areas of the landscape. The lines showing Winter and Year-round predicted probability represent the top five models for each.

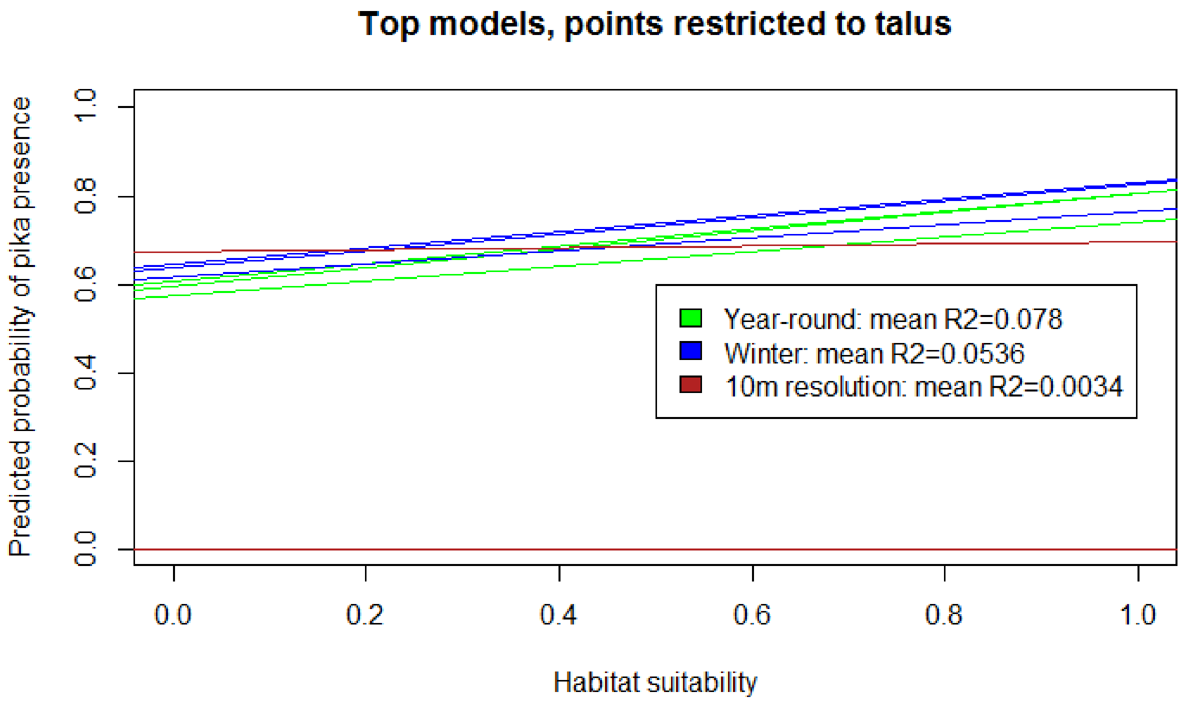


Figure 2.2. Relationship between predicted habitat suitability and predicted winter (blue) or year-round (green) pika presence using supervised models based on high resolution and lower-resolution topographic data (red). In this example, both model predictions were sampled from only talus areas of the landscape. The lines showing Winter and Year-round predicted probability represent the top five models for each.

Land cover plays an important role in terrain characteristics (Table 2.4). For many terrain parameters in our analyses, talus is significantly different from other land cover types.

Table 2.4. Results of t-tests comparing the terrain characteristics of randomly sampled points both on talus (n=12,151) and on all other cover types (n=37,849).

Terrain metric	Talus mean	Off-talus mean	p-value
PointRoughness	3.52	1.70	<0.0001
LocalRoughness	14.49	14.55	0.604
PatchRoughness	9.11	9.69	<0.0001
TPI3	-0.0002	-0.0005	0.366
TPI5	-0.005	-0.0003	0.031
TPI10	-0.014	-0.0009	<0.001
AbsTPI3	0.126	0.114	<0.0001
AbsTPI5	0.178	0.180	0.302
AbsTPI10	0.314	0.335	<0.0001

Discussion

These results suggest several things about pika habitat and about using remotely sensed data to model it. The fact that nearly all of the effective models (and 85% of the top 5 models) had a positive slope shows that these methods using remotely sensed data and expert opinion training data tend to make the same predictions about suitable habitat as models extrapolating from empirical observation. This suggests two sets of predictions and two methods that could be further tested to predict habitat suitability over larger extent. Doing so will allow us to make predictions of pika habitat over unsurveyed areas using expert opinion and remotely sensed data to better inform our understanding of both pika habitat and pikas' role as indicators of ecosystem change.

The analyses we performed do not empirically test either type of model against other observations in NWT. Rather, we compared methods to create suitability models to show the utility of supervised models. It is therefore important that the coefficients for each type of model were derived independently. The pika presence probability surfaces were created based on data from tracking radio-collared pikas and extrapolating across NWT using coefficients from a small subset of NWT. On the other hand, the coefficients in the habitat suitability models were derived from the terrain characteristics of pixels in areas not overlapping with any of the radio telemetry observations. Further, the maximum likelihood models that did not use all the same predictors as the telemetry models still had a significantly smaller ΔAIC than a null model, as well as a smaller ΔAIC than the 10m resolution model in 67% of comparisons overall and in 100% of comparisons where the testing points were not restricted to talus.

When comparing the tests using those points restricted to talus and distributed entirely randomly across the study area, there was a notable difference in which sizes of search window produced predictions most similar to the probability surfaces. When restricted to talus, smaller search windows performed better, while larger windows were better when points were not restricted to talus. It is important that, knowing that talus is a basic requirement for suitable pika habitat, we changed the probability surfaces such that all pixels off talus were equal to 0. Therefore, any random points that are off talus will always have a 0 value. There are some landscape parameters that helped to distinguish talus from the other land cover types. For example, fine scale heterogeneity (e.g. PointRoughness) is greater on talus than off it (Table 2.4). Points with a 0 value on the probability surfaces therefore are fairly distinct in those characteristics, making the presence of talus itself indirectly an important variable. Therefore, when points can appear off talus, a larger search window detects more talus and is more likely to find suitable habitat. On the other hand, when points are restricted to talus the range of values of important terrain metrics are narrower and more representative of talus. A smaller search window therefore better describes the variation of habitat quality on talus. The pixels that are unsuitable by other metrics (and more than 1-3m away from good habitat) are still classified as unsuitable. These data all speak to the importance of talus for pika habitat and therefore, the importance of including talus extent as a predictor variable in suitability models.

The fact that coefficients and R^2 values were higher for the models where points were not restricted to talus reiterates this. There is less clear difference between predicted good habitat and suboptimal habitat when all the points are on talus, yet the fact that those models are still predictive shows that there is variation in habitat quality within talus. Even with high resolution land cover data, using a variety of terrain metrics allows us to address the important fine-scale processes that likely affect pika microtopoclimatic affiliation that would be masked using 10m resolution metrics and those variables most commonly used (aspect, elevation, slope) (Rodhouse et al. 2010, Varner and Dearing 2014). Similarly, there was a clear difference between Models 1-5 and the 10m resolution supervised model. Using the variables and scale commonly used to predict pika habitat, the 10m resolution model was consistently less similar in its predictions to the probability surfaces compared to the 1m resolution models, and even predicted that more than 100% of available talus would be occupied (Table 2.4). This in itself does not make the 10m predictions wrong—those models did predict much of the same suitable habitat as the probability surfaces and the other supervised models—but the fact that they predicted more suitable habitat at NWT than is likely possible suggests that the models would be improved by incorporating biologically relevant data to distinguish the variation within talus. Pikas require talus, so this demonstrates how using coarse scale data may in fact overestimate the extent of suitable habitat.

Multiple-criteria habitat modeling based on remotely sensed data and expert opinion is not in itself novel—this method has been pursued for many different kinds of wildlife, including for pikas. However, it is less common to make predictions for the same area using two methods and at a scale relevant to the movements and survival of individuals of those species (e.g. Rabinowitz and Zeller 2010, Calkins et al. 2012). Understanding these fine scale processes is likely important, and further work should more thoroughly evaluate how the processes at that scale are modulated by macroclimatic drivers in order to make predictions across pika range (Schwalm et al. 2016). This is especially important when considering the differences in winter and summer habitat distinguished both in Chapter 1 and by the greater AIC and lower R^2 values for comparisons between supervised models and the Summer probability surfaces. Because of the apparent importance of both summer and winter habitat, which has been largely excluded to date, we need to determine whether these fine-scale microtopographic and seasonal effects affect occupancy at larger scales and across environmental gradients. Understanding the interaction of macroclimatic and fine-scale drivers will help us better understand this potentially threatened species' role as an indicator of ecosystem change. Testing across greater areas predictions such as those we have produced will provide greater insight into the factors that drive habitat suitability for this indicator species and the relevant scales at which it functions. Testing predictions at various scales will also help elucidate how macroclimatic variables interact with microtopography to foster suitable microhabitat.

As climate changes, microrefugia and the pathways that join them will play a significant role in changes to biodiversity and in overall ecosystem resistance and adaptive capacity (Mackey et al. 2012). It is therefore important to identify potential microrefugia for climate-sensitive species to adequately track suitable habitat and functional connectivity. This is especially true for indicator species such as pikas, as changes in their distribution and connectivity speak more directly to ecosystem change than for more resilient or generalist species (cite). Though broad scale climate factors are important drivers of species distributions (Thomas 2010, Pintor et al. 2015), with the importance of microrefugia it is more fitting to predict suitable habitat for indicator species at both local scales, where microrefugia will persist, and at scales that will drive individual survival (Gillingham et al. 2012, Quintero and Wiens 2013, Valladares et al. 2014, Varner and Dearing 2014). My findings with this climate sensitive indicator species further support that accounting for fine-scale processes will likely improve our understanding of wildlife and ecosystem responses to climate change.

In the first chapter of this thesis I suggested that not all areas of talus are equally hospitable and that quantifiable metrics of terrain and habitat determine the location of suitable habitat. Further, I showed that the important habitat constraints vary seasonally. In this second chapter, I expanded on those findings to predict how microclimatic constraints might affect habitat occupancy across a larger landscape. I included predictions based on variables measured at different levels of spatial resolution to show the effect of model scale on habitat-occupancy predictions.

References

Anderson, B. J., H. R. Akçakaya, M. B. Araújo, D. a Fordham, E. Martinez-Meyer, W. Thuiller, and B. W. Brook. 2009. Dynamics of range margins for metapopulations under climate change. Proceedings. Biological sciences / The Royal Society 276:1415–1420.

Anderton, S. P., S. M. White, and B. Alvera. 2002. Micro-scale spatial variability and the timing of snow melt runoff in a high mountain catchment. Journal of Hydrology 268:158–176.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175–1178.

Ashcroft, M. B. 2010. Identifying refugia from climate change. Journal of Biogeography 37:1407–1413.

Ashcroft, M. B., L. a. Chisholm, and K. O. French. 2009. Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. Global Change Biology 15:656–667.

Ashcroft, M. B., and J. R. Gollan. 2012. Fine-resolution (25 m) topoclimatic grids of near-surface (5 cm) extreme temperatures and humidities across various habitats in a large (200 × 300 km) and diverse region. International Journal of Climatology 32:2134–2148.

Ashcroft, M. B., J. R. Gollan, D. I. Warton, and D. Ramp. 2012. A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. Global Change Biology 18:1866–1879.

Bates, D., M. Maechler, and B. Bolker. 2012. R package lme4. R Foundation for Statistical Computing.

Beever, E. a, C. Ray, P. W. Mote, and J. L. Wilkening. 2010. Testing alternative models of climate-mediated extirpation. Ecological Applications 20:164–178.

Beever, E. a., P. F. Brussard, and J. Berger. 2003. Patterns of Apparent Extirpation Among Isolated Populations of Pikas (Ochotona Princeps) in the Great Basin. Journal of Mammalogy 84:37–54.

Beever, E. a., J. L. Wilkening, D. E. McIvor, S. S. Weber, and P. F. Brussard. 2008. American Pikas (Ochotona princeps) in Northwestern Nevada: A Newly Discovered Population at a Low-elevation Site. Western North American Naturalist 68:8–14.

Bell, K. L., and L. C. Bliss. 1979. Autecology of Kobresia bellardii: Why Winter Snow Accumulation Limits Local Distribution. Ecological Monographs 49:377–402.

Bergman, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, and F. G. R. Watson. 2006. Assessment of Prey Vulnerability through Analysis of Wolf Movements and Kill sites.

Ecological Applications 16:273–284.

Brown, J. H. 1971. Mammals on Mountaintops: Nonequilibrium Insular Biogeography. The American Naturalist 105:467–478.

Brown, J. L., and L. L. Knowles. 2012. Spatially explicit models of dynamic histories: examination of the genetic consequences of Pleistocene glaciation and recent climate change on the American Pika. Molecular Ecology 21:3757–3775.

Calkins, M. T., E. a. Beever, K. G. Boykin, J. K. Frey, and M. C. Andersen. 2012. Not-so-splendid isolation: Modeling climate-mediated range collapse of a montane mammal Ochotona princeps across numerous ecoregions. Ecography 35:780–791.

Chen, I., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species of climate warming. Science 333:1024–1026.

Clark, J. S., C. Fastie, G. Hurtt, S. T. Jackson, C. Johnson, G. A. King, M. Lewis, J. Lynch, S. Pacala, C. Prentice, and others. 1998. Reid’s Paradox of Rapid Plant Migration Dispersal theory and interpretation of paleoecological records. BioScience 48:13–24.

Copeland, S. M., and S. P. Harrison. 2015. Identifying plant traits associated with topographic contrasts in a rugged and diverse region (Klamath-Siskiyou Mts, OR, USA). Ecography 38:569–577.

Costello, J. H., B. K. Sullivan, D. J. Gifford, D. Van Keuren, and L. J. Sullivan. 2006. Seasonal refugia, shoreward thermal amplification, and metapopulation dynamics of the ctenophore Mnemiopsis leidyi in Narragansett Bay, Rhode Island. Limnology and Oceanography 51:1819–1831.

Crimmins, S. M., S. Z. Dobrowski, J. A. Greenberg, J. T. Abatzoglou, and A. R. Mynsberge. 2011. Changes in Climatic Water Balance Drive Downhill Shifts in Plant Species’ Optimum Elevations. Science 331:324–332.

Déry, S. J., W. T. Crow, M. Stieglitz, and E. F. Wood. 2004. Modeling Snow-Cover Heterogeneity over Complex Arctic Terrain for Regional and Global Climate Models*. Journal of Hydrometeorology 5:33–48.

Dobrowski, S. Z. 2011. A climatic basis for microrefugia: the influence of terrain on climate. Global Change Biology 17:1022–1035.

Dullinger, S., A. Gattringer, W. Thuiller, D. Moser, N. E. Zimmermann, A. Guisan, W. Willner, C. Plutzar, M. Leitner, T. Mang, M. Caccianiga, T. Dirnböck, S. Ertl, A. Fischer, J. Lenoir, J.-C. Svenning, A. Psomas, D. R. Schmatz, U. Silc, P. Vittoz, and K. Hülber. 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. Nature Climate Change 2:619–622.

Erb, L. P., C. Ray, and R. Guralnick. 2011. On the generality of a climate-mediated shift in the distribution of the American pika (Ochotona princeps). Ecology 92:1730–1735.

Erb, L. P., C. Ray, and R. Guralnick. 2014. Determinants of pika population density vs. occupancy in the Southern Rocky Mountains. Ecological Applications 24:429–435.

ESRI. 2014. ArcMap. Environmental Systems Research Institute, Redlands, CA.

Ford, K. R., A. K. Ettinger, J. D. Lundquist, M. S. Raleigh, and J. Hille Ris Lambers. 2013. Spatial Heterogeneity in Ecologically Important Climate Variables at Coarse and Fine Scales in a High-Snow Mountain Landscape. PLoS ONE 8:e65008.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Galbreath, K. E., D. J. Hafner, and K. R. Zamudio. 2009. WHEN COLD IS BETTER: CLIMATE-DRIVEN ELEVATION SHIFTS YIELD COMPLEX PATTERNS OF DIVERSIFICATION AND DEMOGRAPHY IN AN ALPINE SPECIALIST (AMERICAN PIKA, OCHOTONA PRINCEPS). Evolution 63:2848–2863.

Gillingham, P. K., B. Huntley, W. E. Kunin, and C. D. Thomas. 2012. The effect of spatial resolution on projected responses to climate warming. Diversity and Distributions 18:990–1000.

Grayson, D. K. 2005. A brief history of Great Basin pikas. Journal of Biogeography 32:2103–2111.

Grayson, D. K. 2006. The Late Quaternary biogeographic histories of some Great Basin mammals (western USA). Quaternary Science Reviews 25:2964–2991.

Grinnell, J. 1917. Field Tests of Theories Concerning Distributional Control. The American Naturalist 51:115–128.

Hafner, D. J. 1993. North American Pika (Ochotona princeps) as a late quaternary biogeographic indicator species. Quaternary Research 39:373–380.

Hannah, L., L. Flint, A. D. Syphard, M. a. Moritz, L. B. Buckley, and I. M. McCullough. 2014. Fine-grain modeling of species’ response to climate change: Holdouts, stepping-stones, and microrefugia. Trends in Ecology and Evolution 29:390–397.

Henry, P., Z. Sim, and M. A. Russello. 2012. Genetic evidence for restricted dispersal along continuous altitudinal gradients in a climate change-sensitive mammal: The American Pika. PLoS ONE 7:1–10.

Holderegger, R., and C. Thiel-Egenter. 2009. A discussion of different types of glacial refugia used in mountain biogeography and phylogeography. Journal of Biogeography 36:476–480.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management 47:893–901.

Howell, A. H. 1924. Revision of the American pikas (Genus Ochotona). North American Fauna 47:1–55.

Hughes, L. 2000. Biological consequences of global warming: Is the signal already apparent? Trends in Ecology and Evolution 15:56–61.

IPCC. 2013. The physical science basis: Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change.

Jeffress, M. R., T. J. Rodhouse, C. Ray, S. Wolff, and C. W. Epps. 2013. The idiosyncrasies of place: geographic variation in the climate-distribution relationships of the American pika. Ecological Applications 23:864–878.

Keppel, G., K. P. Van Niel, G. W. Wardell-Johnson, C. J. Yates, M. Byrne, L. Mucina, A. G. T. Schut, S. D. Hopper, and S. E. Franklin. 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. Global Ecology and Biogeography 21:393–404.

Krear, H. 1965. An ecological and ethological study of the pika (*Ochotana princeps saxatilis bangs*) in the front range of Colorado. University of Colorado Boulder.

Kreuzer, M. P., and N. J. Huntly. 2003. Habitat-specific demography: evidence for source-sink population structure in a mammal, the pika. Oecologia 134:343–349.

Kubota, Y., H. Murata, and K. Kihachiro. 2004. Effects of topographic heterogeneity on tree species richness and stand dynamics in a subtropical forest in Okinawa Island, Southern Japan. British Ecological Society 92:230–240.

Kumar, S., T. J. Stohlgren, and G. W. Chong. 2006. Spatial heterogeneity influences native and nonnative plant species richness. Ecology 87:3186–3199.

Lassueur, T., S. Joost, and C. F. Randin. 2006. Very high resolution digital elevation models: Do they improve models of plant species distribution? Ecological Modelling 198:139–153.

Leopold, M., G. Lewis, D. Dethier, N. Caine, and M. W. Williams. 2015. Cryosphere: ice on Niwot Ridge and in the Green Lakes Valley, Colorado Front Range. Plant Ecology & Diversity 0874:1–14.

Lundquist, J. D., N. Pepin, and C. Rochford. 2008. Automated algorithm for mapping regions of cold-air pooling in complex terrain. Journal of Geophysical Research 113:1–15.

Luoto, M., and R. K. Heikkinen. 2008. Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. Global Change Biology 14:483–494.

MacArthur, R. A., and L. C. H. Wang. 1974. Behavioral thermoregulation in the pika Ochotona princeps: a field study using radiotelemetry. Canadian Journal of Zoology 52:353–358.

Mackey, B., S. Berry, S. Hugh, S. Ferrier, T. D. Harwood, and K. J. Williams. 2012. Ecosystem greenspots : identifying potential drought , fire , and climate-change micro-refuges. Ecological Applications 22:1852–1864.

McLeod, A. I., and C. Xu. 2014. R package Best Subset GLM.

McPhee, H. M., N. F. Webb, and E. H. Merrill. 2012. Time-to-kill: Measuring attack rates in a heterogenous landscape with multiple prey types. Oikos 121:711–720.

Millar, C., K. Heckman, C. Swanston, K. Schmidt, R. D. Westfall, and D. L. Delany. 2014. Radiocarbon dating of American pika fecal pellets provides insights into population extirpations and climate refugia. Ecological Applications 24:1748–1768.

Millar, C. I., and R. D. Westfall. 2010. Distribution and Climatic Relationships of the American Pika (Ochotona princeps) in the Sierra Nevada and Western Great Basin, U.S.A.; Periglacial Landforms as Refugia in Warming Climates. Reply. Arctic, Antarctic, and Alpine Research 42:493–496.

Millar, J. S., and F. C. Zwickel. 1972. Characteristics and Ecological Significance of Hay Piles of Pikas. Mammalia 36:657–667.

Molotch, N. P., T. Meixner, and M. W. Williams. 2008. Estimating stream chemistry during the snowmelt pulse using a spatially distributed, coupled snowmelt and hydrochemical modeling approach. Water Resources Research 44.

Mosblech, N. a S., M. B. Bush, and R. Van Woesik. 2011. On metapopulations and microrefugia: Palaeoecological insights. Journal of Biogeography 38:419–429.

Mosser, A. A., M. Kosmala, and C. Packer. 2015. Landscape heterogeneity and behavioral traits drive the evolution of lion group territoriality. Behavioral Ecology 26:1051–1059.

Nagendra, H., R. Lucas, J. P. Honrado, R. H. G. Jongman, C. Tarantino, M. Adamo, and P. Mairota. 2013. Remote sensing for conservation monitoring: Assessing protected areas, habitat extent, habitat condition, species diversity, and threats. Ecological Indicators 33:45–59.

Nielsen, S. E., G. McDermid, G. B. Stenhouse, and M. S. Boyce. 2010. Dynamic wildlife habitat models: Seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biological Conservation 143:1623–1634.

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology Evolution and Systematics 37:637–669.

Parmesan, C., C. Parmesan, G. Yohe, and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Pauli, H., M. Gottfried, S. Dullinger, O. Abdaladze, M. Akhalkatsi, J. L. B. Alonso, G. Coldea, J. Dick, B. Erschbamer, R. F. Calzado, D. Ghosn, J. I. Holten, R. Kanka, G. Kazakis, J. Kollar, P. Larsson, P. Moiseev, D. Moiseev, U. Molau, J. M. Mesa, L. Nagy, G. Pelino, M. Puscas, G. Rossi, A. Stanisci, A. O. Syverhuset, J. P. Theurillat, M. Tomaselli, P. Unterluggauer, L. Villar, P. Vittoz, and G. Grabherr. 2012. Recent Plant Diversity Changes on Europe’s Mountain Summits. Science 336:353–355.

Pearson, R. G. 2006. Climate change and the migration capacity of species. Trends in ecology & evolution (Personal edition) 21:111–3.

Pepin, N. C., and J. D. Lundquist. 2008. Temperature trends at high elevations: Patterns across the globe. Geophysical Research Letters 35:L14701.

Pintor, A. F. V., L. Schwarzkopf, and A. K. Krockenberger. 2015. Rapoport’s Rule : Do climatic variability gradients shape range extent? 85:643–659.

Quintero, I., and J. J. Wiens. 2013. What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. Global Ecology and Biogeography 22:422–432.

Rabinowitz, A., and K. A. Zeller. 2010. A range-wide model of landscape connectivity and conservation for the jaguar, Panthera onca. Biological Conservation 143:939–945.

Rodhouse, T. J., E. a. Beever, L. K. Garrett, K. M. Irvine, M. R. Jeffress, M. Munts, and C. Ray. 2010. Distribution of American pikas in a low-elevation lava landscape: conservation implications from the range periphery. Journal of Mammalogy 91:1287–1299.

Root, T., J. Price, K. Hall, and S. Schneider. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

Ruel, J.-C., D. Pin, and K. Cooper. 1998. Effect of topography on wind behaviour in a complex terrain. Forestry 71:261–265.

Rull, V. 2009. Microrefugia. Journal of Biogeography 36:481–484.

Rull, V. 2010. On microrefugia and cryptic refugia. Journal of Biogeography 37:1623–1625.

Sandel, B., L. Arge, B. Dalsgaard, R. G. Davies, K. J. Gaston, W. J. Sutherland, and J.-C. Svenning. 2011. The Influence of Late Quaternary Climate-Change Velocity on Species Endemism. Science 334:660–664.

Scherrer, D., and C. K??rner. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. Journal of Biogeography 38:406–416.

Schönswetter, P., a. Tribsch, M. Barfuss, and H. Niklfeld. 2002. Several Pleistocene refugia detected in the high alpine plant Phyteuma globulariifolium Sternb. & Hoppe (Campanulaceae) in the European Alps. Molecular Ecology 11:2637–2647.

Schwalm, D., C. W. Epps, T. J. Rodhouse, W. B. Monahan, J. A. Castillo, C. Ray, and M. R. Jeffress. 2015. Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. Global Change Biology.

Schwalm, D., C. W. Epps, T. J. Rodhouse, W. B. Monahan, J. A. Castillo, C. Ray, and M. R. Jeffress. 2016. Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. Global Change Biology 22:1572–1584.

Shi, H., D. Paull, and S. Rayburg. 2015. Spatial heterogeneity of temperature across alpine boulder fields in New South Wales, Australia: multilevel modelling of drivers of microhabitat climate. International Journal of Biometeorology.

Shimokawabe, A., Y. Yamaura, T. Akasaka, T. Sato, Y. Shida, S. Yamanaka, and F. Nakamura. 2015. The distribution of cool spots as microrefugia in a mountainous area. PLoS ONE 10:1–12.

Simpson, W. G. 2009. American Pikas Inhabit Low-Elevation Sites Outside the Species' Previously Described Bioclimatic Envelope. Western North American Naturalist 69:243–250.

Smith, A. T. 1974. The distribution and dispersal of pikas: consequences of insular population structure. Ecology 55:1112–1119.

Smith, A. T. 1978. Comparative Demography of Pikas (Ochotona): Effect of Spatial and Temporal Age-Specific Mortality. Ecology 59:133–139.

Smith, A. T., and B. L. Ivins. 1984. Spatial Relationships and Social Organization in Adult Pikas: A Facultatively Monogamous Mammal. Zeitschrift für Tierpsychologie 66:289–308.

Smith, A. T., and M. L. Weston. 1990. Ochotona princeps. Mammalian Species 352:1–8.

Solutions, E. V. I. 2014. ENVI. Exelis Visual Information Solutions, Boulder, CO.

Stewart, J. a E., J. D. Perrine, L. B. Nichols, H. James, C. I. Millar, K. E. Goehring, C. P. Massing, and D. H. Wright. 2015. Revisiting the past to foretell the future : summer temperature and habitat area predict pika extirpations in California. Journal of

Biogeography:1–11.

Team, R. C. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Thomas, C. D. 2010. Climate, climate change and range boundaries. Diversity and Distributions 16:488–495.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. De Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. Van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. Nature 427:145–8.

Thornthwaite, C. 1953. A charter for climatology. World Meteorological Organization Bulletin 2:40–46.

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

Valladares, F., S. Matesanz, F. Guilhaumon, M. B. Araújo, L. Balaguer, M. Benito-Garzón, W. Cornwell, E. Gianoli, M. van Kleunen, D. E. Naya, A. B. Nicotra, H. Poorter, and M. A. Zavala. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecology Letters 17:1351–1364.

Varner, J., and M. D. Dearing. 2014. The Importance of Biologically Relevant Microclimates in Habitat Suitability Assessments. PLoS ONE 9:e104648.

Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of Deer Habitat on a Nutritional Basis. Journal of Range Management 30:122–127.

Walter, M., and L. Broome. 1998. Snow as a factor in animal hibernation and dormancy. Snow. A natural history; an uncertain future.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Whiteman, C. D., B. Pospichal, S. Eisenbach, P. Weihs, C. B. Clements, R. Steinacker, E. Mursch-Radlgruber, and M. Dorninger. 2004. Inversion Breakup in Small Rocky Mountain and Alpine Basins. Journal of Applied Meteorology 43:1069–1082.

Wilkening, J. L., C. Ray, E. A. Beever, and P. F. Brussard. 2011. Modeling contemporary range retraction in Great Basin pikas (Ochotona princeps) using data on microclimate and microhabitat. Quaternary International 235:77–88.

Wilkening, J. L., C. Ray, and J. Varner. 2015. Relating Sub-Surface Ice Features to Physiological Stress in a Climate Sensitive Mammal, the American Pika (Ochotona princeps). Plos One 10:e0119327.

Winstral, A., K. Elder, and R. E. Davis. 2002. Spatial Snow Modeling of Wind-Redistributed Snow Using Terrain-Based Parameters. Journal of Hydrometeorology 3:524–538.

Yandow, L. H., A. D. Chalfoun, and D. F. Doak. 2015. Climate tolerances and habitat requirements jointly shape the elevational distribution of the American pika (ochotona princeps), with implications for climate change effects. PLoS ONE 10:1–21.