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Biogeographical implications of climate change for an alpine mammal, the American pika

Marie Louise Westover

Marie Louise Westover

Candidate

Biology

Department

This dissertation is approved, and it is acceptable in quality and form for publication:

Approved by the Dissertation Committee:

Felisa A. Smith, Chairperson

Jessica L. Blois

Joseph A. Cook

Helen J. Wearing

BIOGEOGRAPHICAL IMPLICATIONS OF CLIMATE CHANGE FOR A SMALL ALPINE MAMMAL, THE AMERICAN PIKA

by

MARIE LOUISE WESTOVER

B.S., Biology, Whitman College, 2010
M.S., Biology, University of New Mexico, 2015

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Finally, I thank my lifelong friends and supportive partner; you are all amazing.

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ABSTRACT

Anthropogenic climate change has already impacted a majority of species globally; understanding how animals respond and what mechanisms contribute to shifts in life history, distribution, and ecology are key questions in biology. When faced with changing climate conditions, animals can move to track their niche, adapt to new conditions, or disappear. The aim of this dissertation is to understand how climate and climate change influences animal ecology and evolution across space and time, using pikas (genus *Ochotona*) and particularly the American pika (*O. princeps*) as a model system. Pikas are an ideal study organism for the effects of climate change because their rugged habitat remains largely undisturbed by other anthropogenic activities, are highly detectable within their environment, and have a rich presence in natural history collections.

Body size is a key component animal ecology, as it influences a myriad of other life history traits. Body size evolution is one way that animals adapt to changing climate; temperature influences body size of most mammals studied across diverse spatiotemporal scales. In the first chapter, I ask if pika body size is influenced by different aspects of climate at the interspecific and intraspecific levels. I investigated how climate factors influence body size of *O. princeps* across their range and through historical time using museum specimens and skull measurements, in addition to comparing the mean masses of different species with climate and productivity. Body size in *O. princeps* populations was best related to precipitation and vegetation, and we found no significant correlations between body size and climate at the interspecific level. Our findings suggest that body size evolution may be more related to vegetation and food availability than the direct effects of climate, and that body size is not always a viable adaptation to temperature change.

While temperature change is correlated to species distributional shifts and populations declines worldwide, vegetation and diet may be important factors influencing animal responses to climate change. To investigate the impacts of climate on pika diet across diverse spatiotemporal scales, I used stable isotope analysis (δ^{13}C and δ^{15}N). This was the first study to document the isotopic niche of the American pika. I examined both bone, which averages diet over the course of the animal's life, as well as fur. By comparing populations across their range, though historical time, and across molt lines, I examined spatial, temporal and seasonal changes in isotopic diet. I find pika isotopic diet to be remarkably consistent, given the extensive latitudinal and temporal extent of my study. Population mean isotope values do correlate with local climate conditions; higher

$\delta^{15}N$ values reflected hotter, more arid environmental conditions in both bone and fur; $\delta^{13}C$ was negatively correlated with humidity and precipitation in fur. I suspect that pika's narrow isotopic niche reflects a narrow dietary niche; hence, dietary inflexibility may contribute to pika's ongoing decline across western North America.

Moving to stay within suitable climatic conditions is one way animals can respond to a changing environment. The trailing edge of species distributions are where the populations often decline or disappear, as they sit on the boundary of a species' ecological limits. I examined the climatic, physical and vegetation drivers of pika distribution and occupancy at the southernmost edge of their range through extensive field surveys recording current and old pika evidence. Pikas were most likely to have disappeared from sites with low moisture. The probability of current pika occupancy increased with habitat size, grass cover, and cooler microclimate temperatures. Overall, my studies suggest that aspects of moisture and precipitation are consistently the most influential factors in pika evolution and ecology.

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Chapter 1

Investigating the role of climate in pika *(Ochotona)* body size patterns across intra-and inter-specific levels, space and time

Marie L. Westover[1] and Felisa A. Smith[1]

[1]Department of Biology, University of New Mexico

Abstract

Body size is an important trait in animals because it influences a multitude of additional life history traits. The causal mechanisms underlying body size patterns across spatial, temporal and taxonomic hierarchies are debated, and of renewed interest in this era of climate change. Here, we tested multiple hypotheses regarding body mass patterns of extant *Ochotona* species to determine if direct environmental temperatures, food availability, habitat variability or range area influence body size. We also investigated intraspecific patterns comparing the median body mass of *O. princeps* populations (n=2932 individuals) from across their range with local environmental variables and examined median body mass of populations over time to determine if body size has evolved *in situ* in response to environmental change. We find correlations between body mass and precipitation-related climate variables at the intraspecific level. We found little relationship between temperatures and body mass within the species *O. princeps*, and no relationship between body size and any climate or habitat variable for *Ochotona* species. We find that body size trends in relation to climate are stronger at the intraspecific than

the interspecific level. Our results suggest that body size evolution is not always a viable response to temperature change, as the body size of a climate-sensitive species shows little relation to temperatures. Factors other than environment, such as biotic interactions, may be influential in determining body size over space and time.

Introduction

The geographic range of a species is the spatial reflection of its ecological niche. One important dimension of the niche is climate, and in particular, temperature (Andrewartha and Birch 1954, Grinnell 1917; James et al. 1984). Biotic and abiotic factors are likely influential at different spatial scales to determine a species' distribution (Araújo and Guisan 2006; Boulangeat et al. 2012; Guisan and Thuiller 2005; Elton 1927; Hutchinson 1957; MacArthur 1972; Odum 1953; Sexton et al. 2006; Wisz et al. 2013).

As the climate changes, many animals shift their distributions to track their climatic niche (Brown et al. 1996; Parmesan and Yohe 2003; Tingley 2009). Such ecological niche conservatism leads to large-scale biogeographic patterns and reorganization of communities over time as animals and plants respond individualistically (Graham and Grimm 1990; Sexton et al. 2006; Wiens 2011). While distributional shifts in response to ongoing anthropogenic climate change are well documented (e.g. Parmesan and Yohe 2003; Tingley 2009), adaptation is another possible and underappreciated response to changing conditions (Davis and Shaw 2001; Kozak and Weins 2010). Body size is one important way that animals can adapt to different climatic regimes (Hadly et al. 1998; Pörtner 2002; Sheridan and Bickford 2011; Smith et al. 1995; Smith and Betancourt 2006).

For most mammalian genera, species in cooler climates have larger body sizes than related species in warmer climates, a trend known as Bergmann's rule (Bergmann, 1847; Millien et al. 2006; Salewski and Watt 2017; Watt et al. 2010). While Bergmann's rule was originally postulated to describe geographic variation in species within genera (Blackburn et al. 1999; Watt et al. 2010), other researchers have confirmed the pattern at different levels of taxonomic hierarchy (e.g. Blackburn and Gaston 1996; Clauss et al. 2013; Yom-Tov and Nix 1986), including populations within a single species (e.g., Mayr 1956, 1963; Meiri and Dayan 2003; Rensch 1938). Moreover, Bergmann's rule appears to hold over time in response to climate in certain species (Smith et al. 1995; Smith and Betancourt 2006). Although a fundamental rule of biogeography, the extent to which Bergmann's rule applies across biological hierarchies and the mechanism underlying body size patterns remains elusive (Ashton et al. 2000; Gohli and Voje 2016; Millien et al. 2006; Watt 2010; but see Salewski and Watt 2017).

Typically, thermoregulation is invoked as the mechanism underlying Bergmann's rule (Salewski and Watt 2017). Studies on woodrats *(Neotoma)* support this mechanism over both space and time (Brown and Lee 1969; Smith et al. 1995; Smith and Charnov 2001; Smith et al. 2014); mean annual temperature is positively related to lethal ambient temperature and thermal conductance in woodrats, and inversely correlated with body size. Even over microevolutionary time, woodrat populations consistently evolved smaller size in warmer periods and larger size in cooler periods (Smith et al. 1995, 1998, 2014). Other species have not been studied to this great extent. Other mechanisms have also been proposed for Bergmann's rule, including primary productivity (Huston and Wolverton 2009, 2011; Rosenzweig 1968), fasting endurance (Lindstedt and Boyce

1985) and food availability (Blois et al. 2008; Boyce 1978; Erlinger 1987; Geist 1987; McNab 2010; Meiri et al. 2007; Ochocinska and Taylor 2003; Sepúlveda et al. 2013; Yom-Tov et al. 2003).

We test whether aspects of climate or environmental productivity hypotheses best support Bergmann's rule using pikas *(Ochotona)* at the interspecific and intraspecific levels, as well as over a century of anthropogenic climate change. Previous work on Bergmann's rule has focused on either interspecific or intraspecific patterns, and few studies have investigated the pattern over historic or near time (but see Blois et al., 2008; Brown and Lee 1969; Smith et al. 1995, 1998). Using global climate and net primary productivity data, we aim to disentangle climatic and environmental variables influencing body size patterns and yield new insights into the mechanisms behind this classic ecogeographic rule. We focus on pikas (genus *Ochotona*), a small mammal widely distributed across the Holarctic, inhabiting a wide variety of ecosystems, elevations, and climates (Lissovsky 2016). Our analysis includes 26 species of 30 within the genus (Wilson and Reeder 2005). At the intraspecific level, we focus intensively on *Ochotona princeps,* a widely distributed species in North America known to be sensitive to temperature (Beever et al. 2017; Moritz et al. 2008; Smith 1974; Stewart et al. 2015). We predict that pikas will conform to expectations set by Bergmann's rule, and will exhibit smaller body sizes in warmer climates or more productive areas across space, time and at each level of the taxonomic hierarchy.

Methods

Here, we examine the role of temperature and other environmental factors on

body size of pika (genus *Ochotona)* and of populations within a widely distributed species, *O. princeps*. Pikas (Ochotnonidae) are small (80-290g), round-bodied mammals from the order Lagomorpha, which includes rabbits and hares (Lissovsky 2016; Smith and Weston 1990). The 30 extant pika species belong to a single genus *Ochotona* and inhabit a broad swath of latitudes (25N to ~75N) (Wilson and Reeder 2005) (Fig. 1.1). Most *Ochotona* species live in high elevation plateau or alpine regions, and are well adapted to cold environments due to dense fur and relatively high metabolic rate (Ge et al. 2012; MacAurthur and Wang 1973; Smith and Xie 2008; Smith and Weston 1990). *Ochotona* species live in either rock piles or earthen burrows, which shelter them from predators and ambient temperatures, which can be extremely low (Smith and Xie 2008; Sokolov 2009).
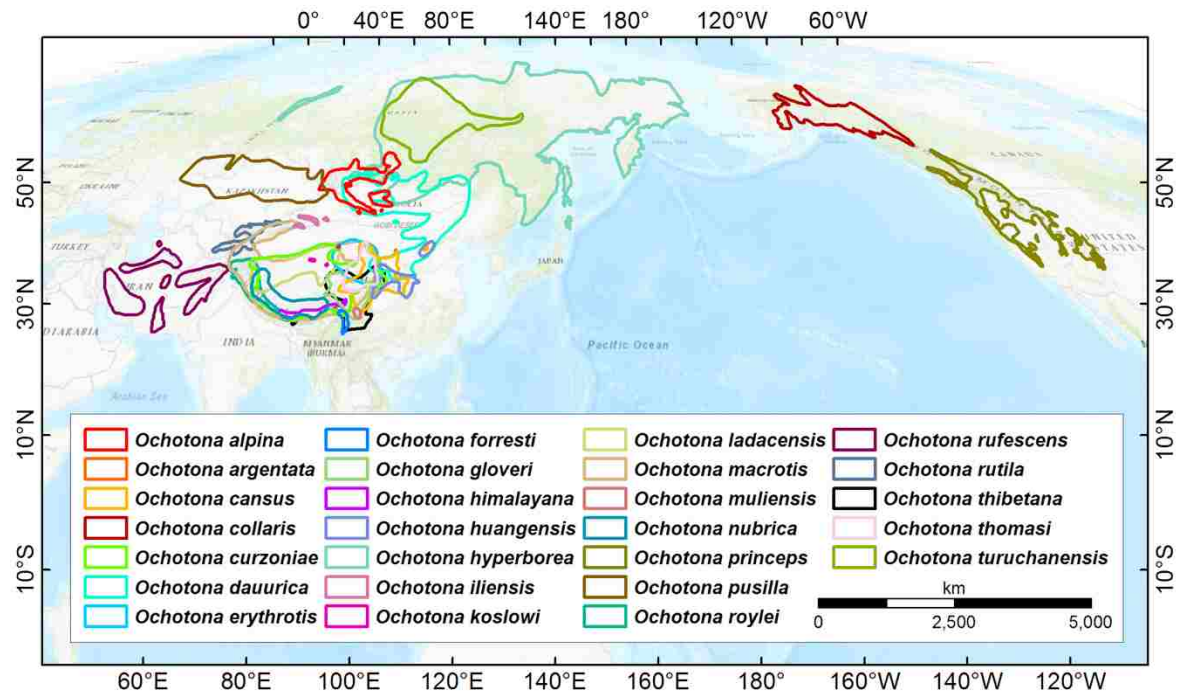
Figure 1.1. Interspecific distribution of extant *Ochotona* species. Species ranges (IUCN.org, downloaded Aug 25, 2014) are mapped on a Mollweide equal area global projection with the central meridian at 140E.

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Alpine and high latitude mammals are more likely to have contracted their range or otherwise have responded to climate change (McCain and King 2014). Given that other small mammals (e.g. woodrats) respond to climate change partly though body size evolution, we might expect cold-adapted mammals to conform to Bergmann's rule. Increased temperatures are implicated in alterations of *O. princeps* distribution, elevation, and behavior (Beever et al. 2017; Moritz et al. 2008; Smith 1974; Stewart et al. 2015). *Ochotona princeps* has experienced disappearances from edges of their range within the last century (Beever et al. 2003, 2016) and from an interior part of their distribution (Stewart et al. 2017), associated with rising temperatures.

Due to the demonstrated sensitivity to warming temperatures, *O. princeps* is considered a bell-weather species for the effects of climate change on animals (Beever et al. 2003, 2016, 2017). *Ochotona princeps* is the more widespread of the two species in western North America (Wilson and Reeder 2005), stretching from 35N to 55N latitude in several discontinuous mountainous regions (Smith and Weston 1990). *Ochotona princeps* distribution is thought to be limited by proximity to cool, mesic high elevation alpine permafrost and further, by availability of talus slopes, which they utilize for protection from the elements and hay storage for winter consumption (Halfner 1994, but see Dearing 1997; Ray et al. 2016; Simpson 2009).

Intraspecific

We compiled an exhaustive dataset of individual *O. princeps* from across their geographic range (n=4093) from natural history collections. Museums included: American Museum of Natural History (AMNH, New York, NY), Denver Museum of Nature and Science (DMNS, Denver, CO), Museum of Southwestern Biology (MSB,

Albuquerque, NM), Museum of Vertebrate Zoology (MVZ, Berkeley, CA), National

Museum of Natural History (NMNH, Washington, D.C.), University of Michigan

Museum of Zoology (UMMZ, Ann Arbor, MI) and the University of Washington Burke

Museum (UWBM, Seattle, WA). For each specimen, we recorded the tag information

written by the collectors, including the location and date collected, sex, stage, total

length, hind tarsus length, and body mass (when available). We measured skull length

(n=2199), zygomatic breadth (n=2284), M1 length and width (n= 2726) of individuals

with digital calipers (Appendix 1 Fig. 1). Not all elements are available for each

specimen. Because of missing elements, we used linear regressions of body mass

reported on the specimen tag compared with each of these measurements to find the most

reliable correlation. This allowed us to estimate the body mass for individuals without

reported mass from skull length.

Individuals determined to be juveniles were removed from analyses. We excluded

juveniles from analyses by removing individuals with reported or estimated mass of 1.5

standard deviations below the median mass value (91.6 g). *O. princeps* did not exhibit

significant sexual dimorphism across its range once juveniles were excluded (Welch 2

sample t-test, female mean mass = 147.84g, male mean mass = 148.04g. t = -0.15, df =

1698, p-value = 0.89). The median body mass of individuals included in our analyses is

148.0 g (mean 147.8 g, sd = 25.2).

Skull length was the single measurement most highly correlated with individual

body mass (Appendix 1 Table 1). We therefore estimated body mass for individuals from

skull length when applicable. Skull width, M1 length, M1 width, total body length and

hind tarsus length were also significantly correlated with body mass (Appendix 1 Table

1). Including multiple measurements in regression models did increase predictive power, but limited the number of samples for which we could estimate mass (Appendix 1 Table 1). Our final dataset contains 2932 individuals spanning across *O. princeps'* distribution from years 1874-2005 with reported mass or estimated mass.

In total, we had 60 geographic populations with 134 unique geographic/temporal populations (Fig. 1.2, Appendix 1 Table 3). We assigned latitude and longitude to specimens without previous georeferenced localities using the information reported on specimen tags. To achieve this, we used Geolocate (www.museum.tulane.edu/geolocate/web/WebGeoref.aspx), and excluded specimens with low likelihood matches. We then assigned *O. princeps* individuals to populations based on geographic barriers such as deserts, valleys, large rivers and mountain passes. Populations with 9 or more individuals were included in subsequent analyses. Populations of 9 or more enabled us to have more historical populations for longitudinal analyses while maintaining adequate numbers of individuals. To avoid temporal averaging, we only included specimens collected within a 10-year time span. For each population, we used the location and year that the majority of individuals were collected from for analysis. We recorded elevations from latitude and longitude for a subset of populations using USGS 7.5' maps (https://caltopo.com).

We extracted climate data for intraspecific analyses from Climate WNA (www.climatewna.com), an interpolated dataset adjusted for elevation and location
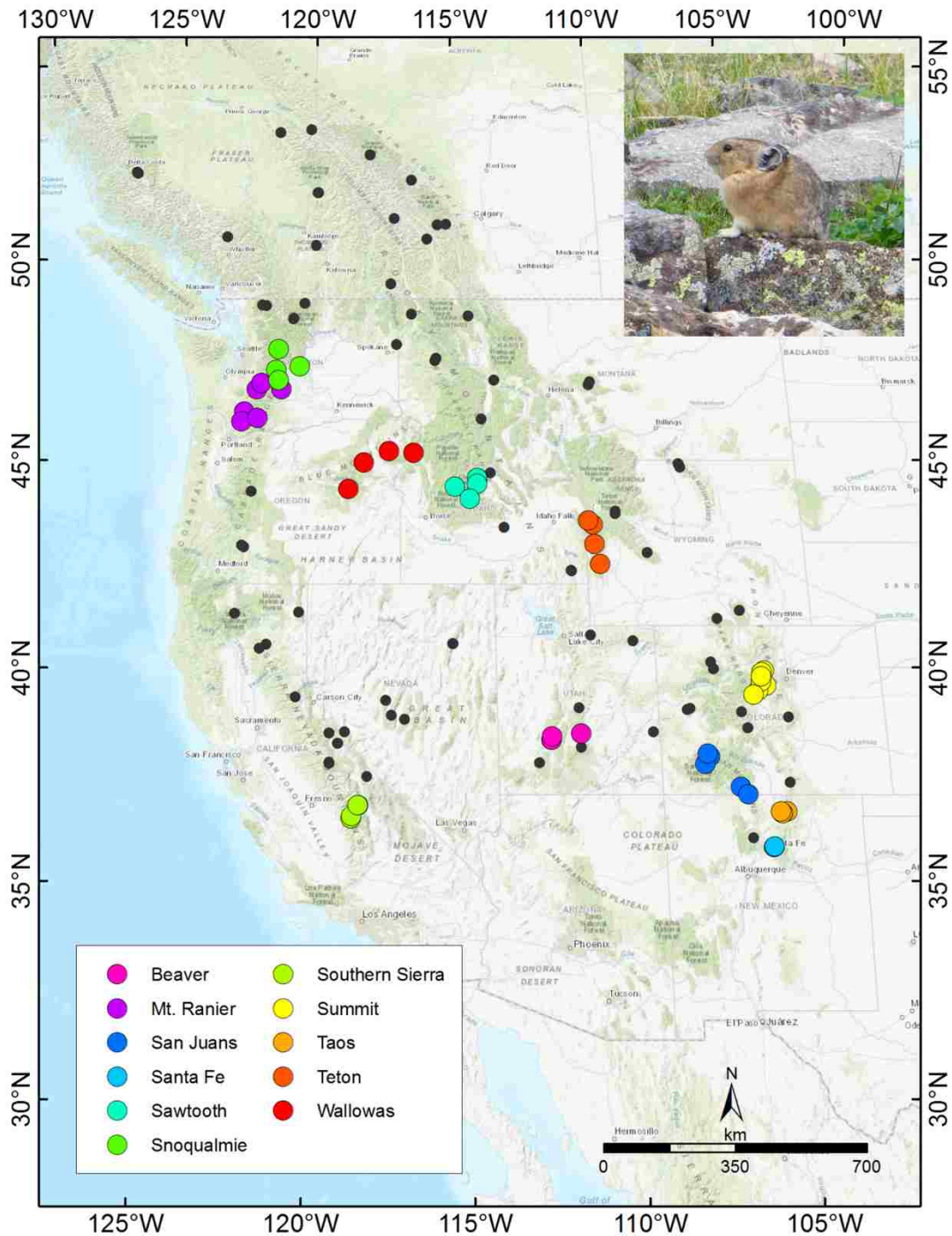
Figure 1.2: Intraspecific *O. princeps* populations. Black dots indicate *O. princeps* populations (1901-2015) used for climate and body size analyses. Large colored dots are the locations of populations with four or more sampled time periods between 1890 and 2005 included in longitudinal elevation and body size comparisons. Populations are mapped on Mollweide equal area projection with the meridian centered at 118W.

(Wang et al. 2016). Climate WNA uses lapse rate algorithms to estimate climate variables to specific geographic locations (Wang et al. 2016). To investigate intraspecific body size patterns, we compared mean body mass of *O. princeps* populations to mean annual temperature, mean annual precipitation, precipitation as snow, number of frost free days, average January temperature and average July temperature. We compiled climate data for each *O. princeps* population dating from 1901-2015 specific to the georeferenced location and year of collection. This allowed us to compare population body sizes over space and the same geographic population over time.

To investigate the influence of vegetation on pika body mass, we used global satellite Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation indices (Didan 2015). Vegetation indices are empirical measures of land surface vegetation photosynthetic activity (Solano et al. 2010). MODIS data contains global monthly composites of Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI). We modeled the influence of vegetation for 22 populations from July of 2004 and 2005 because MOD13C2 is available for dates after 2000. The resolution is 0.05 degrees or 5600m spatial resolution. This was the highest resolution for a global vegetation index found on earthdata.nasa.gov. While NDVI is an older index and can be used to compare historical data, EVI has decreased sensitivity to atmospheric conditions and background variations in snow or leaf litter (Huete et al. 2002).

We ran univariate linear models all pika populations dating between 1901 and 2015 (n=116) for each climate variable we investigated (Table 1.1). We also ran multiple regression models using forward and backward selected AIC to avoid over fitting climate models. We ran univariate linear models for each climate and vegetation variable for pika

populations captured in 2004 and 2005 (n=22) because vegetation data is available for

those years, and it avoids the possible pseudo-replication present in using all populations

where many are from similar geographic areas over different time periods. We also ran

multiple regression models using forward and backward selected AIC on all variables for

populations from 2004 and 2005 (Table1.1).

Table 1.1: Intraspecific body size models for *O. princeps* populations. Multiple regression models shown are the best fit from forward and backward selected AIC. Climate metrics for all *O. princeps* populations are specific to the year and location of each population (Wang et al. 2016). Significance: *p < 0.05, **p < 0.01, ***p < 0.0001

Linear regression models for *O. princeps* populations (n=116)			
Variable/model	Abbreviation	Adj. R^2	Significance
Mean Annual Temperature (°C)	MAT	-0.01	
Mean Annual Precipitation (mm)	MAP	0.19	***
Number of Frost-Free Days	NFFD	0.03	*
Precipitation as Snow (mm)	PAS	0.09	***
Mean January Temperature (°C)	MJanT	-0.01	
Mean July Temperature (°C)	MJulT	0.02	
NFFD + MJulT+ MJanT+ MAP		0.25	***

Linear regression models for *O. princeps* populations from 2004 and 2005 (n=22)			
Mean Annual Temperature (°C)	MAT	-0.03	
Mean Annual Precipitation (mm)	MAP	0.15	*
Number of Frost-Free Days	NFFD	-0.03	
Precipitation as Snow (mm)	PAS	0.28	**
Mean January Temperature (°C)	MJanT	-0.05	
Mean July Temperature (°C)	MJulT	0.08	
Normalized Difference Vegetation Index	NDVI	0.10	
Enhanced Vegetation Index	EVI	0.16	*
PAS + NFFD + MJulT+ MAT		0.45	**

Interspecific

To investigate interspecific body size patterns, we compiled body mass data for

26 out of 30 species within *Ochotona* from a variety of literature sources (See Appendix

1 Table 2). While calculating mean masses from specimens housed in natural history

collections would be ideal, there are very limited museum specimens for many taxa. Thus, we relied upon mean body mass data reported from the literature (Smith and Xie 2008) and the Masses of Mammals database (MOM v. 10.4; Smith et al., 2003). For the single species *(O. turucharensis)* without reported body mass, we estimated mean mass from reported head body length using a linear regression built from average head body lengths reported in literature of other species in the genus *Ochotona*. (Mean mass= head-body average*1.898 -177.608, $r^2 = 0.64$, p< 0.01). The lifestyle of each species, burrowing or rock dwelling, was derived from literature sources (see Appendix 1 Table 2).

We calculated the means of climate and productivity variables for each species' geographic range. We downloaded shapefiles from IUCN.org of each species' geographic range and analyzed them in QGIS (Downloaded Sept 15, 2014, iucnredlist.org). We selected 12 variables to test specific hypotheses about the influence of climate and environment on interspecific body size. To test the influence of average temperature and average precipitation, we used mean annual temperature and annual precipitation. To examine the influences of heat and cold stress we used mean temperature of the warmest quarter, maximum temperature of the warmest month and minimum temperature of the coldest month, mean temperature of the coldest quarter, respectively. To examine the possible influence of habitat variability, we used the standard deviation of net primary productivity, temperature seasonality, precipitation seasonality, and temperature annual range. To test the importance of food availability, we used net primary productivity. To test if geographic range size influenced body size patterns, we used the range size (km^2)

of species geographic distributions. We used R for all analyses (R core development team, version 3.3.2)

All climate variable data came from Bioclim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005: www.worldclim.org/bioclim), a global-scale dataset with approximately one-kilometer square resolution. For net primary productivity (NPP) we used a global version of NASA MODIS spectrometer-derived measures of terrestrial vegetation growth with $500m^2$ resolution from July for the year collected (Running, Mu and Zhao 2015). We used QGIS to calculate the mean values for each climate variable and NPP from each species' geographic range. We also used QGIS to calculate the range size (km^2) from species range maps.

To investigate interspecific body size patterns in *Ochotona* across climatic gradients, we ran linear regressions of mean body mass against selected climate variables. We investigated the relationship between body size and food availability (mean NPP, mean temperature in wettest quarter), range size (range size), climate (mean annual temperature, minimum temperature coldest month, maximum temperature of the warmest month), and habitat variability (standard deviation NPP, temperature seasonality and precipitation seasonality). We ran simple and multiple linear regressions with AIC for all pika species together and also separately for burrow-dwelling and rock-dwelling species.

Results

Intraspecific

We investigated the relationships between climate variables and the median body mass of 116 *O. princeps* populations (n ranged from 9 to 43 individuals) between the
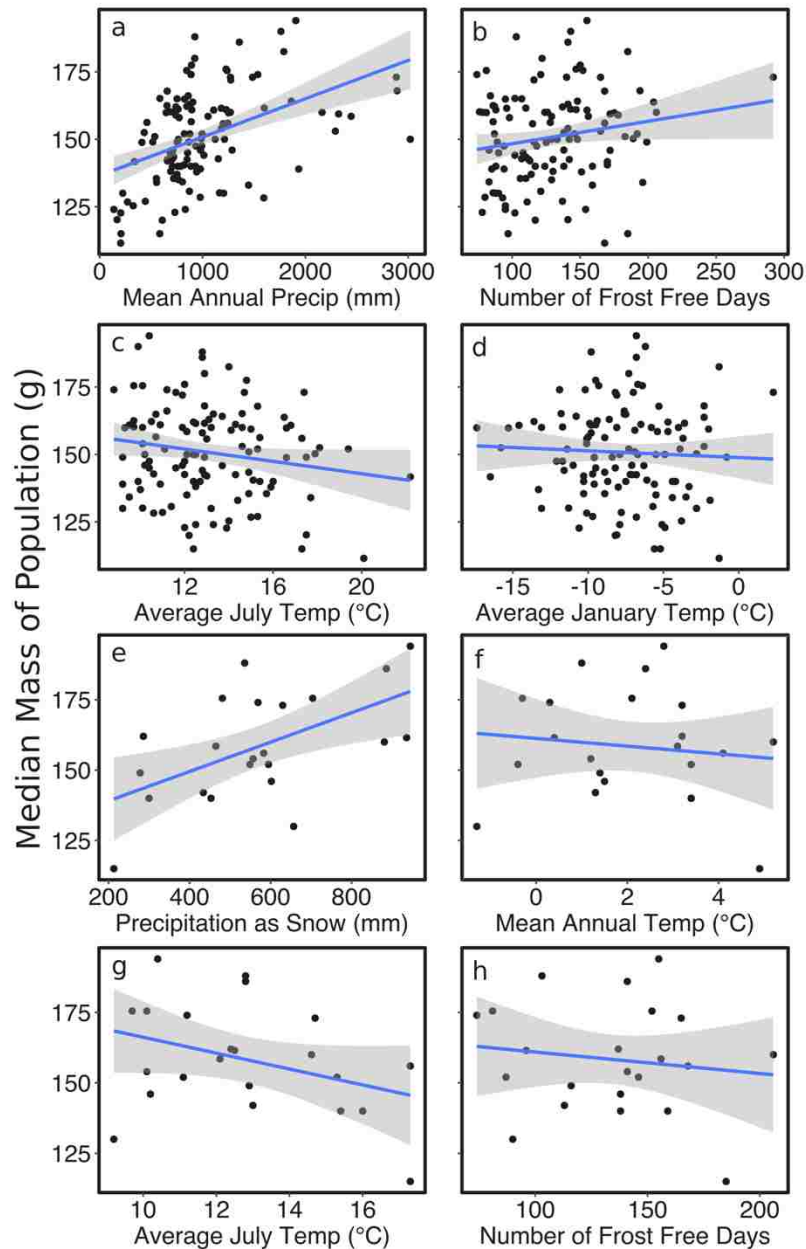
Figure 1.3. Climate variables correlated with *O. princeps* population median body mass. Panels a-d show climate variables included in final multivariate linear model predicting *O. princeps* population median body mass for all populations (n=116) AIC=630.01, df =110, Adj. r^2= 0.25, p < 0.001). Panels e-h show climate and vegetation indexes included in the final AIC model of pika populations from 2004-2005 (n=22, AIC= 121.79, df=17, Adj. r^2= 0.45, p < 0.01). Climate and vegetation data for each population is specific to the year and location collected (ClimateWNA.org, Running et al. 2015).

years of 1901 and 2005. Using linear models, mean annual precipitation was the most explanatory climate variable (Table 1.1, Fig. 1.3a). Precipitation as snow and number of frost free days were also positively correlated with median body mass (Table 1.1, Fig. 1.3a,b). No other individual climate variables were significant. When combined into a multiple regression model using AIC, the highest quality model included number of frost-free days, mean July temperature, mean January temperature and mean annual precipitation (AIC = 630.01, Adj. R^2 =0.25, p< 0.001, Fig. 1.3a-d).

To better understand the role of vegetation in *O. princeps* body size, we also investigated the relationships between climate, remotely-sensed vegetation indices and median mass of pika populations from 2004 and 2005. Enhanced vegetation index (EVI) measurements are available after year 2000, limiting which populations we could test for the influence of vegetation indexes. Investigating this subset of populations removes pseudo-replication of populations from the same place over multiple years and the individuals in these populations were all collected in a single year. Mean annual precipitation, precipitation as snow and EVI are positively correlated with median body size (Table 1.1) in simple linear regression models. When all variables were evaluated with AIC forward-backward stepwise model selection, the final model included precipitation as snow, number of frost-free days, mean annual temperature and average July temperature (AIC= 121.79, Adj. R^2 = 0.45, p < 0.01, Fig. 1.3e-h).

We further investigated *O. princeps* population patterns by comparing the median body mass and median elevation of individuals over time. Eleven populations from the same geographic areas were sampled at 4 or more different times, providing longitudinal
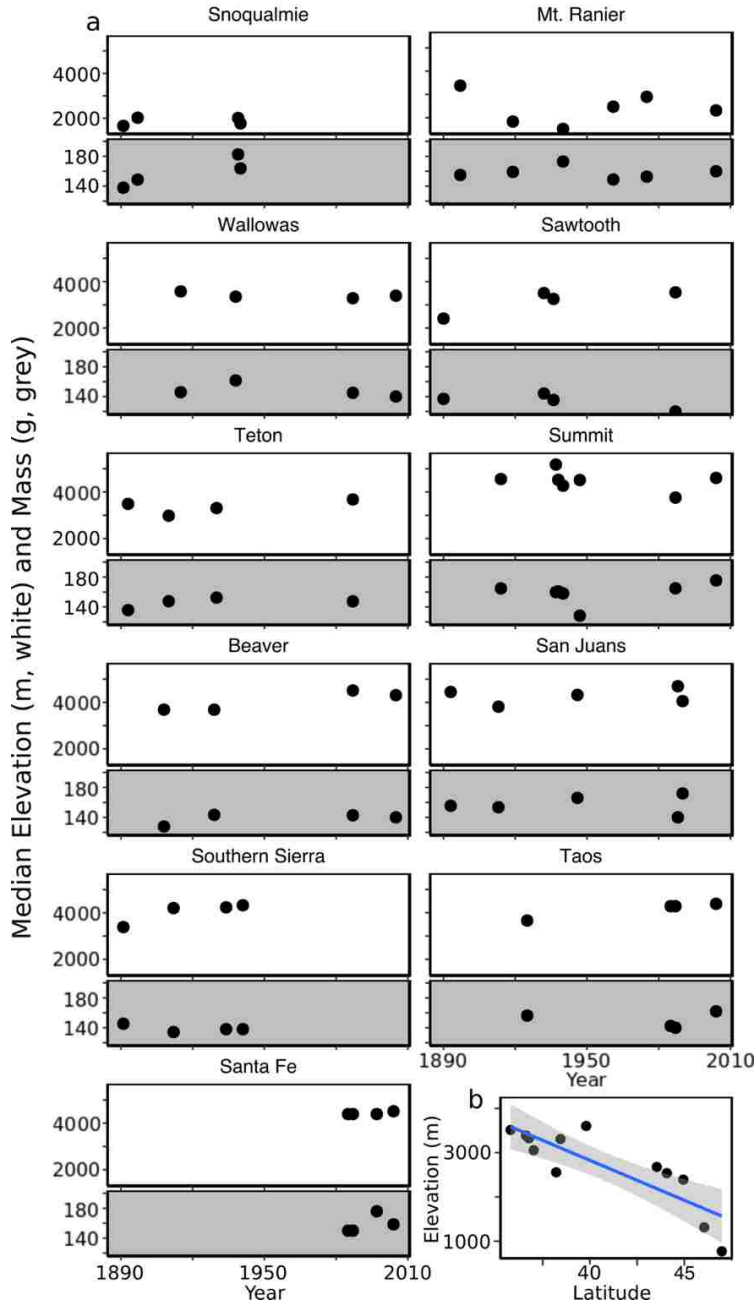
Figure 1.4. a) *O. princeps* populations with 4 or more sampled time periods elevation and body size over time. Across these populations, elevation has increased over time (df= 48, Adj. r^2 =0.09, p < 0.02) while median mass has not (Adj. r^2=0.01, p=0.25). Average elevation of populations with most recent year collected is inversely correlated with latitude (Adj. r^2 = 0.68, p value <0.001). b) Elevation-latitude gradient is apparent in these distinct geographic pika populations (n=12). We plotted median elevation of the most recent population for each longitudinal study site (Beaver, Mt. Ranier, San Juans, Santa Fe, Sawtooth, Snoqualmie, Southern Sierra, Summit, Taos, Teton, Wallowas, Bodie). Ray et al. 2016 also reported a distinct elevation-latitude gradient among 27 range-interior populations.

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body size data (Fig. 1.4a). We found elevation across these eleven populations had increased slightly over time (lm, Adj. r^2 = 0.094, p < 0.05), while median body size did not significantly change (lm, Adj. r^2 = 0.01, p >0.05). Median elevation is inversely related to latitude (Adj. r^2 = 0.68, p value <0.001, Fig. 1.4b).

Because elevation is inversely correlated with latitude, we accounted for this variation by calculating relative elevation compared to the earliest population collection time period. From relative elevation (and relative mass) we can determine the direction of elevation and body mass change for pika populations over time. Relative elevation and body mass of populations compared to past baselines are on average greater than one (one tailed t-test, mean=1.08, df=60, p=0.02 and mean=1.05, df=60, p=0.001, respectively), indicating that elevation and mass of populations both increased over time (Fig. 1.5a,c). We also compared the mean annual precipitation and average July temperatures relative to the first populations collected after 1901 (when climate data was available). Precipitation increased relative to early collections, as did July temperatures (Fig. 1.5b,d). The relative July temperatures decreased between 1950 and 1980, then increased again until 2005. The average July temperature has not significantly increased since the beginning of our population sampling (one tailed t test, t = 0.02, df = 59, p-value = 0.98), nor has mean annual precipitation changed significantly (t = 1.89, df = 59, p-value = 0.06). However, in populations from 1985-1987 to 2004-2005 we see significant changes in July (Welch two sample t-test, t=-2.30, df= 24, p= 0.03) and January temperatures, but not significant changes in mean annual precipitation (MAP) (t=0.74, df=21, p = 0.47), elevation and mass (Welch 2 sample t test, t = -1.01, df = 29.18, p-value = 0.32 and t = 1.34, df = 19.62, p-value = 0.20) for the same time period.

Interspecific

Table 1.2: Interspecific body size body size models for *Ochotona* species. Simple and multiple regression models of environmental variables compared to *Ochotona* species' mean body size. We quantified climate and habitat variables for each species' range by calculating the mean value of each variable within the boundaries of the species' range map (IUCNredlist.org). We classified species' lifestyle from literature (See Appendix 1 Table 2). We found no significant correlations between species' body size and climate or habitat variables, or combinations of variables.

Climate or habitat variable	Abbreviation	All species (n=26)		Burrowing (n=12)		Rock Dwelling (n=14)	
		p	R^2	p	R^2	p	R^2
Mean annual temperature (°C)	MAT	0.8	0.01	0.12	0.27	0.24	0.11
Maximum temp hottest month (°C)	MTHM	0.59	0.12	0.27	0.15	0.13	0.18
Mean temp warmest quarter (°C)	MTWQ	0.7	0.01	0.19	0.2	0.11	0.2
Minimum temp coldest month (°C)	MTCM	0.92	0	0.33	0.12	0.79	0.01
Mean temp coldest quarter (°C)	MTCQ	0.97	0	0.28	0.15	0.65	0.02
Mean net primary productivity (NPP) of range (gCm^{-2}yr^{-1})	MNPP	0.37	0.03	0.14	0.25	0.35	0.07
Standard deviation of NPP	SDNPP	0.38	0.03	0.25	0.16	0.6	0.02
Temperature seasonality	TS	0.76	0	0.93	0	0.64	0.02
Temperature annual range	TAR	0.61	0.01	0.97	0	0.38	0.07
Size of range (km^2)	SR	0.63	0.01	0.54	0.05	0.26	0.11
Precipitation seasonality	PS	0.75	0	0.99	0	0.1	0.2
Annual precipitation (mm)	AP	0.75	0	0.34	0	0.48	0.04
Habitat variability model	SDNPP+ TAR+ TS+PS	0.84	0.06	0.59	0.38	0.26	0.41
Heat stress model	MAT+ MTWQ+ MTWM	0.88	0.02	0.47	0.33	0.47	0.22
Cold stress model	MAT+ MTCQ+ MTCM	0.87	0.03	0.15	0.56	0.05	0.52

Mean body mass for *Ochotona* species ranged from 74.5g *(O. cansus)* to 293g *(O. alpina)* with a median mass of 155g *(O. roylei)* (Appendix 1 Table 2). Linear models found no significant correlations between body size and any variables considered in our study (Table 1.2). Annual mean temperature or temperature seasonality of each species' range had no effect of mean body mass. Precipitation variables (AP, PS) were not

correlated with mean body mass. Maximum and mean hot temperatures (MTMH and MTWQ) had no significant effect, nor did minimum and mean cold temperatures (MTCM and MTCQ). Measures of vegetation (mean and standard deviation NPP) similarly had no effect. The size of each species' geographic range was also not correlated with mean body mass. The single habitat variables have nearly no explanatory power for body size across all species, with the highest r squared value being 0.12 for MTHM. (Abbreviations are defined in Table 1.2).

We found no relationship between body mass and range size of the species (Table 1.2). While we would not necessarily expect to find a linear relationship, we would expect to see larger species occupying larger geographic range sizes (McNab 1963; Gaston and Blackburn 1996). However, the largest bodied species of *Ochotona* have medium sized ranges and the largest ranges belong to medium sized species (~150g).

Examining the effects of single habitat variables of pika subsets with different lifestyles (rock dwelling vs burrow dwelling species) yielded no significant relationships. For burrow-dwelling pikas, MAT, MNPP, and MTWQ had greater explanatory power with r-squared values up to 0.27 (p-values > 0.05). For rock-dwelling pikas, MAT, MTHM, MTWQ had improved explanatory power with r-squared values between 0.1 and 0.2 (p >0.05).

We ran multiple linear regression models for heat stress (MAT+MTWQ+MTWM), cold stress (MAT+MTCQ+MTCM), and habitat variability (SDNPP+TAR+TS+PS) with no significant results for all species, burrow dwelling or rock dwelling pikas (Table 1.2). In addition, log10 transforming mean body mass and predictor variables did not greatly change our qualitative or quantitative results. Since

none of the multiple regression models were significant, we decided not to run AIC tests because we were not concerned about having over fit our models.

Discussion

Our study finds significant patterns among population body size of *O. princeps* populations but not among species of *Ochotona*, suggesting that different processes constrain body size at different taxonomic scales. Within *O. princeps*, combinations of temperature and precipitation factors predicted median body size of populations. However, we found no relationship between environmental factors and the body size of *Ochotona* species within the genus, suggesting that some uninvestigated environmental attribute or biotic interactions may be more influential at the interspecific level.

We do not find strong evidence supporting Bergmann's rule either within a species or across species within a genus. We find more predictable mean body size of pika populations within *O. princeps* than we do between different species within *Ochotona,* but the patterns are not consistent with Bergmann's rule (Table 1.1, 1. 2). Temperature alone was not a significant influence on the body size of *Ochotona* species or *O. princeps* populations (Table 1.1, 1.2). Rather, precipitation variables demonstrate the greatest influence on *O. princeps* body size evolution (Fig. 1.3). Mean annual precipitation is consistently important as the only variable that is significantly correlated with mean body mass among all populations and the subset from 2004-2005 (Table 1.1, 1.2). The importance of precipitation in determining body size of mammals has been described in arid regions of Australia and the Levant, as well as with California ground

squirrels (Blois et al. 2008; Yom Tov and Nix 1986; Yom Tov and Geffen 2006). Our results expand this finding to alpine regions.

Primary productivity or food availability has been implicated in determining animal body size in many studies (Heaney 1978; Kolb 1978; Rosenzweig 1968), but was not directly supported here. Our results did not yield convincing evidence that body size responded directly to precipitation and temperatures over time, but together suggested an influence of vegetation in *O. princeps* body size. We tested this hypothesis by using the vegetation measures of net primary productivity (NPP) and enhanced vegetation index (EVI). However, NPP was not significantly related to intraspecific or interspecific body size (Table 1.1, 1.2). While EVI was a significant predictor of intraspecific body mass in bivariate analyses, this was not true of more complex models (Table 1.1). Given the positive and relatively strong correlation between median body mass and mean annual precipitation, it still seems likely that vegetation (mediated by precipitation) and additional factors that we were unable to adequately capture in this study influence pika body mass.

Forage availability and quality may be an important mechanism through which climate influences *O. princeps* body size. We found patterns consistent with vegetation, along with climate, predicting *O. princeps* density and distribution across their range (Erb et al. 2014; Jeffress et al. 2013; Millar and Westfall 2010; Ray et al. 2016; Yandow et al. 2015). Beyond pikas, food availability is often related to body size in mammals (Blois et al. 2008; Boyce 1978; Erlinge 1987; Geist 1987; Ochocinska and Taylor 2003; McNab 2010; Meiri et al. 2007; Sepulveda 2013; Yom-tov et al. 2003). Vegetation in alpine and sub-alpine environments is heavily influenced by snowpack (Wipf and Rixen 2010).

Increased snowpack and later snowmelt leads to larger plants, higher NDVI and increased forb productivity (Walker et al. 1994; Wipf and Rixen 2010), which might select for larger body size. Our results are consistent with this idea; mean annual precipitation and precipitation as snow (Table 1.2) are the most important variables to population median body size. While we did not directly test the impact of forage quality on body mass in this study, it remains a possible mechanism and deserves further inquiry.

While there is some direct or indirect role of climate on population body size among populations of *O. princeps,* we find no such patterns among species of *Ochotona.* Species within the genus *Ochotona* do not conform to Bergmann's rule. We find no evidence that temperature, environmental seasonality, precipitation, NPP, resources, or range size influence average body size in pika species. While all species of pika exhibit burrow-dwelling or rock-dwelling lifestyles (Smith and Xie 2008, Smith and Weston 1990; Sokolov et al. 2009), use of micoclimate shelter does not explain their lack of body size trends. The use of thermal shelters by animals is often highly associated with Bergmann's rule or some body size response to climate (Ashton et al. 2000; Gür and Gür 2012; Medina et al. 2007; Meiri and Dayan 2003). For example, woodrats *(Neotoma)* use dens as climate refuges which can ameliorate surface temperatures by as much as 20°C (Murray and Smith 2012). Still, *Neotoma* strongly adhere to Bergmann's rule both at the interspecific and intraspecific levels, as do hibernators like marmots to some extent (Brown and Lee 1969; Murray and Smith 2012; Panteleev et al. 1998; Smith et al. 1995; Smith and Charnov 2001). Thus, absence of a temperature-body mass correlation in *Ochotona* is not likely due solely to their burrowing and rock-dwelling lifestyle sheltering them from thermal extremes.

Biotic interactions may be an important and underestimated factor in body size trends. Many pika species have overlapping ranges (Fig. 1.1) perhaps leading to strong interspecific competition. The competitive exclusion principle, that closely related species diverge in body size so as to not compete directly for resources, may be influential in segregating body sizes at the interspecific level (e.g. Brown and Nicoletto 1990; Hutcinson 1959; MacArthur 1972). Additionally, there is evidence that pressure from predation can influence body size of small mammal species, a possible mechanism not investigated here (Lomolino 1984; Smith 1992). We suspect interspecific competition and predation pressure may be stronger than energetic benefits of adapting to local temperatures or productivity at the interspecific level.

Despite Bergmann's rule originally being conceived for temperature influencing body size at the interspecific level, we find more support for body size patterns at the intraspecific level and that precipitation, and presumably vegetation, are most related to body size patterns. The processes influencing interspecific and intraspecific body size are different in our study. Our results suggest that climate likely impacts *O. princeps* body size both directly and indirectly though vegetation, but biotic factors such as competitive exclusion may be more influential at the species level. While extensive in scale, our study has limitations in the type and quality of data incorporated, particularly at the interspecific level. The spatial and temporal resolution of most data for North American climate and *O. princeps* is better than for *Ochotona* species worldwide, which likely hampered interspecific analyses. *O. princeps* has disappeared from warmer, drier sites (Galbreath et al. 2009, Beever et al. 2011, Stewart et al. 2017) while not adapting body size in response to warmer temperatures across their range or through time. While we

find evidence for some local adaptation to climate, specifically precipitation, the pace of climate change may be too much for local adaptation. Body size evolution is shown here not to be a universal response to global warming, even among temperature-sensitive taxa.

Chapter 2

Pikas are picky: Isotopic niche conservatism in the American pika

over space and time

Marie L. Westover[1], Kelly A. Lizewski[1], Kelly B. Klingler[2,3] and Felisa A. Smith[1]

[1]Department of Biology, University of New Mexico
[2]Department of Biology, University of Nevada, Reno
[3]Ecology, Evolution, and Conservation Biology Program, University of Nevada, Reno

Abstract

Anthropogenic climate change is influencing the ecology and distribution of animals. Pikas are considered model species for studying the effects of climate change on small alpine mammals and have already experienced multiple extirpations within the southwestern part of their range. However, what drives these extirpations is unclear; abiotic factors such as temperature and precipitation alone may not be sufficient to explain recent declines in pika distribution. We investigate the role of diet by characterizing the isotopic carbon and nitrogen niche of pika populations across their range and over historic time. We find pika isotopic diet to be remarkably invariant across both space and time, suggesting that they specialize on a subset of available forage. We do find a small, but significant seasonal difference in $\delta^{13}C$ consumption, which may be explained by microbial enrichment of haypiles they eat during the winter and early spring. Environmental factors explain some of the small isotopic variation across the pika's range. We conclude that the constrained isotopic dietary niche of pikas may make

them particularly sensitive to climate shifts and contribute to range declines as alpine vegetation shifts in response to a warming climate.

Introduction

Climate change is disrupting species and communities worldwide through range shifts, local extirpation and population declines (Beever et al. 2003; Parmesan and Yohe 2003; Pearce-Higgins et al. 2010). While there are now multiple studies documenting latitudinal and elevational shifts in response to climate change (e.g., Moritz et al. 2008; Lennoir and Svenning 2015), the mechanisms underlying these distributional changes are not as well understood (Chen et al. 2011). The specific mechanisms are likely to be diverse, and may include factors such as physiological limits, drought stress, and reductions in food sources (Cahill et al. 2012). In this contemporary era of climate change, a synoptic understanding of the mechanisms influencing species distributions is more pressing than ever (Cahill et al. 2012; Wisz et al. 2013; Rapacciuolo et al. 2014).

Anthropogenic climate change has altered geographic ranges for many species (Parmesan and Yohe 2003; Moritz et al. 2008; Thomas 2010; Chen et al. 2011; McCain and King 2014). A wide variety of taxa have expanded their ranges poleward and/or upslope in elevation, consistent with expected responses to warming temperatures (Parmesan and Yohe 2003; Hickling et al. 2006; Moritz et al. 2008; Tingley et al. 2009, 2012; La Sorte and Jetz 2010, 2012; Chen et al. 2011; Lenoir and Svenning 2015). Low latitude and low elevation, or "trailing edge" extirpations are also common, impacting nearly half of plant and animal species surveyed (Wiens 2016). Species are tracking their climatic niche through distributional shifts, but many populations appear unable to keep

pace with climate change and succumb to local extinction. (Thomas 2010; Beever et al. 2011; Wiens 2016; Panetta et al. 2018).

Temperature and precipitation often determine species distributions (Grinnell 1929; Andrewartha & Birch 1954; Thomas 2010; Lesica and Crone 2017), but biotic interactions such as food availability, predation, competition or mutualisms are also important contributors (Hutchinson 1957; Guisan and Thuiller 2005; Wisz et al. 2013; Louthan et al. 2015). Potential mechanisms behind climate-induced distributional shifts and local extinctions include temperature or drought stress, as well as changes in the strength and direction of biotic factors (Tylianakis et al. 2008; Blois et al. 2013; Cahill et al. 2014). For example, habitat-specialists are limited by the availability of suitable habitats and vegetation communities, which may themselves be constrained by climate (Van der Putten et al. 2010). While species interactions are more commonly implicated as a proximate cause for local extinction, the extent to which climate change is impacting animals directly or indirectly through exacerbating changes in biotic interactions is not well known, and deserves increased investigation (Guisan and Thuiller 2005; Sexton et al. 2009; Anderson 2013; Cahill et al. 2014).

One way that climate change can cause distributional shifts and local extinction is by altering food webs. Reduced food availability, in particular, was identified as the most common proximate cause of climate-related extirpation (Cahill et al. 2014). Temperature changes can alter the availability and abundance of food species, thus initiating indirect impacts on the distribution and abundance of consumers (Pörtner and Farrell 2008; Graham et al. 2009; Stirling and Derocher 2012). Climate change can also rearrange food webs by causing the loss or decline of species in a community, which can lead to changes

in ecosystem function (Petchey et al. 1999; Lurgi et al. 2012). Reduction in food availability or quality may be an under-appreciated mechanism behind climate change related extirpations and population declines.

Here, we examine the diet of a climate-sensitive alpine mammal through space and time to test the hypothesis that climate-mediated changes in forage are contributing to extirpations. Pikas *(Ochotona princeps)* are small, cold-adapted lagomorphs that have experienced well-documented extirpations and range contractions due to contemporary climate change (Beever et al. 2003, 2011, 2016; Wilkening et al. 2011). Local extirpations across their range, including parts of the southern Rocky Mountains, Great Basin, and Sierra Nevada, are associated with warming temperatures or decreased precipitation in the past few decades (Erb et al. 2011; Beever et al. 2016; Stewart et al. 2017). Additional studies suggest forage availability and quality may be the primary factors influencing pika occupancy and persistence (e.g., Rodhouse et al. 2010; Ray et al. 2016). Pikas appear to selectively occupy sites with higher forb cover, and lower graminoid cover (Rodhouse et al. 2010; Ray et al. 2016) and their presence and persistence in multiple environments is often best predicted by vegetation indexes including forbs (Erb et al. 2014; Yandow et al. 2015; Ray et al. 2016). While vegetation appears to play an important role in pika ecology, the extent that pika diet changes through space and time is not well known.

We suspect that the availability of quality vegetation and diet may be important factors influencing pika populations across their range and during the past century of climate change. Pikas independently select for two different types of diet:, summer forage which they consume immediately, and winter forage that they collect during the summer

months and cache in haypiles for use in the winter and early spring (Conner 1983; Dearing 1997). In fact, pikas may preferentially collect high quality forbs (e.g., higher nitrogen and nutrient content, greater percent phenolic compounds, lower fiber) for haypile storing, which could lead to seasonal variation in diet between the winter and summer months (Huntly et al. 1986; Dearing 1996, 1997). As central-place foragers that collect food from a small radius around well-defended territories, pikas may be particularly susceptible to changes in the composition and diversity of the local vegetation community (Huntly et al. 1986; Bhattacharyya and Ray 2015). Pika diet and haying behavior may also be affected by warming climate, through limiting the active surface time spent foraging or reducing the quality of food available (MacArthur and Wang 1974; Smith 1974; Dearing et al. 2008; Bhattacharyya and Ray 2015). As alpine vegetation communities shift due to climate change, pika dietary options may be altered, with potential consequences that further limit pika distribution.

To investigate the extent to which climate influences pika diet across this species' range and over time, we employ stable isotope analysis. Stable isotope analysis (SIA) of carbon and nitrogen is an accepted technique in animal ecology to determine approximate dietary composition (Crawford et al. 2008; Ben-David & Flaherty 2012). Different plant types differentially uptake carbon isotopes, which are then incorporated into an animal's tissues, providing a signature of what types of plants the individual ate (Deniro and Epstein 1978, 1981; O'Leary 1988). While $\delta^{13}C$ is typically used to distinguish between C_3 and C_4 plants, it can also be used to distinguish categories within C_3 plants, such as graminoids and forbs (O'Leary 1988; Farquhar et al. 1989). In addition, carbon isotopes are considered indicators of past climatic patterns such that C_3 plants demonstrate a

negative relationship between $\delta^{13}C$ and both precipitation and humidity across varying

spatial and temporal scales (Sternberg et al. 1984; Kohn 2010). Globally, plant $\delta^{15}N$

values are negatively correlated with precipitation and positively correlated with

temperature (Amundson et al. 2003; Craine et al. 2015).

Our study is unique in that we investigate isotopic diet by analyzing multiple

tissue types and museum specimens sampled at different timescales across the last

century. Stable isotopes from bone collagen capture the lifetime average of a mammal's

diet (Ben-David and Flaherty 2012). Analysis of fur can be used to study diet at the time

when fur growth occurred and thus characterize seasonal variation (West et al. 2004;

Cryan et al. 2004; Chambers and Doucett 2008). Seasonal molts are easily

distinguishable in pikas; the summer molt typically begins in late June or July and is

shorter and lighter in color than the winter molt, which begins in September and remains

through much of the year (Howell 1924; Krear 1965)(Fig. 2.5). Rates of carbon isotope

turnover in pika fur specifically are not known, but are likely ~48 days (Tieszen et al.

1983). From this, we are able to investigate if pikas consume different isotopic diets for

summer forage (via fall-onset molt) and haypiles and/or spring forage (via summer-onset

molt) (Fig. 2.5). Our study is the first to document the American pika's isotopic dietary

niche. It is unique in that we compare historical pika diet spanning the early twentieth

century with modern diets of extant populations, as well as comparing seasonal diets.

We hypothesize that climate change may impact pika populations through

reductions in dietary quality, which could further limit their distribution via several

mechanisms including higher rates of overwinter mortality due to insufficient haypiles or

the forced retreat upslope where high quality forage may fail to exist. We predict that if

climate influences pika dietary niche, the isotopic diets of populations will reflect environmental differences through space and time. Based on global isotope trends in plants, we predict that pika population δ^{15}N values will be negatively correlated with precipitation and positively correlated with temperature (e.g., Craine et al. 2015). We predict that populations in warmer, drier areas will have isotopic diets that are more enriched in ^{13}C, due to increased water stress of plants and increased graminoid consumption relative to forbs (Ehleringer and Cooper 1988; O'Leary 1988; Farquhar et al. 1989; Tieszen 1991). Since North America has warmed an average of 1.5°C since the beginning of the 20th century, we expect that more recent pika populations will have isotopic dietary signatures of higher δ^{13}C associated with higher temperatures and increased drought stress relative to more historical populations (Pachauri and Meyer 2014). Populations along the trailing edge of the species' range (low elevation, low latitude) are likely to show the strongest initial responses to warming climate, as they tend to sit on the boundary of a species' ecological limits (Hampe and Petit 2005; Sexton et al. 2009). We therefore predict that populations at the trailing elevation and/or latitudinal edge will have distinct isotopic diets with higher δ^{13}C values, indicating less nutritious diets and increased environmental stress, compared to more central populations. As pikas are known to preferentially cache more nutritious forbs for winter consumption, we expect that the summer-onset molt will have lower δ^{13}C values, reflecting a more forb-rich diet than fall-onset molt (Dearing 1997).

Methods

Study Design
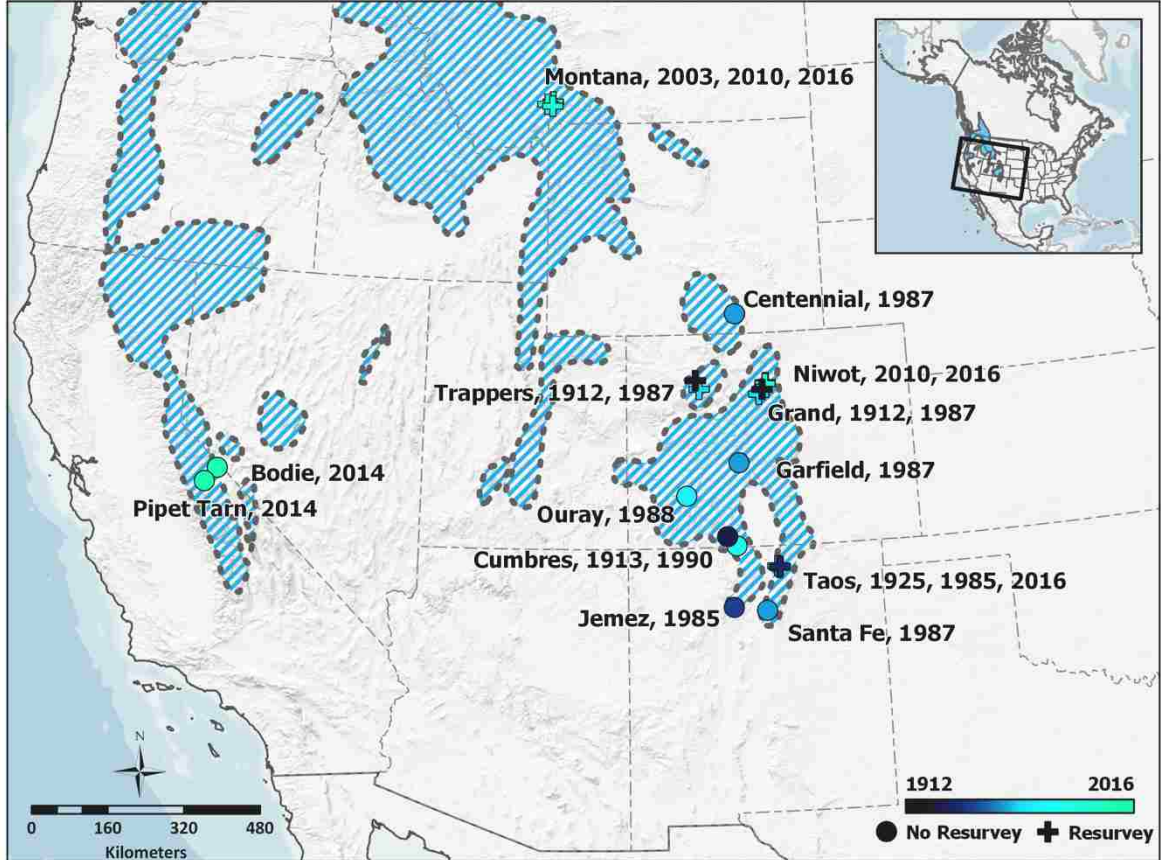
Figure 2.1. Locations of *Ochotona. princeps* populations sampled for SIA. The distribution of *O. princeps* is outlined and hatched in blue (IUCNredlist.org). Circles denote locations of populations that were sampled from one time period, and crosses denote locations that were sampled multiple decades for temporal comparison. Darker colors indicate earlier years of sampling, and lighter colors indicate more recent sampling. Years of sampling are indicated next to the population names on the map.

We investigated isotopic dietary trends in pikas across their range and historical time using museum collections, in addition to modern field-collected pika fur (Appendix 2 Fig. 1). Collaborators supplied fur samples from pikas that live-trapped for other studies in 2003-2014. All specimens were caught during the summer months of June to September. We grouped pikas into "populations," defined as individuals (n=8-26)

collected from the same locality (e.g. the same mountain massif with no valleys or major rivers separating individuals) within three years of each other. Typically, populations were collected in the same summer with the same location reported on specimen tags. To investigate isotopic trends across their range, our pika specimens range in latitude from 35.8 to 45.4 N (Fig. 2.1, Appendix 2 Table 1).

To compare trailing edge population isotopic diets to central populations, we included specimens from the southernmost pika populations (Jemez and Santa Fe), as well as lower elevation and comparatively xeric sites. We analyzed bone samples (n=195), as well as summer-onset and fall-onset molts (n=203, 278) for δ^{13}C and δ^{15}N isotope composition (Appendix 2 Table 2). We used GeoLocate (http://www.geo-locate.org/) software and Google Earth (https://www.google.com/earth/) to determine latitude and longitude from recorded location data on specimen tags when GPS coordinates were not recorded. Our populations ranged over a century from 1912 to 2016, including six populations that were surveyed across multiple time periods (Appendix 2 Table 4). Thus, in total we analyzed 21 distinct spatiotemporal pika populations from 13 geographic locations across a century.

Fur

We were able to obtain both fur and bone from museum specimens for 13 populations, and fur alone from eight live-trapped populations (Appendix 2 Table 4). Since pika specimens were all collected in the summer, we were able to take advantage of molt lines to characterize seasonal diet variation. For museum specimens, we sampled small clumps of fur (~1-2g) with tweezers and scissors from both sides of the molt line, near the shoulder for summer-onset fur and the rump for fall-onset fur to analyze seasonal

variation in isotope ratios (Fig. 2.5). We analyzed paired summer-onset and fall-onset molts for 14 populations. The summer-onset molt and previous year fall-onset molt were usually easily distinguished, but if not then we sampled only fall-onset molt. For pikas from Pipet Tarn and Bodie, we collected a small hair sample (~2.0 cm x 1.0 cm square patch) using scissors on the dorsal side of the animal near the rump. Additional collaborators pulled a small amount of fur from the rump of pikas at Niwot Ridge, Colorado and Montana using tweezers.

We rinsed fur samples in 2:1 chloroform methanol two times before drying for at least 24 hours in a fume hood. We weighed fur samples to 0.5-0.6 or 0.9-1.0mg depending on the amount of available material and wrapped in tin capsules for SIA. All isotope ratio analysis for fur, bone and plant materials was completed at the Center for Stable Isotopes at the University of New Mexico. Isotope ratios were quantified using a Thermo Scientific Delta V Plus mass spectrometer with a dual inlet and Conflo IV interface connected to a Costech 4010 elemental analyzer. Analytical precision was estimated via repeated measurements of reference materials calibrated to internationally accepted standards; within-run standard deviation for all reference materials was ≤ 0.2‰ for $\delta^{15}N$ and ≤ 0.04 for $\delta^{13}C$‰.

Bone collagen

We analyzed bone collagen from nine modern and four historical populations (Appendix 2 Table 1) to study the lifetime average of pika isotopic diet. We collected 25-100mg bone samples from a rib, or bone collagen samples from samples of ribs when available, or taken from the condylar process with a low speed dremel tool if post-cranial skeleton was unavailable. We placed samples in glass vials with foil-lined caps and

demineralized them in 0.25 HCL for 24-72 hours. We rinsed samples in DI water (x3) and then bathed in 2:1 chloroform methanol for 24 hours three times, rinsing with DI water 6-8 times in between each chloroform methanol bath. After the final DI water rinse, we moved the samples to micro-centrifuge tubes with the caps secured closed with parafilm and two small holes created in the cap for moisture to escape. We freeze-dried samples for at least six hours, and then weighed out 0.9-1.0 mg samples for SIA as described above.

Plants

We analyzed plants from seven localities in order to estimate pika diet composition (collected 2014-2016, n=128, Appendix 2 Table 3). Plant collection locations included the Sangre de Cristo Mountains in northern New Mexico, the Rocky Mountains near Niwot Ridge, CO and Emerald Lake, MT, as well as two localities in the Sierra Nevada Mountains in California (Pipet Tarn and Cabin Slope), and span from latitude 35.8018N to 45.41100N and elevations from 2609 to 3722m. Plant collection sites align with contemporary fieldwork locations. In the Sangre de Cristos, we collected representative plant samples from within 5m of pika-inhabited talus from locations within the Pecos Wilderness, Columbine Hondo Wilderness and Latir Peak Wilderness. We sampled vegetation including roots and flowers when possible and transferred specimens to a plant press for drying and identification at the Museum of Southwestern Biology Herbarium. Representative plant samples from the Sierra Nevada Mountains were collected from Pipet Tarn and nearby Cabin Slope at the talus-vegetation interface of pika-occupied territories. Plant samples from Niwot Ridge and Emerald Lake came from vegetation growing within 10m of a pika haypile (see Bhattacharyya and Ray 2015). We

stored dried plant samples in coin envelopes until processing. For stable isotope analysis, we preferentially selected plant genera that were common across different sampling localities and belonged to one of three main functional groups: forb, woody and graminoid. We cleaned plant samples with DI water and paper towels to remove dirt, dried them in an oven at 40°C overnight and weighed 3.5-3.6mg samples (based on 2.9-3.0mg test run not having enough nitrogen content) before isotope analysis as described above.

Climate

We obtained climate data specific to the year and location of each population from ClimateWNA software, which adjusts for elevation lapse rates (http://www.climatewna.com/,Wang et al. 2016). We analyzed the mean annual temperature, mean annual precipitation, and relative humidity to determine the effects of climate on pika bone isotope values (Appendix 2 Table 2). To study the relationships between climate seasonality and seasonal differences in fur, we calculated temperature seasonality as the difference between average summer temperature and average winter temperature. We generated precipitation and relative humidity seasonality variables by subtracting seasonal averages from the annual total precipitation and relative humidity annual mean values.

Statistical analyses

We calculated the mean and standard deviations for $\delta^{13}C$ and $\delta^{15}N$ values of each population's winter fur, summer fur and bone samples. We performed all statistical analyses in R (R Core Team, 2016), and calculated standard ellipse areas (SEA) as a quantitative measure of isotopic niche size using the R package SIBER (Jackson et al.

2011). We corrected for the increase of $\delta^{13}C$ in the atmosphere since nuclear testing (Suess effect) by applying the following equation: if younger than 1960, (2016-year)*(-0.022), if between 1860 and 1960, (1960-year)*(-0.005)-1.21, thus standardizing all $\delta^{13}C$ values to 2016 (Chamberlain et al. 2005).

To determine the relationships of climate and geography to pika isotopic dietary niche, we ran univariate linear regressions and multiple linear models between selected climate variables and population mean $\delta^{13}C$ and $\delta^{15}N$ values from fur and bone (see Appendix 2 Table 3 for full list of models). Since many climate variables are related to each other, we removed those with correlations of $r^2 > 0.5$ to other variables, keeping the variable with a higher r^2 in a univariate model, before running multiple linear models. We used AIC to select the most explanatory models for each isotope and pika tissue sample type.

Since the range of temperature and precipitation may also influence the breadth of pika isotopic dietary niche, we examined if climate seasonality variables correlated with the SEA of pika population bone and fall-onset fur isotopes. To investigate isotopic trends in pika populations over historical time, we calculated the difference between historical and most recent population mean $\delta^{15}N$ and $\delta^{13}C$ values. We studied shifts in isotopic composition over seasonal time by calculating the differences in $\delta^{13}C$ and $\delta^{15}N$ from summer onset and fall onset fur molts with student's t-test. To test whether seasonal changes in weather contributed to seasonal differences in fur isotope values, we compared the magnitude of average seasonal differences in $\delta^{13}C$ and $\delta^{15}N$ of populations with temperature, precipitation and RH seasonality.

We used ANOVA to determine if plant functional types (forb, graminoid and woody) have distinct $\delta^{13}C$ and $\delta^{15}N$ values, which could then inform our ability to determine what proportions of plant types pika population diets are comprised of. To explore how climate may directly impact plant isotopic values, we ran linear mixed effects models using *lme4* (Bates et al. 2015) with climate variables as fixed and plant functional type as random effects. Data limitations precluded estimating dietary proportions of pika populations with mixing models (Stock et al. 2018).

Results

Environmental variables

Environmental variables, rather than geography, tend to be associated with pika stable isotope values. Pika population $\delta^{13}C$ and $\delta^{15}N$ isotope values do not uniformly meet expectations set by global isotope trends. Moisture-related variables of relative humidity (RH) and precipitation were consistently correlated with $\delta^{13}C$ and $\delta^{15}N$ isotope values at both annual and seasonal time scales for fall-onset molts and bone. The best single climate variable was relative humidity of the year prior to collection, which demonstrates a negative relationship with $\delta^{13}C$ mean population values, as expected (Table 2.1, Fig. 2.2). Fall onset fur, but not summer onset fur or bone, conformed to our predictions that $\delta^{15}N$ would correlate negatively with moisture (Appendix 2 Table 2). Bone $\delta^{15}N$ was positively correlated with temperature, but contrary to our expectations, this metric increased instead of decreased with precipitation (Appendix 2 Table 2).
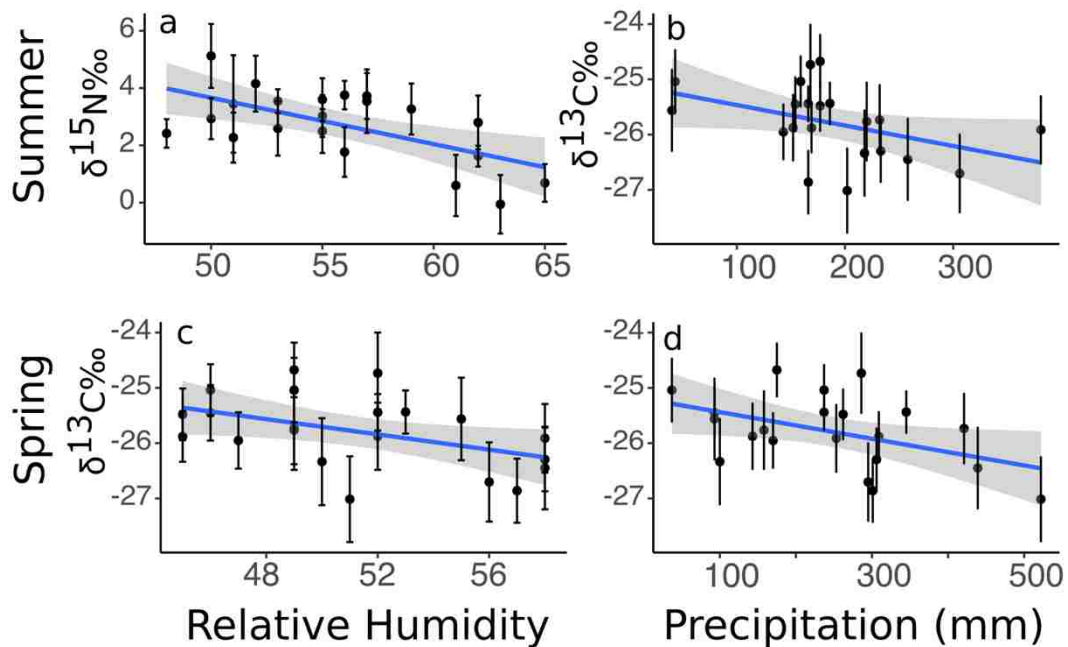
Figure 2.2. Fall-onset pika fur stable isotope values are negatively correlated with seasonal climate variables from the year prior to collection. Dots show the population mean isotope values, and lines indicate one standard deviation. A) Pika population $\delta^{15}N$ values are negatively correlated with average summer relative humidity ($r^2 = 0.35$, p < 0.001, Table 1). B) Summer precipitation is negatively correlated with average $\delta^{13}C$ of pika populations ($r^2 = 0.14$, p= 0.005, Table 1). C) Spring relative humidity ($r^2 = 0.17$, p < 0.05, Appendix 2 Table 2), and D) precipitation ($r^2 = 0.17$, p < 0.05, Appendix 2 Table 2), are significantly related to $\delta^{13}C$.

Precipitation and temperature annual variables strongly related to bone collagen $\delta^{15}N$ but not $\delta^{13}C$ (mean values for bone isotopes in Appendix 2 Table 1). Mean annual temperature and mean annual precipitation from the year prior to collection together explain most of the variation in population mean $\delta^{15}N$ values (Table 2.1, Fig. 2.3).
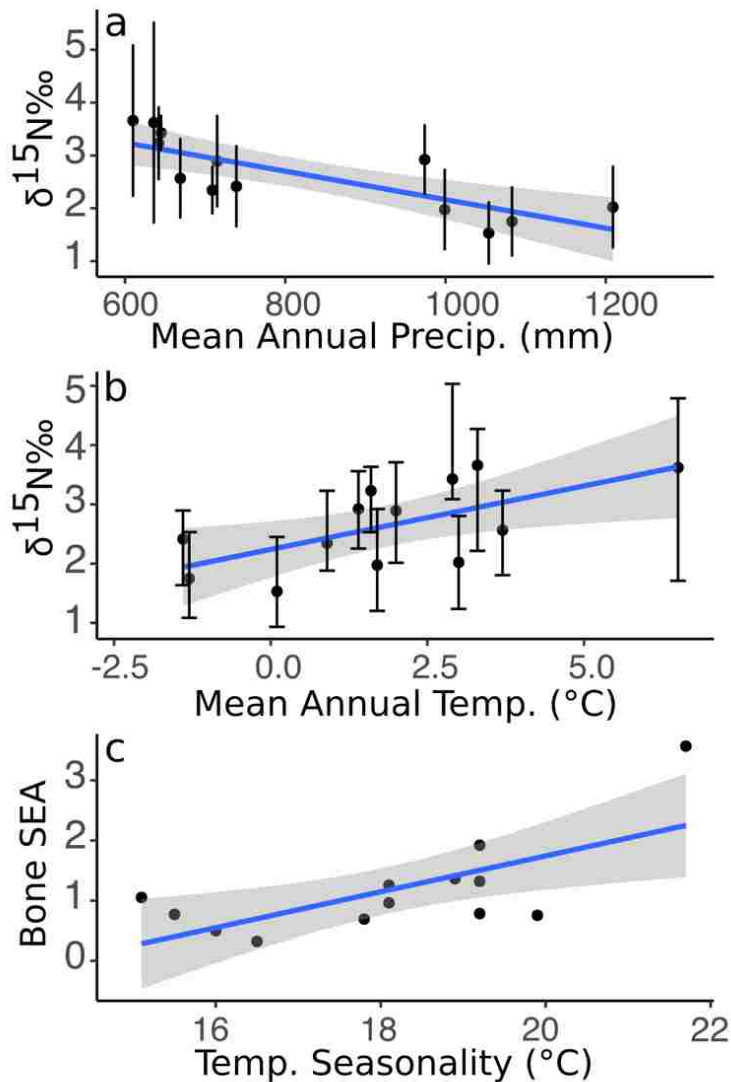
Figure 2.3. Pika bone collagen $\delta^{15}N$ and SEA values relate positively to measures of temperature and negatively with precipitation. Dots show population mean values and lines indicate one standard deviation. A) Population mean $\delta^{15}N$ exhibit a negative relationship with mean annual precipitation (mm) from the year prior to collection (r^2 =0.59, p=0.001). B) Population mean $\delta^{15}N$ values positively correlate with mean annual temperature from the year prior to collection ($r^2 = 0.35$, p= 0.001). C) Population bone collagen $\delta^{15}N$ and $\delta^{13}C$ standard ellipse area (SEA) positively correlates with temperature seasonality, which we calculated as the difference in mean summer temperature and mean winter temperature (r^2=0.41, p=0.010).
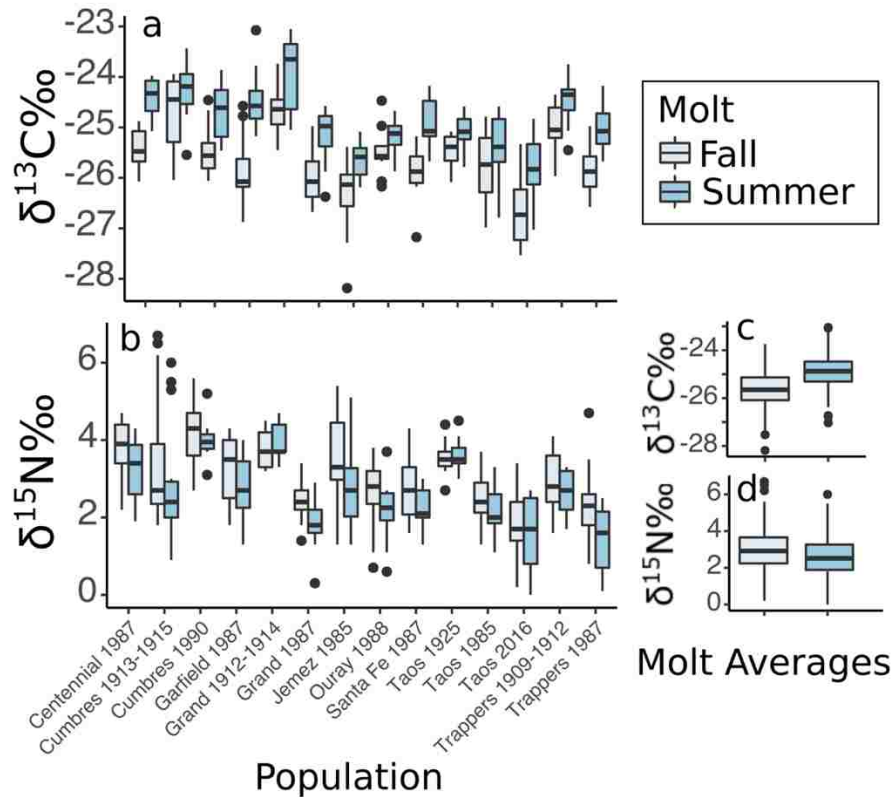
Figure 2.4. Fall-onset molt and summer-onset molt isotopic differences. Mean $\delta^{13}C$ value for summer-onset molt (-24.9‰ ± 0.7‰) is significantly higher than fall-onset molt (-25.7‰ ± 0.8‰) in populations with both molts sampled (Welch 2 sample t-test, t = 10.35, df = 401.4, p-value < 2.2e-16). $\delta^{13}C$ values are Suess-corrected to 2016. Mean summer and fall molts $\delta^{15}N$ values are not significantly different across populations (mean $\delta^{15}N$ = 2.7±1.3‰, t = -0.55, df = 24.99, p-value = 0.59).

Spring was the most relevant season to pika fur $\delta^{13}C$ values. Spring RH and precipitation negatively correlated with fall-onset fur $\delta^{13}C$ values (Table 2.1). Summer RH had a strong positive relationship to fall-onset fur $\delta^{15}N$ values, which was the opposite direction we predicted based on global $\delta^{15}N$ being negatively correlated with moisture (Table 2.1, Fig. 2.2). Since we had fewer summer-onset molt fur samples in our data compared to winter molt samples (Appendix 2 Table 4), we analyzed only the seasonal relationships of summer onset molt isotopes. Average temperature in the winter was negatively

correlated with summer onset δ^{13}C values, which is the opposite relationship we expected (Table 2.1). Summer molt δ^{15}N values did not correlate to any seasonal climate variables tested (p > 0.05, Appendix 2 Table 2). While we expected larger SEAs to be associated with greater climate seasonality, seasonality in temperature, precipitation and relative humidity did not influence pika fur SEA (p> 0.05). We found no impact of elevation or latitude on pika δ^{13}C or δ^{15}N values, seasonal fur differences, or SEA (p > 0.05, Appendix 2 Table 2).

Table 2.1. Models that best describe variability in pika population mean isotope values as ranked by AIC.

Isotope	Model[1]	Expectation	Result	R^2	P	df	AIC
Fall onset fur δ^{13}C	RH_sp_prev+ PPT_sp_prev	Decrease/ Decrease	Decrease/ Decrease	0.26	0.03	18	40.13
Fall onset fur δ^{13}C	PPT_sm_prev	Decrease	Decrease	0.14	0.05	19	42.45
Summer onset fur δ^{13}C	Tave_wt	Increase	Decrease	0.48	0.00	12	17.65
Fall onset fur δ^{15}N	RH_sm_prev	Decrease	Decrease	0.35	0.00	19	64.33
Bone SEA	Temperature Seasonality	Increase	Increase	0.41	0.03	11	29.01
Bone δ^{15}N	MAT_prev+ MAP_prev	Increase/ Decrease	Increase/ Increase	0.70	0.00	10	17.07

[1]Abbreviations are as follows: SEA= standard ellipse area, RH= relative humidity (%), MAT= mean annual temperature (°C), MAP = mean annual precipitation (mm), PPT= precipitation (mm). Seasonal variables are listed as _at = autumn, _wt = winter, _sp = spring, _sm = summer. Expectations are the direction of the relationship based on global patterns and mechanisms of δ^{13}C and δ^{15}N discussed in the introduction, and the result directions are the relationships between isotope values and climate variables in our data. Additional results are listed in Appendix 2 Table 2.

Over time

Pika populations exhibit small but consistent changes in isotope values over both seasonal and historical time. Across the 21 populations we sampled, δ^{13}C mean fall-onset fur values ranged only 2.3‰ (Appendix 2 Table 1). Seasonally, population mean δ^{13}C

values were on average 0.8‰ higher in the summer onset fur compared to the fall onset

molt (t = 3.35, df = 24.83, p-value = 0.003, mean values reported in Fig. 2.4, molts

illustrated in Fig. 2.5). Seasonal mean $\delta^{15}N$ values were not significantly different across

molts (mean $\delta^{15}N$ = 2.7±1.3‰, t = -0.55, df = 24.99, p-value = 0.59, Fig. 2.4). Climate

variables or seasonality in temperature or precipitation do not explain seasonal variation

in fur isotopic values (p> 0.05, Appendix 2 Table 2).
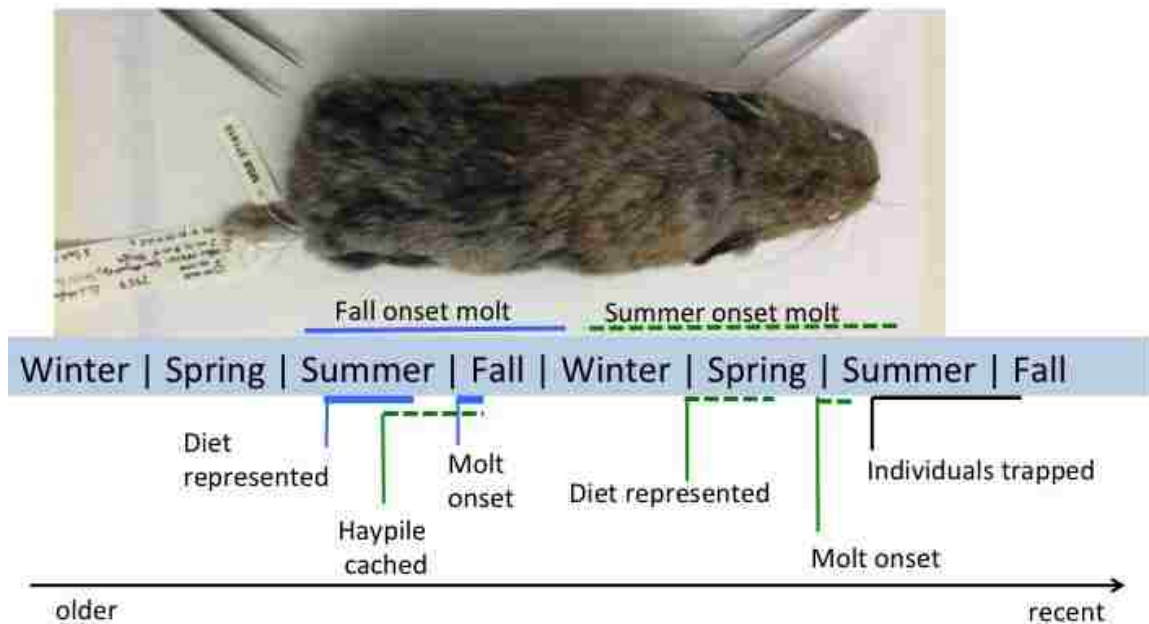
Figure 2.5. Timeline illustrating the influences of $\delta^{13}C$ and $\delta^{15}N$ signatures in pika winter and summer molts. Fall-onset molt likely reflects summer forage from the year prior to pika specimen collection. Summer onset molt may represent early spring forage or diet from haypiles cached the summer prior to collection.

However, seasonality appears to have an impact on pika bone isotopic niche

space. Temperature seasonality from the year of collection was significantly correlated

with the standard ellipse area of pika population bone (Table 2.1). Across the five

populations that were resampled over decades, mean $\delta^{13}C$ values significantly decreased

in fall onset fur for all populations and $\delta^{15}N$ values also decreased in a majority of the

resampled populations (Appendix 2 Table 1, Appendix 2 Table 5, two-sample t-tests p < 0.05). However, the direction of climate change among these resampled populations was not consistent. The population sites did not have significantly different mean annual temperature or precipitation in historical and modern samples (ANOVA, MAP df=2, F-value=2.11, Pr=0.17, MAT df=2, F-value =0.19, Pr = 0.83). We also found no significant relationships between changes in climate variables most relevant to pika isotope ratios (Spring and summer precipitation, relative humidity) and changes in stable isotope values at the resampled pika population sites over time (linear regressions, p > 0.05).

Plant isotopes

Forbs and graminoids had distinct isotope values. The mean $\delta^{13}C$ value of C_3 graminoids in our study are 2‰ higher than those of forbs and woody vegetation, which is a significant difference (mean $\delta^{13}C$ values: graminoids: -25.8 ± 1.5‰, forbs: -27.8 ±1.7‰, woody vegetation: -27.9 ± 1.3‰. ANOVA, p < 0.001, Tukey HSD, p < 0.05). Forbs have higher mean $\delta^{15}N$ values compared to other plant types (graminoid: -1.8 ± 2.4‰, forb: -0.6 ± 1.8‰, woody: -2.2 ± 2.7‰. ANOVA, p < 0.005, Tukey HSD p<0.05, Appendix 2 Fig. 4). The part of the plant (flower or leaf) sampled did not influence isotope values except for $\delta^{13}C$ in forbs, where flowers average 1.8‰ higher than leaves (t-test, p<0.05). Graminoids contain significantly lower percent nitrogen content than woody vegetation or forbs (df=2, p< 0.001). Average summer temperatures slightly affected $\delta^{13}C$ values (X^2 =7.54, p=0.006) while summer relative humidity slightly lowered $\delta^{15}N$ (X^2=9.46, p= 0.002) across plant types in linear mixed models (significance tested by likelihood ratio tests).

Pika fur isotope values do not fall within the isotopic values of plants collected, as would be expected from generalist herbivores (e.g., Stock et al. 2018) (Appendix 2 Fig. 2). The mismatched position of pika isotopic values relative to dietary sources suggests that the best estimate of pikas' trophic discrimination factor (the difference in isotopic diet and tissues) sourced from rabbits on a diet of alfalfa (Sponheimer et al. 2003a, b) is not suitable for pikas in the wild. California and New Mexico fur values display limited overlap with local dietary sources, but were still not sufficient to accurately determine proportions of food sources to diets through mixing models (Stock et al. 2018) (Appendix 2 Fig. 2). It is also possible, but unlikely given what we know of pika diets, that we failed to collect one or more isotopically distinct food sources contributing to pika diet (Dearing 1997; Bhattacharyya and Ray 2015).

Discussion

Despite the broad latitudinal, elevational, and environmental gradients represented by our study - as well as over a century of climate change- we find that pika isotopic diets are surprisingly invariant. The lack of isotopic dietary diversity among pika populations from xeric Bodie to high elevations of central Colorado indicates that even as environments change, pika diet does not (Table 2.1). Contrary to our initial expectations, we find no evidence that trailing edge or marginal populations are consuming isotopically distinct, nutritionally inferior diets. However, pikas do appear to be tracking a specific dietary niche, which could have distribution and conservation implications if climate change results in changes in alpine plant distribution.

While few stable isotopic dietary studies have encompassed the geographic and temporal range of our research, other small mammal isotopic diets are often broader than the isotopic variation found in pika diets from across their range and over a century of climate change. Other lagomorphs, *Lepus* and *Sylvilagus,* exhibited greater isotopic niche breadth and higher values in both $\delta^{13}C$ and $\delta^{15}N$ than pikas (Somerville et al. 2018). *Lepus californicus* populations show much greater population $\delta^{15}N$ variability in bone collagen within the state of Utah than pikas do across their entire range (Ugan and Coltrain 2011). Voles (Arvicolinae) showed little intra-population variation in $\delta^{13}C$ values, with similarly small standard variations to those of pikas from one sampling event at one locality (Gehler et al. 2012). Murid rodents had greater isotopic variability, and indicate a more generalist diet, from one sampled population than pikas exhibited across their range and over nearly a century (Gehler et al. 2012). In larger mammals, stable isotopes from caribou and moose spanned similar ranges in $\delta^{13}C$ and $\delta^{15}N$ to pikas but at a much smaller geographic scale, limited to Denali National park and over only two years of sampling (Ben-David et al. 2001). Thus, we conclude that pika inter-population isotopic variation is low compared to the intra-population isotopic dietary niche of other mammals.

We do find a significant, but small, influence of season on pika isotopic values across all populations. Summer onset molts are invariably higher in $\delta^{13}C$ compared to fall onset molts, with an average increase of 0.8‰ (Fig. 2.4). Animals may be expected to have seasonal changes in diet, particularly in environments with high seasonal variability. Similar to pikas, moose and caribou also exhibit a 0.5-0.6‰ enrichment of $\delta^{13}C$ in winter, attributed to seasonal shifts in diet (Ben-David et al. 2001). Alternatively,

seasonal variation in pika isotopes could potentially be attributed to seasonal changes in water availability impacting isotope values of forage, not dietary changes (Zazzo et al. 2015). While we find changes in $\delta^{13}C$ over time, our results are consistent with previous findings that $\delta^{15}N$ does not change seasonally in herbivorous mammals, suggesting that $\delta^{15}N$ may not be a good indicator of seasonal diet (Ben-David et al. 1999, 2001)(Fig. 2.4).

Pika diet is known to vary seasonally, with pikas selecting forbs with greater concentrations of secondary phenolic compounds for winter caching compared to less specific summer grazing (Dearing 1997; Varner and Dearing 2014). We therefore expected the summer molt isotopic signature to reflect increased forb consumption from haypiles with lower $\delta^{13}C$, and relatively higher $\delta^{13}C$ in fall onset molt from less selective summer grazing (Dearing 1996; Varner and Dearing 2014). However, summer onset molt is enriched in $\delta^{13}C$ compared to fall onset molt, which is the opposite trend we would expect if the isotopes were reflecting increased forb consumption from winter hay piles (Fig. 2.4). Our results indicate that seasonal differences in pika $\delta^{13}C$ isotope ratios are not likely derived from isotopically distinct diets in summer forage and winter hay piles.

One potential explanation of seasonal shifts in pika $\delta^{13}C$ is that microbial respiration of cached hay piles result in consistent $\delta^{13}C$ enrichment of summer fur in pikas. Experimental hay piles lose mass over winter, indicating significant microbial decomposition that could alter hay pile isotopic values (Dearing 1997). More decomposed leaves tend to be moderately enriched in $\delta^{13}C$, with an average (but variable) enrichment of ~0.5‰ compared to fresh leaves (Wedin et al. 1995). However, microbial decomposition has a varied effect on C_3 plant material ranging from -6‰ to

8‰. Microbes and fungi are enriched in $\delta^{13}C$ by ~1.6 ± 0.3‰ compared to soils, so microbes that occur on hay pile vegetation may contribute to higher pika $\delta^{13}C$ values in summer molt (Dijkstra et al. 2006; Bowling et al. 2008). Therefore, we suggest that microbial decomposition of hay pile vegetation is a likely factor leading to the consistent $\delta^{13}C$ enrichment of summer onset fur compared to fall onset fur, rather than seasonal dietary differences as we originally predicted.

Plant isotope values differ seasonally, which may also be a factor influencing the small but consistent seasonal variation in pika fur $\delta^{13}C$ values. Plants seasonally discriminate less against $\delta^{13}C$ as water becomes less available, (Smedley et al. 1991; Ehleringer and Dawson 1992). Pika molt $\delta^{13}C$ should mimic the seasonal variation in plants, but we observed the opposite trend expected if pika were eating early season forage before the summer-onset molt, which would coincide with increased moisture from snowmelt (Zazzo et al. 2015). However, if summer onset molts are reflective of pikas relying more heavily on late-summer procured hay piles than early spring forage, then seasonality in alpine plant $\delta^{13}C$ could also contribute to the observed summer enrichment in pika molts.

While there was limited variation in pika isotope values across both fur and bone tissues, the variation that exists appears to be related to climate. Moisture influences pika isotope values, particularly for $\delta^{13}C$ in fall-onset fur and $\delta^{15}N$ in bone. For fall-onset fur, relative humidity and precipitation are important to $\delta^{13}C$ values at both the seasonal and annual time scales. MAP and RH have a negative effect on average $\delta^{13}C$ values, as do spring RH and PPT (Table 2.1). We attribute these trends to plants increasing carbon discrimination in environments with more moisture available (Ehleringer and Cooper

1988; O'Leary 1988; Farquhar et al. 1989; Tieszen 1991). Summer fur $\delta^{13}C$ values relate to winter temperatures in the inverse direction from what we initially predicted if water stress in plants results in higher $\delta^{13}C$ (Table 2.1). However, higher winter temperatures lead to reduced snow accumulation and increased precipitation as rain, which could provide more moisture for early spring forage and possibly explain this unpredicted result (Stewart 2009). We predict that under future climate change, pika populations in areas that experience decreased precipitation and relative humidity will eventually have higher $\delta^{13}C$ values in fur.

Herbivore $\delta^{15}N$ isotope values can be challenging to interpret because plants have high $\delta^{15}N$ variability and multiple mechanisms influence $\delta^{15}N$ values (Kielland et al. 1998; Ben-David et al. 1998; Craine et al. 2015). In our study, precipitation and temperature correlate most strongly with bone collagen ^{15}N. Previous studies on leporids also found positive relationships of bone collagen $\delta^{15}N$ with temperature (Ugan and Coltrain 2011; Somerville et al. 2018). We report, as other studies have, a negative relationship between precipitation and $\delta^{15}N$ of pika bone collagen, suggesting that water stress may have an impact on pika bone collagen $\delta^{15}N$ values (Cormie and Schwarcz 1996; Somerville et al. 2018)(Table 2.1).

While overall populations from low latitudes and elevations were no different isotopically from more central populations, pika fur from our most arid site, Bodie, had significantly higher $\delta^{15}N$ values than all other sites, suggesting possible water or nutritional stress (Appendix 2 Fig. 1). In addition, bone mean $\delta^{15}N$ values are negatively correlated with MAP across the species' range, indicating that precipitation has a significant impact on lifetime isotope values (Fig. 2.3). Plants grown in arid

environments tend to have lower nitrogen content, perhaps adding to nutritional stress of herbivores (Sealy et al. 1987; Cormie and Schwarcz 1996). While pikas still occupy the atypical, sagebrush dominated habitat of Bodie Hills in eastern California, pikas from similar sites nearby have become extirpated within the 20th century and as recently as 2015, providing further evidence that pikas in this habitat are under stress (Stewart et al. 2015; Nichols et al. 2016). Our data offer support to the hypothesis that the isotopic fractionation of nitrogen in animal metabolism is larger in arid environments (Schoeniger & Deniro 1984; Ambrose & DeNiro 1986, but see Cormie & Schwarcz n.d.; Murphy & Bowman 2006). With this in mind, pikas from Bodie are likely under water stress compared to other populations. If pikas become extirpated from Bodie in the near future, analyzing $\delta^{15}N$ may be a way to predict which pika populations are at greater risk of extirpation due to a combination of nutrient and water stress.

Throughout their range and across time, pikas appear to be strict C_3 specialists, which may one day pose challenges for pika conservation. C_3 plants, including C_3 graminoids, have higher nutritional quality compared to C_4 plants (Barbehenn et al. 2004). Multiple pika species appear to be averse to consuming C_4 plants, even when they are available in the environment (Ge et al. 2012). *O. curzoniae*, the only other pika species to have its isotopic niche documented, also consumes an overwhelmingly C_3 based diet that varies little across regions of the Tibetan Plateau (Yi and Yang 2006). The expansion of C_4 grasses in the late Miocene coincided with mass extinction of pika genera and a severe range contraction of remaining pika taxa to the C_3 dominated refugia of alpine areas in Asia (Ge et al. 2012). C_4 plants are well adapted to arid environments, and thus may expand further into alpine environments with increasing temperatures and

aridity (Sage and Kubien 2003; Angelo and Daehler 2013). Thus, pika aversion to C_4 plants may increasingly impact their distribution and abundance.

Our study, by identifying the American pikas' isotopic dietary niche, illustrates that dietary inflexibility may limit pika populations. Being a small hindgut herbivore is energetically challenging, and our study suggests that pikas may be physiologically restricted to a diet containing higher quality vegetation sources like nutrient-rich forbs (Geist 1974; Smith 1992; 1995 but see Varner and Dearing 2014). Climate change may precipitate nutritionally challenging environments for pikas, as increasing temperatures and drought stress can lead to lower nutrient content in plants and relative increases in less-nutritious graminoids (Barbehenn et al. 2004; Venn et al. 2014; Rosenblatt and Schmitz 2016). Such climate-induced shifts in alpine vegetation communities pose ecological consequences for pikas and other alpine mammals. Nutritional stress from climate change, with increases of graminoids and C_4 grasses in particular, may increasingly limit pika distribution in the future.

Chapter 3

Living at the edge: The importance of climate to occupancy trends at the

trailing range edge of an alpine mammal

Marie L. Westover[1], Erik A. Beever[2], Lindsey Thurman[2], and Felisa A. Smith[1]

[1]Department of Biology, University of New Mexico
[2]U.S. Geological Survey, Northern Rocky Mountain Science Center

Abstract

Populations along the trailing range edge (low elevation or latitude) of

species' distributions are positioned at the boundary of species' ecological limits,

and thus may show the strongest initial responses to climate warming. As climate

has changed over the last century, American pikas *(Ochotona princeps)* have

disappeared from parts of their range. This habitat specialist is an ideal indicator

species for studying effects of climate change because its preferred habitat (alpine

talus) is largely spared the confounding effects of other anthropogenic disturbances.

Here, we examine the factors most influential in determining *O. princeps* distribution

at the southernmost limit of its range, including climate, biogeography and forage.

We conducted extensive field surveys, documenting evidence of current pika and

past pika occupancy, used high-resolution near-surface climate data and within-

talus temperature sensors to analyze determinants of occupancy. Pika site

occupancy was best characterized by low winter vapor pressure deficit (VPD, a

measure of atmospheric moisture demand), higher grass and forb cover, and greater

talus patch size. At the southern limit of their range, pikas are more likely to have

disappeared from sites with higher winter moisture stress, and warmer mean August within-talus temperatures. Our results emphasize that if anthropogenic climate change leads to warmer, drier conditions as expected, pika distribution will likely be negatively impacted. We find a combination of biotic and abiotic factors including climate, forage, and habitat area influence species distribution at the trailing edge.

Introduction

Determining the factors that most influence the distributions of species is a central aim of biogeography, which has gained urgency in the face of anthropogenic climate change. Climate is often considered a key dimension in the niche and distribution of animals (Grinnell 1917; Andrewartha and Birch 1954; Wiens and Graham 2005). Indeed, there is abundant evidence that warmer temperatures are already causing latitudinal and elevational changes in the geographic distributions of animals, as well as local extirpations and population declines worldwide (Parmesan and Yohe 2003; Moritz et al. 2008; Thomas 2010; Chen et al. 2011; Freeman et al. 2018b; Rumpf et al. 2019). However, we lack consensus in understanding the specific mechanisms underlying observed distributional and ecological changes (Cahill et al. 2012). The mechanisms influencing species distributional limits are likely diverse, and their relative importance likely varies across taxa, space and time (Cahill et al. 2012). The changing distributions of plants, animals and pathogens hold consequences not only for natural communities, but also for human health and well-being (Pecl et al. 2017). Therefore, it is imperative to

investigate climate-related mechanisms driving distributional changes, particularly among species that stand to be most impacted by climate change.

Although direct effects of temperature and precipitation are more often thought to determine species' distributions, there is considerable debate whether climate, directly or indirectly through altering species interactions, will prove most detrimental to organisms (Wiens 2011; Cahill et al. 2012; Wisz et al. 2013; Ockendon et al. 2014; Rapacciuolo et al. 2014). For example, physiological responses to increases or decreases in temperature may cause shifts in distribution, especially at the edges of distributions where species are already near their limits (Pörtner and Farrell 2008). Extreme temperatures or droughts can increase mortality rates (e.g., McKechnie and Wolf 2010), and sub-optimal climate conditions can also have detrimental effects such as limiting reproduction (Hansen 2009). However, the indirect effects of climate change, such as limiting dispersal ability, or altering biotic interactions like competition and forage availability must be considered (Smith 1974; Wisz et al. 2013). For example, shifts in temperature or precipitation may alter animal behaviors such as time spent foraging or dispersal ability, which in turn can affect diet choice, genetic diversity, geographical distribution, and ultimately population viability (Dearing et al. 2008; Galbreath et al. 2009; Wilkening et al. 2011; Murray and Smith 2012; Smith et al. 2016b; Varner et al. 2016; Castillo et al. 2016; Mathewson et al. 2017; Beever et al. 2017). Identifying the underlying mechanisms is essential for predicting or mediating the influence of anthropogenic climate change on species' distributions worldwide.
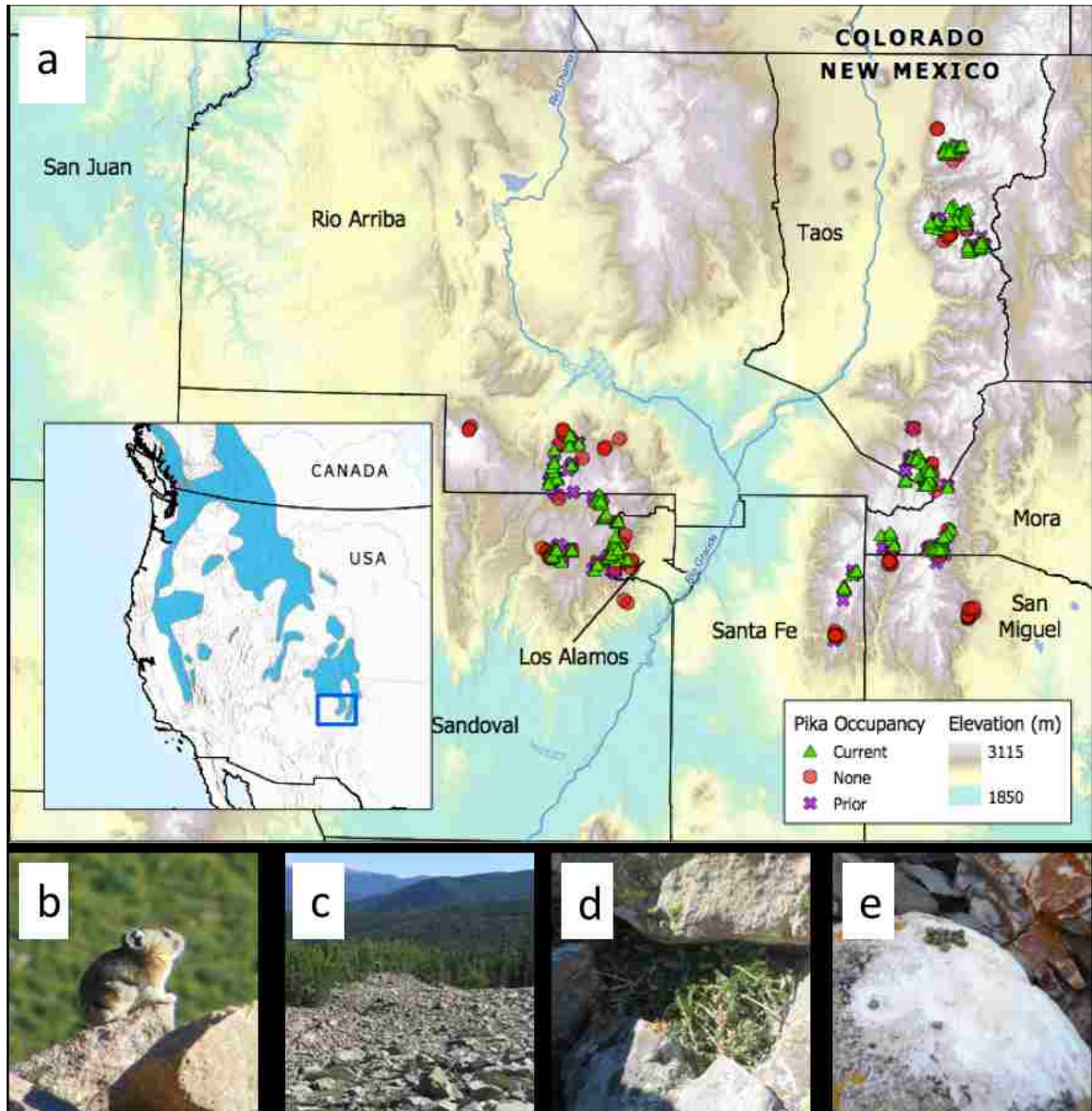
Figure. 3.1. (a) Map of pika survey sites in northern New Mexico 2016-2018. The Jemez mountains lie within Sandoval, Los Alamos and Rio Arriba counties. The Sangre de Cristo survey sites fall within Mora, Santa Fe, San Miguel and Taos Counties. A pika sighting (b) in typical subalpine talus slope habitat (c). A fresh haypile with green vegetation (d) and fresh pepper corn-shaped pika fecal pellets on a urine stain (e) also indicate current pika occupancy. Old, dry pellets may be found in rocky crevices, or just hidden under dirt and, in the absence of any recent sign, indicate previous pika occupancy.

There are likely different mechanisms contributing to species' distributional limits at the trailing and leading edges. The leading edge of a species distribution is where the distribution is expanding due to colonization into new territory, while the trailing edge contains populations where extirpation is more likely to occur (Root 1997; Parmesan and Yohe 2003; Hampe and Petit 2005; Hickling et al. 2006; Thomas 2010). Abiotic factors such as temperature extremes are historically thought to limit the leading edge while biotic processes and species interactions may be more influential at the trailing edge (Dobzhansky 1950; MacArthur 1972). However, recent research indicates that species at the trailing edge show equally strong responses to climate warming (Rumpf et al. 2019). Populations found near the ecological limits of a species' niche may have locally adapted genotypes to more diverse or extreme climatic conditions, and trailing edge populations in particular are more likely than others to have evolved in isolation (Hampe and Petit 2005; Rehm et al. 2015). Trailing edges are therefore often exceptionally important for the evolution and survival of taxa but remain relatively understudied (Hampe and Petit 2005; Rumpf et al. 2019). Therefore, trailing edge populations deserve special consideration and increased study from biogeographic and conservation perspectives.

Species occupying high elevation ecosystems are at particular risk from global warming. Alpine and arctic ecosystems form the cornerstone of conservation areas and priorities in North America and are already experiencing greater magnitude of climate change than other parts of the landscape (Gonzalez et al. 2018). While lowland species can expand their distributions higher in response to

warming temperatures, for many alpine-dwelling species an upslope movement leads to range contraction, and they may even run out of suitable habitat at the highest elevations available (Brown 1971; Hampe and Petit 2005; Moritz et al. 2008; Rowe et al. 2014). Competition from lower-elevation species dispersing into alpine terrain may lead to replacement of mountain-top species (Urban 2015). Nearly a quarter of high-elevation mammal species in the Sierra Nevada Mountains experienced range contractions over the 20th century with warming temperatures (Pachauri and Meyer 2014; Rowe et al. 2014). Globally, climate change has reduced the elevational extents of over half of mountaintop species by shifting their lower elevational limits upwards without a corresponding increase in upper elevational extent (Freeman et al. 2018a). Yet, there have been few studies on the precise mechanisms driving elevational range contractions as seen in alpine animals.

To address the need for a mechanistic understanding of the selective forces acting on species distributions, we focused on a climate-sensitive animal at the southern limits of its geographic range. Our study aims to determine what factors limit species' distribution at their trailing range edge by using the American pika *(Ochotona princeps)* as an indicator species. We conducted extensive field surveys at 353 sites across northern New Mexico from June to September of 2016 and 2017 (Fig. 3.1a), where we systematically documented sites as having current, previous or no evidence of pika occupancy. By collecting both biotic and abiotic habitat data, recording site-level microclimate, as well as incorporating multi-year climate datasets, we analyzed determinants of pika occupancy, and examined if the drivers of current and past pika occupancy are distinct. We predicted that heat and/or

moisture stress or forage availability would influence pika occupancy along the trailing edge, and also considered the effects of biogeography and within-talus temperatures. Determining the factors important for alpine mammal persistence at the edge of their range can help inform alpine conservation needs.

Methods

Study organism

Our study focuses on the ecology of an alpine mammal, the American pika *(O. princeps).* The American pika (hereafter, "pika") is a small (~121-176g) alpine lagomorph, typically found in mountainous areas of western North America (Smith and Weston 1990). However, pika persistence in non-alpine habitats such as lava fields of Craters of the Moon and low elevations in the Columbia Gorge, complicates our understanding of their ecological limits (e.g., Rodhouse et al. 2010; Varner and Dearing 2014; Ray et al. 2016; Smith et al. 2016a). These unconventional pika populations highlight the possible importance of microclimates that are strongly decoupled from regional and surface temperatures. The distribution of pikas is thought to be strongly determined by climate at multiple spatial and temporal scales (Smith 1974; Beever et al. 2003, 2011; Grayson 2005; Stewart et al. 2017). Within their range, pika habitat is typically limited to patches of broken rock talus, which they utilize for protection from extreme temperatures and predators (Hafner 1994). Pika talus habitats are conspicuous within the environment, easily identified, and stable across ecological timescales (Hafner 1994). As temperatures have warmed over the last century, pikas have disappeared from many areas, including

populations in southern Utah and what were long considered core parts of their range in the Sierra Nevada Mountains (Henry et al. 2012; Nichols et al. 2016; Beever et al. 2016; Stewart et al. 2017). Thus, pikas are considered indicator species for the effects of climate change on other alpine animals (e.g., Hafner 1994; Beever et al. 2003; Galbreath et al. 2009; Holtcamp 2010).

Here, we focus on pika populations at their southern distributional limit in northern New Mexico. By examining pika occupancy across the Jemez and Sangre de Cristo mountains, we provide a detailed understanding of pika occupancy at their southernmost limit (Fig. 3.1a). Our approach is to survey and record current and previous occupancy of pikas and characterize numerous measures of physical environment, localized near-surface climate, microclimate, and biotic factors within their habitat. We investigate which biotic and abiotic factors contribute to the likelihood of pika occupancy, as well as if the factors influencing the likelihood of pika occupancy have changed for previously occupied sites and currently occupied sites.

Surveys

We chose 353 sites in northern New Mexico to extensively survey. These sites were selected to encompass the latitudinal and elevational extent of pika habitat, as well as contain different aspects (e.g., north-facing) of each mountain range. Localities where pika specimens had been previously collected (www.gbif.org, accessed Aug. 2015) were prioritized for surveys. Potential pika survey sites were identified by mapping and collecting geographic coordinates of talus slopes and rocky habitat on satellite imagery (caltopo.com). At each site, we

conducted a thorough survey to determine if the site was currently occupied by

pikas and searched for evidence of previous pika occupancy. We then recorded

abiotic habitat properties like habitat patch size and aspect, as well as biotic factors

of vegetation and animal species present (see below for further details).

Our team surveyed each site for evidence of pikas, and categorized them as

either currently occupied, formerly occupied, or having no evidence of pika

occupancy. We utilized previously published survey methods for continuity and

comparability across regions (Beever et al. 2003, 2011, 2016). Upon reaching a talus

slope, surveyors would walk 50m transects along isoclines separated by ~15m in

elevation (Fig. 3.1c): special care was taken to search under large boulders within

the talus for pika hay piles and fecal pellets; flashlights were used to search in dark

crevices. We considered talus patches to be distinct sites if separated by >25m of

non-talus habitat at the nearest point.

Pika occupancy:

Each site was categorized as containing current, old, or no evidence of pikas

after survey. Evidence of current pika occupancy included sightings, vocalizations,

and fresh haypiles with fresh pika fecal pellets (Fig. 3.1b, c, d). Old evidence of pika

occupancy was determined by the presence of old haypiles or fecal pellets and no

evidence of current occupancy. Pika fecal pellets are distinctly spherical, and

unmistakable with any other small animal feces (Stewart and Wright 2012). In

addition, pika fecal pellets can persist in the talus environment for decades,

providing unequivocal evidence of prior occupancy (Nichols 2011; Millar et al.

2014). A patch was categorized as having no evidence of occupancy if thoroughly

searched, with all potential home ranges crossed in transects. We considered all types of pika evidence within 30m to be the same individual to avoid counting the same individual multiple times.

Physical factors:

The abiotic factors we collected during surveys included physical habitat features, patch size, and microclimate temperatures. At the location of each pika evidence, we recorded the geographic coordinates and elevation with a handheld GPS unit (WGS84, 3-7m accuracy). We recorded physical habitat variables of aspect, overall slope of the talus patch, local slope within 2m of the evidence, and number of potential home ranges (each 20m diameter area of pika-suitable rocks). Potential solar insolation of each site was calculated from the mean slope and mean aspect using the following formula: (sine(slope) * cosine(aspect)). To document the weather conditions during each survey, we recorded the time searched, percent cloud cover, wind speed, and estimated temperature.

Climate:

To record microclimate temperatures, we placed 100 small temperature sensors (Maxim iButton, GS1921G-F5# Thermochron 4k. Resolution 0.5°C, accuracy ± 1°C) within talus interstices of surveyed sites during June-September of 2016. These small temperature sensors directly record temperatures within pika-relevant talus interstices. iButton sites were selected to cover a broad geographic and elevational range within the study area. Each iButton was placed in a PVC capsule and wrapped with Teflon tape around the PVC plug to waterproof the chamber. We then wrapped wire around the iButton capsule and placed it an arm's length (40-

80cm) within an interstice of the talus slope, dangling the chamber from the wire wrapped around a rock to avoid contact with rock, dirt, or sunlight at any time of day. We recorded the location of the iButton with a GPS, as well as at least three triangulation directions so that it could be found the following year. We downloaded data from 92 iButtons collected in summer 2017, which we programmed to record the temperature every 4 hours for a full year. However, most iButtons ran out of memory after recording temperatures 342 days. Of the iButtons we collected, 66 sensors had been placed in June, 15 in July, 2 in August and 9 in September of 2016.

To test aspects of temperature, precipitation, and atmospheric moisture that could be influencing pika occupancy, we characterized the prevailing climate at each site using PRISM (Parameter-elevation Relationships on Independent Slopes Model) version AN81d at 30 arcseconds spatial resolution, available as continuous rasters of daily values (Daly et al. 2008). We selected climate predictors for an *a priori* model set to represent potential mechanisms important to pika occupancy, including seasonal metrics of heat stress, cold stress, precipitation, and moisture (Table 1). To obtain the desired climate predictors, we batch imported and stacked the PRISM raster files, then performed raster calculations on the raw daily values. The derived climate values were then extracted by sampling locations (with appropriate spatial projections) for use in analyses. Climate variables from PRISM were averaged for the seven years prior to the most recent survey year, to capture the climate that would be experienced by pikas assuming maximum pika life span (Smith and Weston 1990).

We investigated atmospheric moisture using vapor pressure deficit (VPD), as moisture may be particularly limiting in arid climates. VPD is the measurement of the deficit between saturation vapor pressure and actual vapor pressure and increases exponentially as temperature increases and humidity remains constant (Will et al. 2013). Low VPD means the air is more saturated with water, and high VPD means the air is more dehydrated (Massmann et al. 2018). To derive sub-lethal and acute cold stress and heat stress values, we calculated maximum duration of days exceeding predetermined temperature thresholds. For cold stress values, we calculated exceedances based on winter year, which we defined as October 01 through September 30. We used calendar year (January 01 – December 31) for heat stress values, since calendar year captures the entire summer season. Leap-years were accounted for in all exceedance calculations. All analyses on PRISM data were done in R version 3.4.1 using packages *raster* (Hijmans 2017), *rgdal* (Bivand et al. 2018), *tidyverse* (Wickham 2017), *heatwaveR* (Schlegel and Smit 2018), and *gtools* (Warnes et al. 2015). All code for extracting and calculating climate variables is available in a supplemental file (PRISM_data_extraction_in_R.Rmd).

Biotic factors:

Biotic factors of vegetation cover and animals present were also recorded at each survey site. To document the local vegetation at each location of pika evidence, we recorded the percent cover for the four most common species at the site within a 12m radius of the evidence. To consistently record pika forage available, we recorded the percent cover of total grasses and total forbs at each site. Plants and vertebrate animals observed at the site were identified to species, or lowest

taxonomic unit determined by the surveyor. If the surveyor was unable to identify a

plant or animal, they would photograph or sketch the organism for later

identification with the help of field guides or PIs.

Analyses

We hypothesized that aspects of climate, forage, and/or habitat connectivity

influenced current and former pika occupancy. Our predictions were that cooler,

wetter climates, (MacArthur and Wang 1974; Galbreath et al. 2009; Beever et al.

2011; Johnston et al. 2019), greater availability of forage from forbs and/or grasses

(e.g., Erb et al. 2014; Ray et al. 2016), and/or habitat size and connectivity (e.g.,

Lomolino 1986; Beever et al. 2003) would best predict pika occupancy (Table 3.1).

We used logistic regression and log-odds to determine which variables influenced

probability of a site being currently occupied by pikas, compared to all unoccupied

sites and sites determined to be formerly occupied. The predictors we tested for all

sites include: measures of cold stress, heat stress, moisture, precipitation, forage,

patch size and potential solar energy (Table 3.1). Within the subset of sites that had

within-talus microclimate records, we similarly analyzed mean August, annual, and

December temperatures, days below 4°C, inferred snow cover, and distance to

nearest patch (Table 3.3). We ran all variables as univariate logistic regressions and

ran *a priori* selected models as multiple logistic regressions (Table 3. 2). For

multiple regression models, we excluded any variables that linear correlations (r^2 >

0.5). To have equal sample sizes among models, we included only the 327 sites that

had complete data recorded. For sites that were resurveyed between years, we used

the most recent survey data in our analyses.

Table 3.1. Variables we tested for influence on pika occupancy on sites surveyed (n=327). The variables below the line are climate variables derived from PRISM. The variables above the line are non-climate variables and represent data collected directly from survey sites.

Variables	
Solar energy	
Potential solar insolation (sine(slope) * cosine(aspect))	
Biogeography	
Patch size (number of 20m diameter home ranges)	
Forage-mediated	
Forage (mean%Grass + mean%Forb)	
Forb:Grass ratio	
Mean grass	
Mean forbs	
PRISM near-surface data	
Cold stress	
Chronic cold	Mean winter temperature 1 Nov through 31 March
Sub-lethal cold	The largest number of consecutive days when Tmin <-5°C
Acute cold	Total days with Tmin <-8 °C
Heat stress	
Acute heat	Total days when > 26°C
Sub-lethal heat	The largest number of consecutive days $\geq$ 22°C
Chronic heat	Mean summer temperature °C Jun-Sept
Measures of moisture	
Chronic moisture stress	Daily VPD (kPa) min 1 June – 31 August
Growing moisture stress	Daily VPD (kPa) min 1 May – 31 Sept
Peak moisture stress	Daily VPD (kPa) min, 1 Sept -31 November
Winter moisture stress	Daily VPD (kPa) max, 1 Dec – 31 March
Precipitation measures	
Growing-season precip	Total PPT May-September (mm)
Monsoon precip	Total PPT received, 15 Jun – 31 August (mm)
Winter precip	Total PPT received 1 Dec – 31 March (mm)
Annual precip	Total PPT per year (mm)

Across a subset of 92 sites with talus microclimate temperature records, we evaluated the relative importance of temperatures, inferred snow cover, and patch isolation. iButton temperature data was retrieved from 58 occupied sites, 26 formerly occupied sites, and 7 sites with no pika evidence. We used logistic regression and AIC values to determine which microclimate variables best predicted current pika occupancy among the subset of sites. Temperature variables considered included mean annual temperature, mean monthly temperatures of August and December, as well as inferred snow cover. The mean temperature of a month was not included if there were fewer than 15 days recorded. We calculated the total number of readings below -4°C to test the impact of cold stress. To infer snow cover, we calculated the number of days where the daily temperature range was less than 2°C and the temperature reached below 2°C. Patch isolation was measured as the distance of each site to the nearest visible talus patch using caltopo.com.

Results

Of 353 sites, 177 were currently occupied, 108 formerly occupied and 65 sites had no evidence of pika occupancy. The mean elevation of occupied sites (3253m) is significantly higher than formerly occupied (2998m) and sites with no pika evidence (2933m) (Anova, $p < 0.001$, F= 10.8). Formerly occupied and no evidence sites were not found to have significantly different mean elevation (Tukey HSD, $p = 0.741$). Larger patch size (number of 20m diameter home ranges) had a small but significant positive effect on pika occupancy ($p < 0.001$, OR = 1.03,

Appendix 3 Table 1). Potential solar insolation had no discernable impact on

whether a site was likely to be occupied by pikas (p=0.823, OR = 1.05, Appendix 3

Table 1).
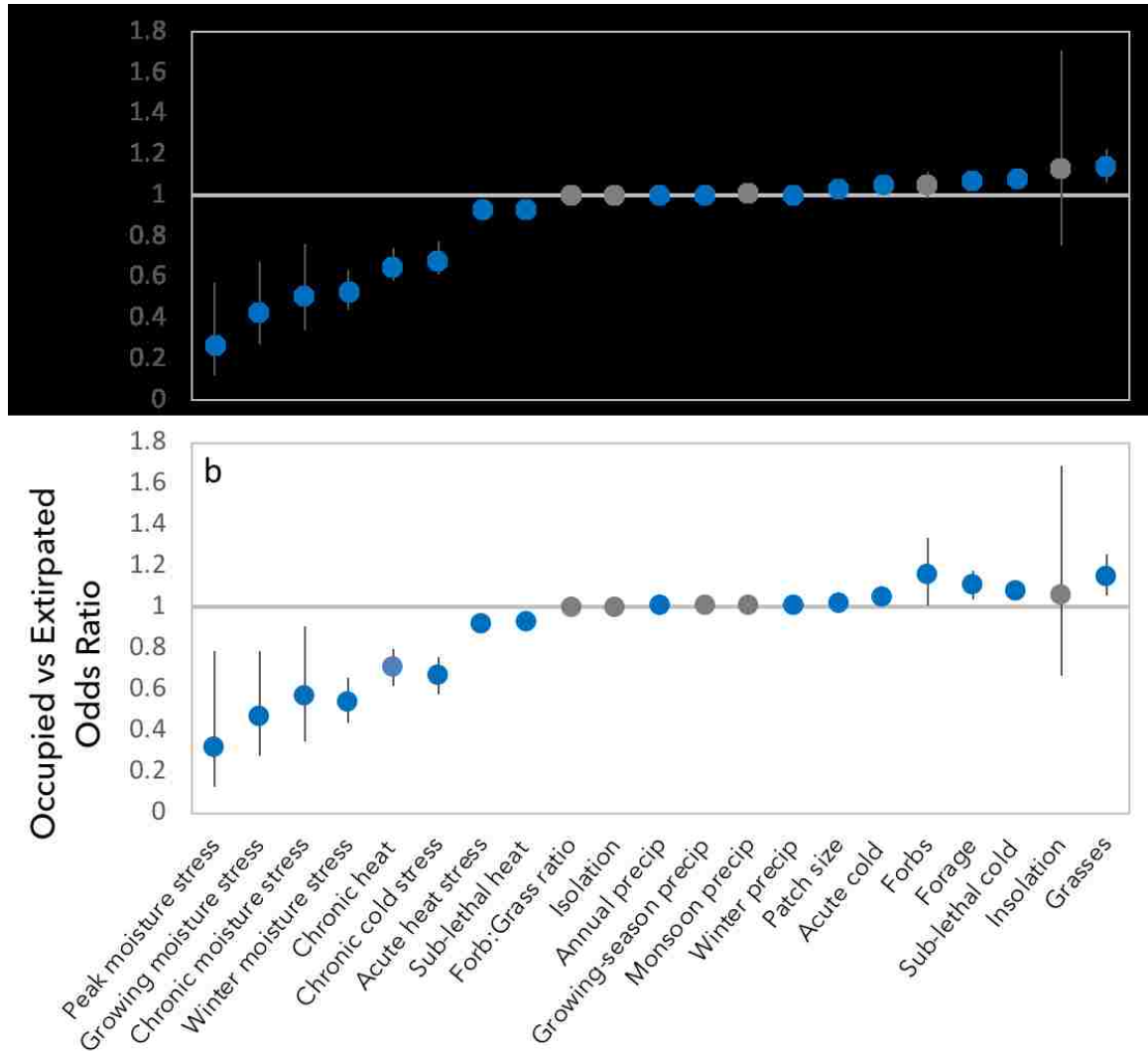
Figure 3.2. Odds ratios of variables predicting a) pika-occupied sites compared to unoccupied sites (n=353) and b) occupied compared to extirpated sites only (n=310). Dots indicate the odds ratio of each variable and lines indicate 95% confidence intervals. Blue dots indicate significant logistic regressions (p < 0.05) and red dots indicate non-significant relationships (p > 0.05). Variables with odds ratios below 1 have a negative impact on probability of occupancy, odds ratios above 1 indicate a positive impact on probability of pika occupancy.

Overall, climate factors had the greatest impacts on the likelihood of pika occupancy. Winter moisture stress (as measured by vapor pressure deficit) was the most important (as determined by AIC) predictor of pika occupancy at the southernmost edge of the pika's range ($p < 0.001$, OR = .54, Fig. 3.2a, Fig. 3.4a, Appendix 3 Table 1). Pikas were more likely to be found at sites with lower mean winter temperatures (chronic cold, $p < 0.001$, OR = 0.66, Fig. 3.2a), greater numbers of acute cold days below -8°C (acute cold, $p < 0.001$, OR = 1.05, Fig. 3.2a) and number of consecutive days below -5°C (sub-lethal cold, $p < 0.001$, OR = 1.08, Fig. 3.2a). While hot temperatures significantly decreased the likelihood of site occupancy, they were not as predictive of pika occupancy as cold temperatures (logistic regression test statistics in Appendix 3 Table 1). Acute heat ($p < 0.001$, OR = 0.93, Fig. 3.2a), number of consecutive days where the temperature reached 22°C or higher (sub-lethal heat duration, $p < 0.001$, OR= 0.93, Fig. 3.2a) and mean summer temperature (chronic heat, $p < 0.001$, OR= 0.68, Fig. 3.2a) negatively impacted pika occupancy (Fig. 3.2a). Total annual precipitation was the most explanatory precipitation variable, with a slight positive impact on pika occupancy ($p < 0.001$, OR= 1.003, Fig. 3.2a, Fig 3.4f, Appendix 3 Table 1). Winter precipitation and growing season precipitation also slightly increased the likelihood of pika occupancy ($p < 0.001$, OR = 1.01, $p=0.010$, OR = 1.005, Fig. 3.2a, Fig. 3.4e, g). Monsoon season precipitation was the only climate variable that had no effect on pika occupancy ($p = 0.118$, OR=1.005, Appendix 3 Table 1).

Warmer within-talus microclimate temperatures were most influential in determining pika occupancy among sites with temperature sensors. Mean August

within-talus temperature was the most explanatory variable, significantly decreasing the probability of pika occupancy (p < 0.001, OR = 0.56, Fig. 4.3a, Table 3.3). Higher mean annual temperature and mean December temperature also decreased pika occupancy (p < 0.001, OR = 0.64, and p = 0.011, OR = 0.72, respectively, Fig 3.4b, c). Days of inferred snow cover and number of sensor readings below 4°C slightly increased the probability of sites being occupied (p = 0.006, OR = 1.01, and p = 0.007, OR = 1.004, Fig. 3.3d, Table 3.3). However, distance to the next nearest talus patch had no significant effect on pika occupancy (p = 0.153, OR = 1.00, Table 3.3). One caveat is that our temperature sensor readings do
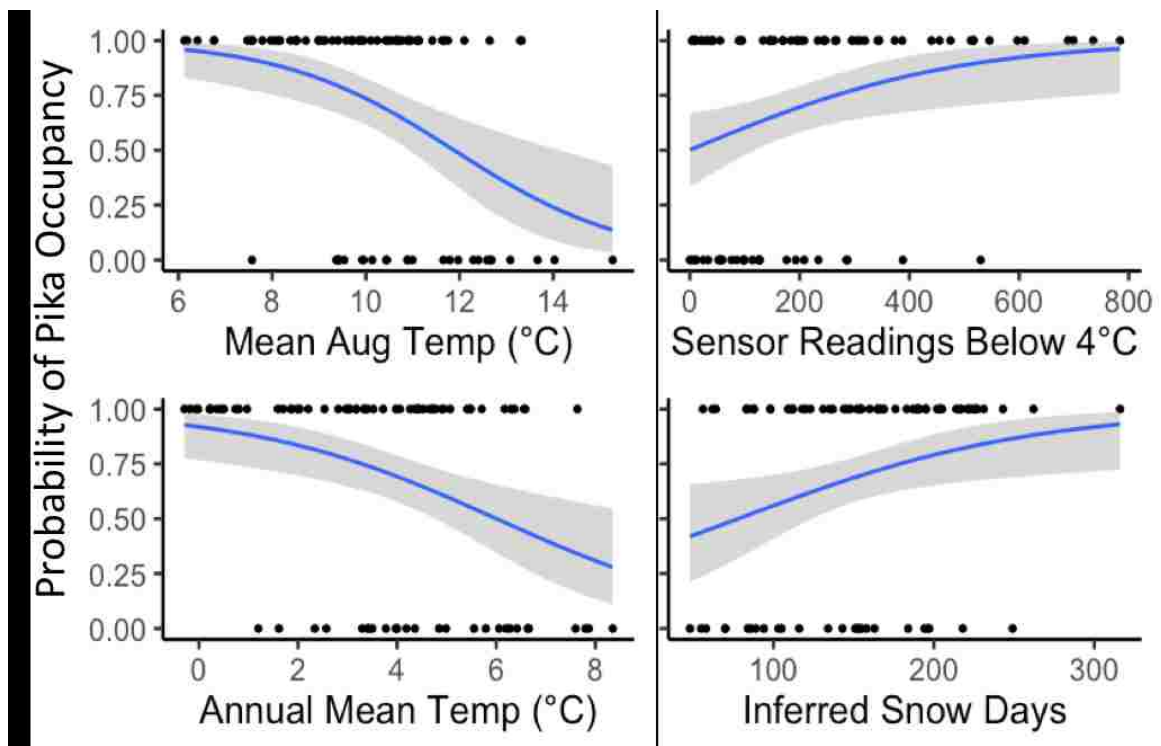
Figure 3.3. Probability of a sites being pika-occupied vs extirpated as predicted by iButton temperature sensor data. Probability of pika site-level occupancy compared to unoccupied sites modeled from iButton temperature sensor within-talus data. Gray lines indicate 95% confidence intervals. Mean August temperature (a) was the most predictive

of pika occupancy. Both high mean August and annual mean temperatures (b) negatively

impact probability of pika occupancy while inferred snow days and cold sensor readings

increase probability of pika occupancy.

not encompass the exact same overlapping dates during the summer months of

June-September, as they were placed throughout the summer of 2016. Therefore,

for a mean July, mean August and mean annual temperatures may encompass either

2016 or 2017 summer temperatures. We decided maintaining a greater sample size

of average temperature recordings would be more beneficial for describing pika

within-talus temperatures than limiting our analyses to a smaller number of sensors

placed in a short amount of time. In addition, our remotely-sensed measure of

isolation as the distance to the nearest visible talus patch could be skewed in

forested areas where small talus patches could be hidden from view in satellite

imagery and during field work.

Several of the biotic variables we tested here were important in predicting

pika occupancy. Mean grass cover had the greatest positive impact on pika

occupancy, followed by overall forage ($p < 0.001$, OR = 1.13, and $p = 0.002$, OR =

1.06, respectively, Fig. 3.2, Fig. 3.4h, i, Appendix 3 Table 1). Forb cover and forb to

grass ratio both had no significant effect on pika occupancy ($p = 0.146$, and $p = 0.804$,

Fig. 2, Appendix 3 Table 1, all significant regressions are plotted in Appendix 3 Fig.

1).

We created our multivariate logistic model suite to include models with

aspects of climate only, aspects of temperature only, biotic variables only, and

combinations of climate, vegetation cover, and physical habitat variables to predict

current pika occupancy against formerly occupied sites and sites with no evidence.

The top-ranked multivariate models included aspects of climate, forage, and habitat

connectivity. Winter moisture stress, patch size, and forage availability best

predicted current pika occupancy (all coefficients significant $p < 0.05$, null deviance

453.3 on 326 df, AIC = 382.8, Table 3.2). The second-best model performed almost

equally well; it included patch size, forage availability, and mean summer
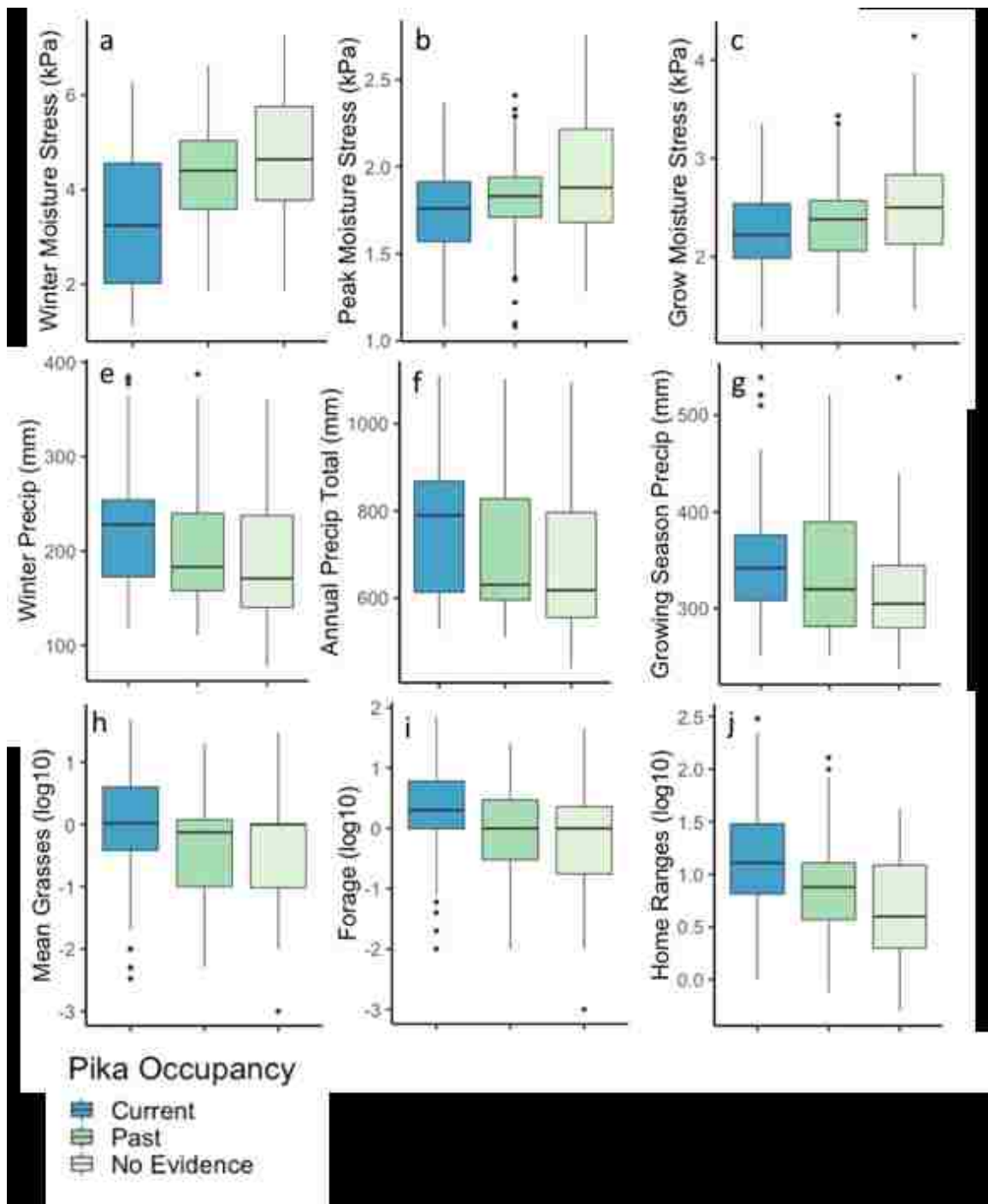
Figure 3.4. Sites with current pika occupancy had lower winter (a), peak (b), and growing season moisture stress (c) than both previously occupied sites and sites with no evidence. Currently occupied pika sites had more winter (e), annual (f) and growing season (g) precipitation. Currently occupied sites tended to have a higher percent of grass cover (h) and higher overall forage (grasses and forbs combined, i). Sites with more home ranges (j) were more likely to be currently occupied than those with old and no evidence.

temperature (p < 0.05, AIC = 383.3, Table 3.2). The other multivariate models that

were more explanatory than winter moisture stress alone each included two climate

variables. The third best model combined mean summer temperature and winter

precipitation (p < 0.05, AIC = 390.6, Table 3.2) and fourth best model included the

variables that influenced pika disappearance, comparing sites with current pika

occupancy with sites that had old evidence of pikas, were essentially the same as

those predicting current occupancy against all sites with no evidence and old

evidence. When we compared current pika occupancy to sites where pikas are

extirpated, all variables have the same direction of positive or negative influence

(Fig. 3.2b). The order of importance was largely the same as well, with a few small

exceptions. Winter moisture stress remains the most explanatory variable, and

chronic cold temperature remained the second most explanatory variable as

determined by AIC (p < 0.001, OR = 0.56 and p < 0.001, OR = 0.68, respectively, Fig.

3.2b, Appendix 3 Table 1). Although grasses are still the most explanatory positive

variable for pika occupied compared to extirpated sites, forbs also have a significant

influence (p = 0.002, OR = 1.15 and p = 0.04, OR = 1.16, Fig. 3.2b, Appendix 3 Table

1). The within-talus temperature variables have essentially the same influences on

pika occupied compared to extirpated sites as pika occupied compared to

unoccupied sites (Table 3.3). winter moisture stress and winter precipitation (p <

0.05, AIC = 405.8, Table 3.2).

Table 3.2. The highest-ranked multivariate logistic regression models were selected from competing hypotheses explaining pika current occupancy versus all unoccupied sites. ΔAIC is the difference from the top-ranked model. Multivariate models with AICs higher than univariate models were not included. P values of coefficients are all significant (p < 0.05).

Model name	Variables	AIC	ΔAIC
Moisture, space, forage	Winter moisture stress + Home ranges + Forage	382.8	0.0
Dispersal stress	Chronic heat + Home ranges + Forage	387.7	4.9
Snow and heat	Chronic heat + Winter precip	390.6	7.8
Winter recharge	Winter moisture stress + Winter precip	396.1	13.3
Winter moisture stress	Winter moisture stress	405.8	23.0
Null model		455.3	72.5

Table 3.3. We analyzed microclimate using within-talus temperature sensors in pika habitat from summer 2016-2017 (n=92). Isolation we measured as distance to nearest visible talus patch (m) using caltopo.com. Logistic regression models of currently occupied sites compared to unoccupied and formerly occupied. No multiple regression models tested improved AIC and were significant (p < 0.05).

Within-talus microclimate							
Variable	AIC	P (Wald's test)	d.f.	Odds Ratio	L95%CI	U95%CI	Log Likelihood
Mean Aug temp	103.69	< 0.001	89	0.56	0.41	0.76	-49.84
Mean annual temp	109.62	< 0.001	91	0.64	0.50	0.82	-52.81
Readings below 4°C	116	0.007	91	1.00	1.00	1.01	-56.00
Snow days	116.8	0.006	91	1.01	1.00	1.02	-56.40
Mean Dec temp	117.92	0.011	91	0.72	0.55	0.93	-56.96
Isolation (m)	120.99	0.153	91	1.00	1.00	1.00	-58.50
Null model	123.21	0.013	91	1.00	1.00	1.00	-60.60

Discussion

Our study indicates that climate has a profound impact on pika occupancy at their trailing edge in the southern Rocky Mountains (Appendix 3 Table 1, Fig. 3.2). Although temperature is often demonstrated to be a main driver of distribution for pikas and many other mammals (e.g., Beever et al. 2011; Chen et al. 2011), we find

that atmospheric moisture is more influential than temperature alone in the southernmost Rocky Mountains (Fig. 3.2). Temperature does have an important impact; after moisture stress, warmer summer and winter temperatures have the greatest negative impacts on pika occupancy (Fig. 3.2). Cooler microclimate temperatures, particularly cooler mean August temperatures, increased the likelihood of pika occupancy and persistence in our study (Fig. 3.3). However, the factors that influenced pika occupancy were complex and included both physical and biotic habitat features. Increased talus patch size and forage cover were also important factors influencing the likelihood of pika occupancy (Table 3.2). Here, we demonstrate that low atmospheric moisture and warmer microclimates have in part led to pika disappearance. Thus, warmer and drier climates in the future may have further negative impacts on pika occupancy, through impacting pikas directly as well as the forage they depend on.

High winter VPD was the single most important variable negatively impacting pika occupancy; both univariate and multivariate analyses revealed that VPD increased the likelihood of local disappearance (Table 3.2, Appendix 3 Table 1). Interestingly, a recent study also identified winter moisture as a climate feature important to pikas. In North Cascades National Park, nearly 2000 km northwest of northern New Mexico, increased snow pack duration interacting with minimum winter VPD was significantly related to pika abundance (Johnston et al. 2019). However, during the winter months, pikas are likely to be under the snow, so ambient winter VPD is unlikely directly influencing their physiology. Rather, we

suspect the significance of winter VPD reflects moisture available to vegetation at an important time.

The importance of moisture and specifically winter daily maximum VPD is a departure from typical explanations of animal distribution. Atmospheric moisture has received little attention both in climate and species distribution modeling, although it can influence biologically relevant processes including plant functioning and drought response (Daly et al. 2015). The physiological effects of VPD on plant function are generally understood. For example, stomatal closure in dry atmospheric conditions can stunt growth and even lead to plant mortality (Oren et al. 1999; Breshears et al. 2013; Will et al. 2013; Massmann et al. 2018). Many plant species distributions are likely explained by atmospheric moisture, since VPD is reportedly responsible for large scale vegetation and productivity changes (Williams et al. 2010, 2014; Konings et al. 2017). Thus, it is possible that high winter VPD impacts pikas' food supply by dehydrating plants or otherwise impacting the pika-relevant plant community.

The dehydrating effects of low atmospheric moisture can directly impact animals through physiological stress. Low air moisture can result in dehydration across the skin and mucous membranes, requiring additional water and limiting activities (Lillywhite 2006). Atmospheric moisture directly impacts animal ecology by limiting foraging and breeding activities to times of lower VPD (Ludwig 1945; Bellis 1962; Riddell and Sears 2015). Water loss can be a major factor in animal energy balance, activity time, and geographic niche (Riddell et al. 2017). Thus, VPD can influence species distributions, potentially directly through physiological

restrictions or indirectly by influencing activity time for foraging or the vegetation animals rely on. Atmospheric moisture is not frequently tested as a factor in animal distribution studies, likely due to large-scale data being unavailable until fairly recently (Daly et al. 2015). Although we suspect that atmospheric moisture is more likely impacting pikas indirectly through vegetation, further study investigating the influence of VPD on animals is an important avenue of future investigation.

Although insulation from snowpack might be an important factor in northern parts of the pika's range (Beever et al. 2011; Yandow et al. 2015), extreme cold exposure due to a lack of snowpack is less of a concern for pika populations along the trailing edge. Our study found inferred snow cover and potential snowfall, while significant, have little effect on pika population occupancy in the southern part of their range (Table 3, SI Table 1). Snow can impact pika ecology through influencing the growing season, in addition to insulating their sub-talus habitat. Pikas subsist on cached vegetation throughout the winter months, and typically need to wait until spring snowmelt to begin active foraging (Dearing 1997). Early snowmelt is associated with higher rates of survival in closely-related collared pikas *(O. collaris)* in Yukon Territory (Morrison and Hik 2007). Snowpack appears to be a less-influential variable along the trailing edge, perhaps due to warmer winters and earlier snow melt in the spring, suggesting context-dependency of climate factors influencing pika survival.

Although not as important as moisture, temperature did influence pika occupancy and persistence (Fig. 3.2, Appendix 3 Table 1, Fig. 1). This finding is consistent with previous studies of pika ecology (Beever et al. 2010; Calkins et al.

2012; Stewart et al. 2017). Rather than extreme cold temperatures being detrimental to pika occupancy (Beever et al. 2011; Yandow et al. 2015), we found both chronic cold and acute cold winter temperatures were beneficial for pikas. Here, we find that mean winter temperature was the second-best univariate model for predicting current pika occupancy, where warmer winter temperatures had a negative influence (Appendix 3 Table 1, Fig. 1). Sub-lethal cold and acute cold temperatures were also high-ranking univariate models (Appendix 3 Table 1). Cooler temperatures, including acute cold, were also found to positively predict pika occupancy across four northern mountain ranges in Oregon, Idaho, and Montana (Thompson 2017). It was somewhat surprising that hot summer near-surface temperatures were less influential than other factors in univariate models, considering our study encompassed the southernmost, warm-edge of pika distribution (Appendix 3 Table 1). However, mean summer temperature was the key climate variable in the second-best multivariate model, suggesting that summer temperatures may still play a role in determining pika occupancy (Table 3.2).

Microclimate refuge appears to be especially important to pikas in the hot summer months. Mean August temperature was the best within-talus factor predicting pika occupancy, followed by mean annual temperature (Fig. 3.2, Table 3.3). Pika populations are able to persist in more hot and arid environments where exceptionally cool thermal refuge is available (Rodhouse et al. 2010; Jeffress et al. 2013; Varner and Dearing 2014; Ray et al. 2016). It appears that pikas are less likely to occupy, and more likely to disappear from, sites where the thermal refuge available is relatively warm, especially during the warmest part of the year (Fig.

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3.3). Given the results from our study and others, adequate thermal refuge from warm temperatures seems important to pika occupancy and persistence.

Although we expected increased habitat area and connectivity to positively correlate with pika presence, we found only talus patch size influenced pika occupancy (Table 3.3, Appendix 3 Table 1). Under metapopulation dynamics and island biogeography theory, larger and better-connected habitat areas should contain more individuals (Lomolino 1986; Moilanen et al. 1998; Beever et al. 2003; Franken and Hik 2004). Pikas are a classic example of metapopulation dynamics, with subpopulations connected through dispersal events (Hanski 1998). When talus patches are small or have fewer home ranges, juveniles are more likely to disperse away from their natal patch, and conversely are more likely to disperse within their natal patch if more home ranges are available (Peacock and Smith 1997; Castillo et al. 2016). As predicted, the number of home ranges in the talus patch was positively correlated with pika presence (Fig. 3.2, Appendix 3 Table 1), and was included as a variable in the two best multivariate models predicting pika occupancy (Table 3.2). However, the distance of each surveyed site to the next nearest talus patch did not have a significant effect on whether the patch was occupied (Table 3.3). Long-term population studies would clarify the local extinction and colonization dynamics of pika populations in the southern Rocky Mountains.

Vegetation had small, but positive, effects on pika occupancy at the southernmost limit of their range. We predicted that vegetation was an important variable influencing pika ecology and evolution, based on factors related to body size evolution (Westover and Smith, *in revision*) and stable isotope dietary studies

(Westover et al., *in review*). In addition, previous studies had found that forbs and forb to grass ratio helped predict pika occupancy (Erb et al. 2014; Ray et al. 2016). We found that grass cover was the best vegetation predictor of pika occupancy (Appendix 3 Fig. 1, Table 1). Overall forage also positively correlated with pika occupancy and was included in the two best multivariate models (Fig. 3.2, Appendix 3 Fig. 1, Table 2). However, the influence of forbs alone was not significant (Fig. 3.2, Appendix 3 Table 1). This was somewhat unexpected, as forbs are more nutritious and reportedly, an important component of pika diet in the Rocky Mountains (Bhattacharyya and Ray 2015, Westover et al., *in review*). Perhaps grasses are more important than previously thought in New Mexico pika diets, or certain species of forbs are influential in pika occupancy. Other than grasses and forbs, we did not incorporate community-level aspects of biotic interactions such as competition (e.g., woodrats), predation (e.g., weasels), or parasite load, which could be important influences at the trailing edge of the pikas' range (Louthan et al. 2015).

Across the geographic range, drivers of occupancy and distribution might vary in strength and importance. Indeed, it is evident from the body of scientific studies on the American pika that distinct mechanisms are more influential to pika distribution in different parts of their range (Varner and Dearing 2014; Ray et al. 2016; Johnston et al. 2019). This idea reaches back to the foundations of evolution and biogeography, yet remains highly relevant in today's era of anthropogenic climate change (Darwin 1859; Grinnell 1917; Dobzhansky 1950; MacArthur 1972). Temperatures in western North America are projected to increase 2-3°C by the end of the 21st century, with a concomitant decrease in annual precipitation (Field et al.

2007). Since increasing temperature has an exponential increase on VPD, warming will lead to thermal effects on biota but also increasingly dehydrating effects (Will et al. 2013). According to our study, such decreasing atmospheric moisture may have the strongest detrimental impact on pika occupancy at trailing edges. As different pressures may have led to distinct local adaptations, studies should consider populations from multiple parts of species ranges to best understand animal responses to environmental change. Including more-explicit tests for the relative importance of biotic and abiotic factors driving geographic distributions and range shifts is important to understand how individual species and communities respond to climate change.
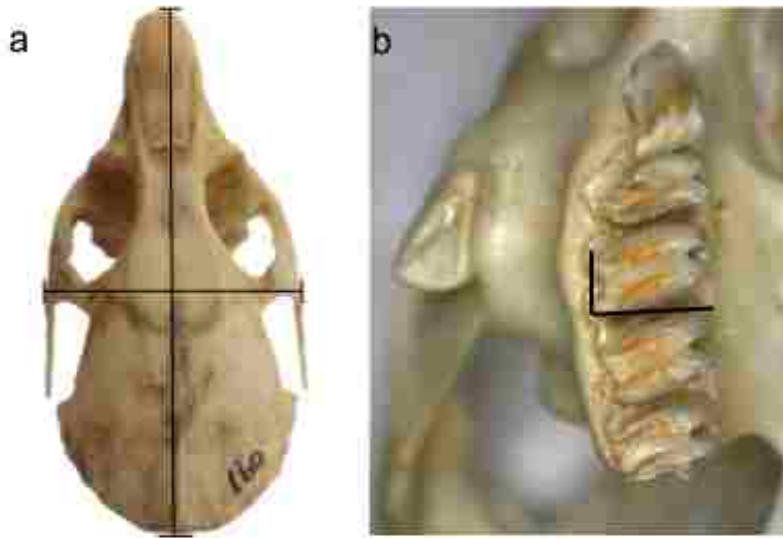
Figure 1. Measurements of *O. princeps* specimens taken with digital calipers included skull length, skull width (a), upper M1 length and M1 width (b).
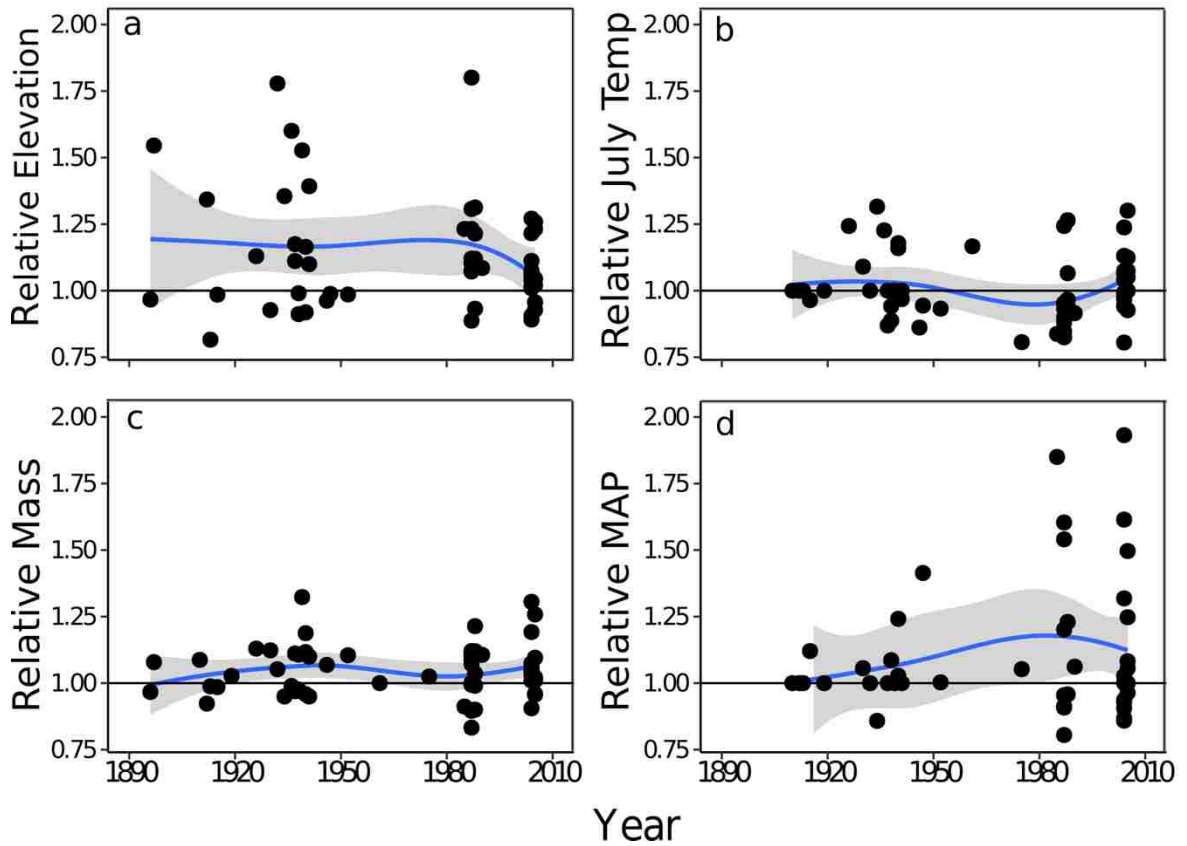
Figure 2. Mean elevation, mean mass, mean July temperature and mean annual precipitation of *O. princeps* populations over time compared to the first record at each geographic location. We plot the relative median elevation and body mass of populations for all subsequent populations. These data are fit by loess smoothing to aid visualization.

Table 1. Correlations between body measurements of *O. princeps* specimens and reported mass. We measured skull length, skull width, M1 length and M1 width with digital calipers. Total body length, hind tarsus length and mass we collected from specimen tags. We used the reported mass for 1633 specimens and we used skull length to estimate mass for 874 additional specimens used in intraspecific body size analyses. Significance: *p < 0.05, **p < 0.01, ***p < 0.0001.

Measurement	Intercept	Slope	Degrees of freedom	Adjusted r^2	Significance
Skull length	-268.06	9.73	1017	0.63	***
Skull width	-349.98	23.45	1009	0.58	***
M1 length	-10.72	122.33	1295	0.29	***
M1 width	-40.23	70.51	1295	0.22	***
Total body length	-65.17	1.19	2025	0.41	***
Hind tarsus length	-107.47	8.52	1379	0.31	***
Log10 skull length	-2.44	2.82	1017	0.64	***
Skull length + skull width	-257.23	7.33, 4.27	972	0.72	***

Table 2. Body size data for *Ochotona* species. Species included are found in Ge et al., 2012. Mean mass was calculated as the mean of mass range reported in Smith and Xie, 2008 or reported from Smith et al., 2003. *O. turuchanensis* mass was calculated by using a linear regression from the head-body length average and mean mass of other species (mean mass= head-body average*1.9 -177.61, $r^2 = 0.64$, $p < 0.0001$). Head-body average was calculated as the mean of the highest and lowest head-body lengths reported in the literature. Lifestyle (rock or burrow-dwelling) was reported in the literature. Citations: 1. Smith and Xie 2008, 2. MacDonald and Jones 1987, 3. Smith et al., 2003, 4. Smith and Weston 1990, 5. Smith, Formozov, Hoffmann, Changlin, & Erbajeva, 1990. 6. Sokolov, Ivanitskaya, Gruzdev, & Heptner, 2009 7. Fulk and Khokhar 1980, 8. Lissovsky 2003. Geographic range sizes calculated in QGIS from species range maps downloaded Sept 15, 2014, from iucnredlist.org.

Species	Mass range (g)	Mean mass (g)	Head-body length (mm)	Head-body average (mm)	Lifestyle	Citations	Species citation	Range (Log^{10} Km^2)
O. alpina	226-360	293	152-235	205.5	rock	1	Pallas 1773	5.95
O. argentata	176-236	206	208-235	221.5	rock	1	Howell 1928	2.09
O. cansus	50-99	74.5	116-165	140.5	burrow	1	Lyon, 1907	5.93
O. collaris	117-145	129	178-198	188	rock	2, 3	Nelson, 1893	6.26
O. curzoniae	130-195	162.5	140-192	166	burrow	1	Hodgson, 1858	6.43
O. daurica	110-150	130	150-210	180	burrow	1	Pallas, 1776	6.47
O. erythrotis	184-352	268	181-285	233	rock	1	Buchner, 1890	5.83
O. forresti	110-148	129	155-185	170	burrow	1	Thomas 1923	4.64
O. gloveri	140-300	220	160-220	190	rock	1	Thomas 1922	5.69
O. himalayana	120-175	147.5	140-186	163	rock	1	Feng, 1973	5.14
O. huangensis	52-108	80	125-176	150.5	burrow	1	Matschie 1908	5.55
O. hyperborea	122-190	156	150-204	161.9	rock	1	Pallas 1811	7.27
O. iliensis	217-250	233.5	203-204	203.5	rock	1	Li and Ma 1986	4.66
O. koslowi	150-180	165	220-240	230	burrow	1	Bucher 1894	3.78
O. ladacensis	190-288	238	180-229	204.5	burrow	1	Gunther 1875	5.99
O. macrotis	142-190	166	150-204	177	rock	1	Gunther 1875	6.55
O. muliensis	235	235	222	222	rock	1	Pen and Feng 1962	4.32
O. nubrica	96-135	115.5	140-184	162	burrow	1	Thomas 1922	5.76
O. princeps	121-176	157.627	162-216	189	rock	4, 3	Richardson 1828	6.11
O. pusilla	95-277	142.5	153-210	181.5	burrow	5, 3	Pallas 1769	6.38
O. roylei	130-180	155	155-204	179.5	rock	1	Ogilby 1839	5.77
O. rufescens	NA	250	150-220	190	rock and burrow	6, 7	Gray, 1842	6.05
O. rutila	220-320	270	196-230	213	rock	1	Severtzov 1873	5.44
O. thibetana	72-136	104	140-180	160	burrow	1	Milne-Edwards 1871	5.93
O. thomasi	45-110	77.5	105-165	135	burrow	1	Argyopulo 1948	5.60
O. turuchanensis	NA	152.6	158-190	174	rock	8	Naumov 1934	6.55

Table 3. Intraspecific population summaries *(O. princeps)* used in analyses. We calculated median masses for populations of nine or more individuals determined to be within nearby localities and collected within a ten-year time period. Latitude and longitude, and year represent the most common locality and year within each population of specimens. Tables of climate data and contributing specimens are available upon request from the corresponding author.

Population	Median mass (g)	Latitude	Longitude	Elevation (m)	Year	Province/state
Banff 1935-1941	125.8	50.888326	-115.641303	NA	1941	British Columbia
Banff 1988	137.0	50.911347	-115.321504	NA	1988	Alberta
Beaver 1908	127.8	38.29444	-112.40139	2685	1929	Utah
Beaver 1929-1939	143.4	38.29444	-112.40139	2685	1929	Utah
Beaver 1987	142.8	38.378118	-112.382135	3509	1987	Utah
Beaver 2005	140.0	38.44038889	-111.4829444	3307	2005	Utah
Bighorn 1987	140.0	44.836027	-107.817732	NA	1987	Wyoming
Bighorn 2004	149.0	44.92313611	-107.8687194	NA	2004	Wyoming
Bitterroot 1985-1987	142.5	46.02263	-114.303251	NA	1987	Montana
Bodie 1946	125.4	38.211724	-119.01162	2556	1946	California
Bodie 1947	124.0	38.211724	-119.01162	2556	1947	California
Bodie 1948	130.0	38.211724	-119.01162	2556	1948	California
Bodie 1949	122.0	38.211724	-119.01162	2556	1949	California
Bodie 1950-1952	126.6	38.211724	-119.01162	2556	1950	California
Capitol Reef 1988-1990	158.0	38.124983	-111.500733	NA	1988	Utah
Cariboo 1928-1930	161.2	53.2667	-121.2667	NA	1928	British Columbia
Clearwater 1988	161.0	51.712726	-119.844873	NA	1988	British Columbia
Clearwater 2005	154.0	51.72105556	-119.858525	NA	2005	British Columbia
Copenhagen 1937	160.8	42.3292	-111.5725	NA	1937	Idaho
Copenhagen 1987	177.5	42.321868	-111.552441	NA	1987	Idaho
Craters 1936-1937	141.7	43.3704	-113.6661	NA	1937	Idaho
Elko 1987	124.0	40.583036	-115.402063	NA	1987	Nevada
Elko 2005	156.0	40.57883056	-115.3932083	NA	2005	Nevada
Fishlake 1987	166.4	37.764197	-112.805114	NA	1987	Utah
Glidden Creek 1932-1937	159.8	47.5203	-115.7764	NA	1937	Idaho
Golden 1988	174.0	51.048329	-117.152432	NA	1988	British Columbia
Grand Mesa 1987	180.0	39.019726	-108.158814	NA	1987	Colorado
Grand Mesa 2004	188.0	39.04319444	-108.0734917	NA	2004	Colorado
Great Basin 1933	127.0	38.78833	-116.93167	NA	1933	Nevada
Great Basin 1934	111.5	39.23639	-117.52556	NA	1934	Nevada

Great Basin 2004	115.0	38.8769694	-117.3496639	NA	2004	Nevada
Gunnison 1983-1985	145.0	38.579337	-106.327638	NA	1985	Colorado
Gunnison 1987	162.5	38.577288	-106.325016	NA	1987	Colorado
Gunnison1950-1956	160.2	38.9649885	-106.4827907	NA	1952	Colorado
Hagensborg 1988	190.0	52.239501	-126.390662	NA	1988	British Columbia
Hagensborg 2005	194.0	52.2113972 2	-126.3645833	NA	2005	British Columbia
Henry House 2005	146.0	53.3482611	-120.1358083	NA	2005	British Columbia
Huerfano 1985-1987	139.0	37.306665	-105.154973	NA	1985	Colorado
Jasper 2005	130.0	52.0372777 8	-116.5157528	NA	2005	Alberta
Jemez 1985-1992	157.5	36.007594	-106.396421	NA	1992	New Mexico
La.Sal 1987	160.0	38.481442	-109.244247	NA	1987	Utah
Manti 1987	163.0	39.053386	-111.519579	NA	1987	Utah
Medicine Bow 1987	160.0	41.370656	-106.29615	NA	1987	Wyoming
Medicine Bow 2004	161.5	41.1778055 6	-107.0159139	NA	2004	Wyoming
Missoula 1974-1975	137.9	46.97684	-113.83794	NA	1974	Montana
Mt. Ranier 1917-1919	159.2	46.751158	-121.814218	833	1919	Washington
Mt. Ranier 1939-1943	173.0	45.9654142	-122.2906807	518	1940	Washington
Mt. Ranier 1959-1965	149.0	46.7583	-120.9753	1473	1961	Washington
Mt. Ranier 1974-1983	152.7	46.9114	-121.6558	1898	1975	Washington
Mt. Ranier 2004	160.0	46.0524306	-121.759025	1313	2004	Washington
Neihart 1987	135.0	46.869937	-110.669192	NA	1987	Montana
Neihart 2004	142.0	46.9351972 2	-110.6249111	NA	2004	Montana
North Cascades 1973-1977	150.0	48.8375	-121.575	NA	1977	Washington
North Cascades 1988	168.0	48.860927	-121.703735	NA	1988	Washington
Northern Sierra 1923-1924	133.0	40.4690676	-121.4934073	NA	1923	California
Northern Sierra 1925-1928	150.3	40.5606452	-121.2876191	NA	1926	California
Okanagan 1912-1920	142.5	48.897858	-120.251478	NA	1920	Washington
Okanagan 1988	173.0	48.533991	-120.622542	NA	1988	Washington
Okanagan 2004	186.0	48.5063083 3	-120.6263306	NA	2004	Washington
Ovando 1987	150.0	46.870114	-110.66902	NA	1987	Montana
Panhandle 2004	173.0	48.6294805 6	-116.5915306	NA	2004	Idaho
Payette 2004	152.0	45.1755388 9	-116.5679917	NA	2004	Idaho
Pemberton 2005	175.5	50.5818861 1	-123.0281389	NA	2005	British Columbia
Pike 1987	149.0	38.84054	-105.04442	NA	1987	Colorado
Rock Creek 1938	152.0	47.8706	-117.1014	NA	1938	Washington
San Juans 1908-1915	153.6	37.199896	-106.664005	2815	1913	Colorado
San Juans 1946-1952	166.1	37.737721	-107.697808	3320	1946	Colorado
San Juans 1988	140.0	37.979262	-107.616266	3695	1988	Colorado
Santa Fe 1981-1985	150.0	35.79062	-105.789473	3393	1985	New Mexico
Santa Fe 1987	150.0	35.79062	-105.789473	3393	1987	New Mexico

Santa Fe 1990-1997	176.0	35.79062	-105.789473	3393	1997	New Mexico
Santa Fe 2004	158.5	35.79780833	-105.7773889	3513	2004	New Mexico
Sawtooth 1932	144.1	44.3658	-115.2357	2506	1932	Idaho
Sawtooth 1936	135.5	44.4271	-114.4926	2255	1936	Idaho
Sawtooth 1987	120.0	44.072447	-114.757148	2537	1987	Idaho
Sisters 1932-2941	164.1	42.9389	-122.1444	NA	1937	Oregon
Sisters 1983-1990	153.0	44.247191	-121.880887	NA	1988	Oregon
Snoqualmie 1938-1939	182.5	47.7494	-121.1194	1011	1939	Washington
Snoqualmie 1940	163.8	46.98286	-121.09337	771	1940	Washington
Southern Sierra 1911-1916	134.2	36.76896	-118.35945	3205	1912	California
Southern Sierra 1927-1936	138.1	36.507684	-118.575203	3235	1934	California
Southern Sierra1933-1942	138.1	36.7704575	-118.3891075	3324	1941	California
Summit 1907-1915	164.9	39.9329689	-105.6831856	3558	1914	Colorado
Summit 1927-1937	159.9	39.5899051	-105.6437898	4180	1937	Colorado
Summit 1938-1939	160.9	39.456403	-105.90163	3524	1938	Colorado
Summit 1940-1941	158.0	39.6721987	-105.7975494	3269	1940	Colorado
Summit 1947	128.3	39.361655	-106.062519	3515	1947	Colorado
Summit 1987-1989	165.0	39.891654	-105.763062	2759	1987	Colorado
Summit 2004	175.5	39.80141667	-105.7908778	3603	2004	Colorado
Sweetwater 1946	122.2	38.461747	-119.279393	NA	1946	California
Taos 1925	156.3	36.613309	-105.319574	2664	1925	New Mexico
Taos 1985	142.5	36.583874	-105.459315	3282	1985	New Mexico
Taos 1987	140.0	36.583874	-105.459315	3282	1987	New Mexico
Taos 2004	162.0	36.61471111	-105.502175	3385	2004	New Mexico
Teton 1910-1911	147.6	42.978094	-110.769249	1978	1910	Wyoming
Teton 1930-1939	152.5	43.4372	-110.79439	2306	1930	Wyoming
Teton 1987	147.5	43.540878	-110.935232	2676	1987	Wyoming
Trappers Lake 1909-1912	146.0	40.13972	-107.33278	NA	1912	Colorado
Trappers Lake 1987	156.5	39.975499	-107.244433	NA	1987	Colorado
Trappers Lake 2004	174.0	39.97155833	-107.25785	NA	2004	Colorado
Uinta 1928-1929	165.2	40.64408	-109.72205	NA	1929	Utah
Uinta 1987	160.0	40.786866	-111.051919	NA	1987	Utah
Umatilla 1988	140.5	44.948065	-118.202692	NA	1988	Oregon
Wallowas 1915	145.9	44.312998	-118.712148	2576	1915	Oregon
Wallowas 1937-1938	161.6	45.2269	-117.3874	2349	1938	Oregon
Wallowas 1987	145.0	45.18824	-116.559638	2286	1987	Idaho
Wallowas 2005	140.0	44.94482778	-118.2122278	2390	2005	Oregon
Warner 1925-1926	133.2	41.3349759	-120.2675673	NA	1926	California
Wassuk 1947	115.0	38.48806	-118.7975	NA	1947	Nevada
Westwold 1988	151.0	50.358771	-119.890827	NA	1988	British Columbia
White Mountains 1917	120.2	37.432159	-118.099737	NA	1917	California

Yellowstone 1987	147.5	43.757188	-110.049824	NA	1987	Wyoming
Yellowstone 2004	152.0	43.71141389	-110.0452944	NA	2004	Wyoming
Yosemite 1901	129.7	37.739375	-119.271536	NA	1901	California
Yosemite 1915-1919	127.8	37.7769743	-119.2608776	NA	1915	California
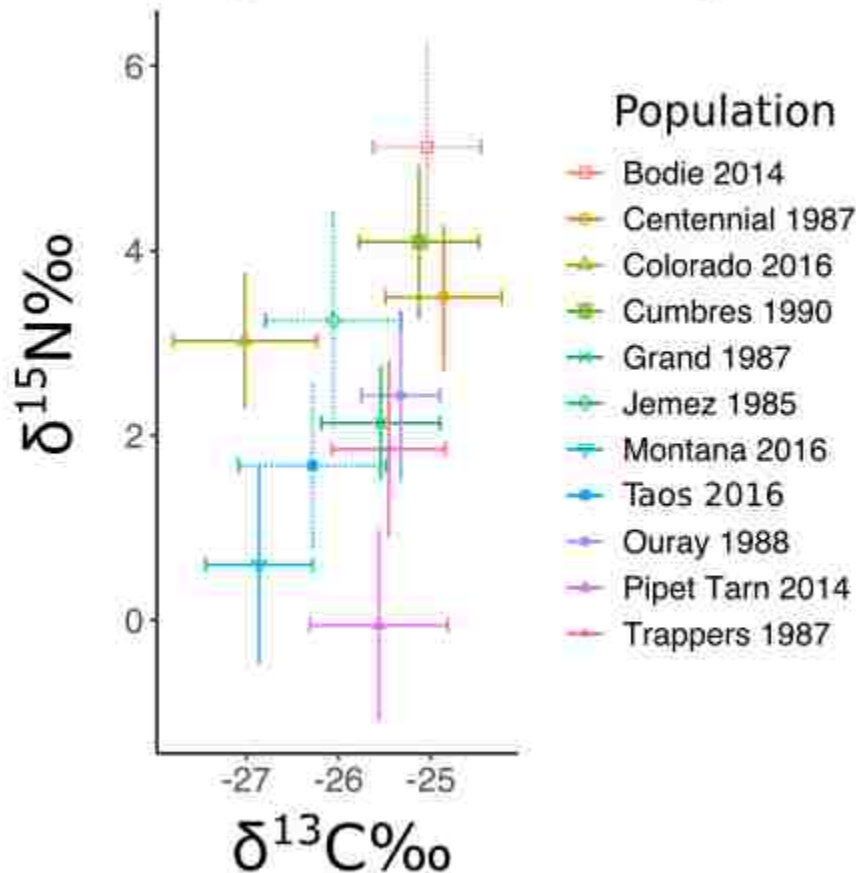
Figure 1. A comparison of edge and central population fall onset fur mean $\delta^{13}C$ and $\delta^{15}N$ values. Lines indicate one standard deviation from the mean. "Edge" populations of Bodie, Jemez, and Northern NM lines are shown with dashed lines, "central" populations are solid lines. Each population has significant overlap with multiple other populations in $\delta^{13}C$ values (Tukey-Kramer HSD, p >0.05). In $\delta^{15}N$, Bodie is distinct from all populations, and Pipet Tarn is distinct from all populations except Montana (Tukey-Kramer HSD, p >0.05). We did the above analyses in JMP Pro 12.
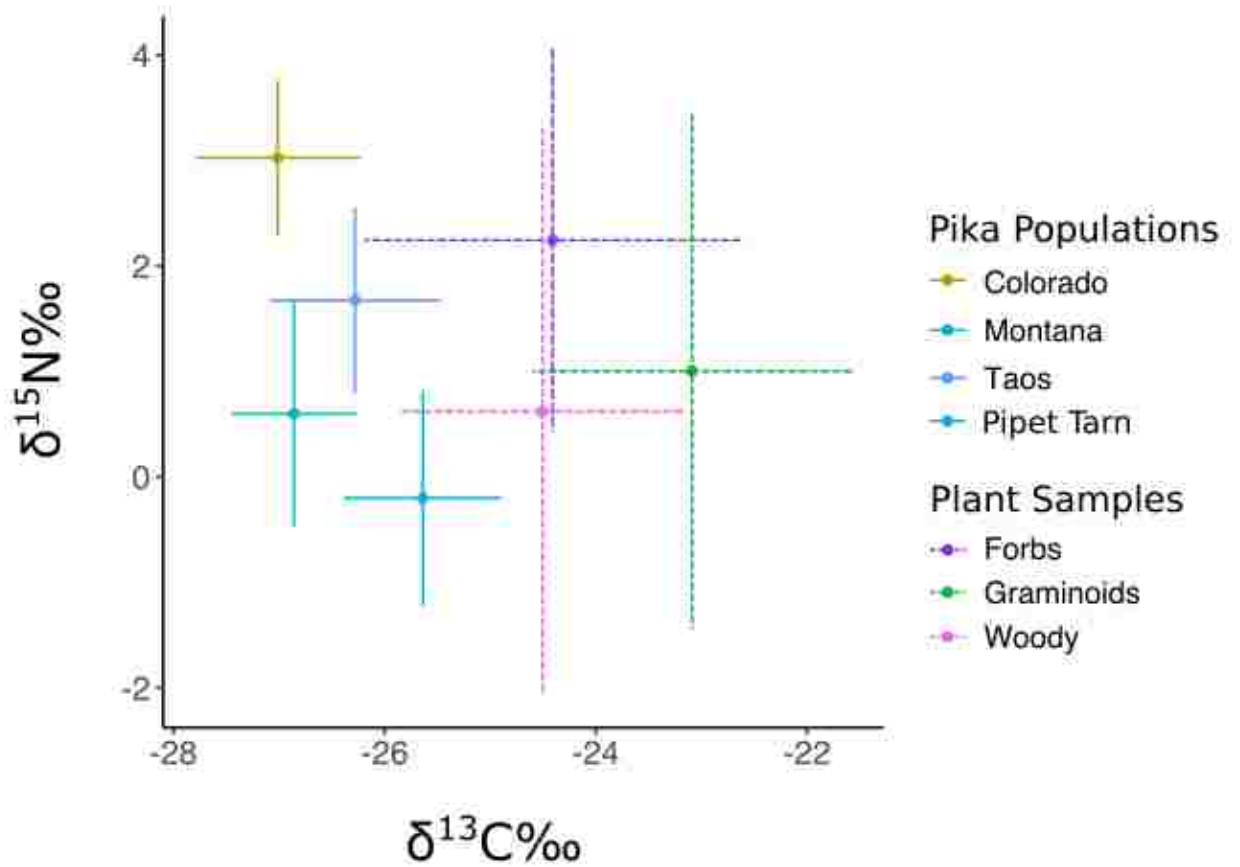
Figure 2. Plant functional types sampled from New Mexico (2016), California (Pipet Tarn 2014), Colorado and Montana (2010-2011) are shown with dashed lines. corrected for trophic discrimination, (Sponheimer et al. 2003) Pika fall-onset fur values from the same year and locations as plant samples. Dots indicate the population mean values and bars indicate one standard deviation from the mean.
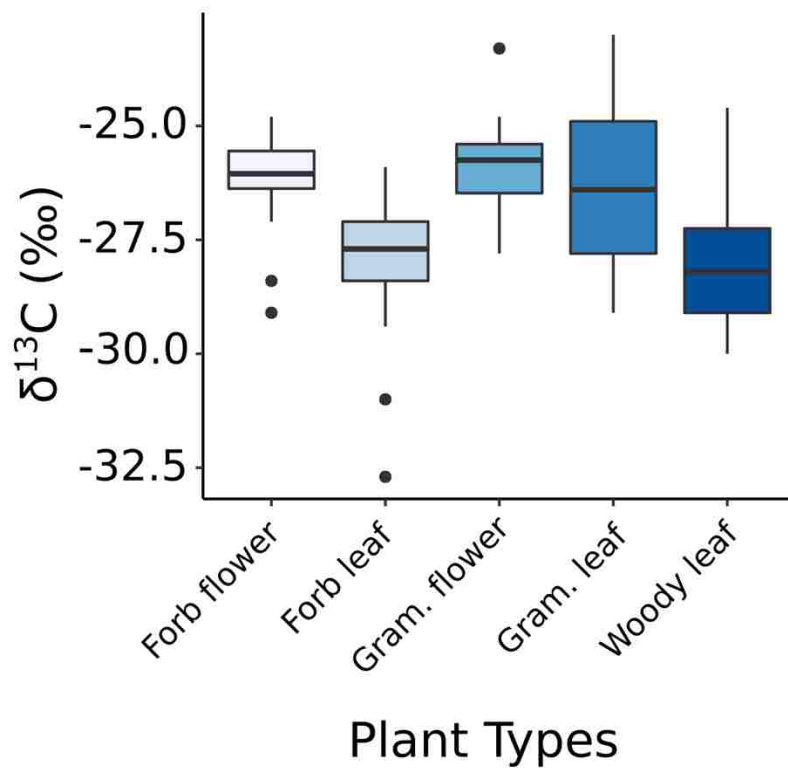
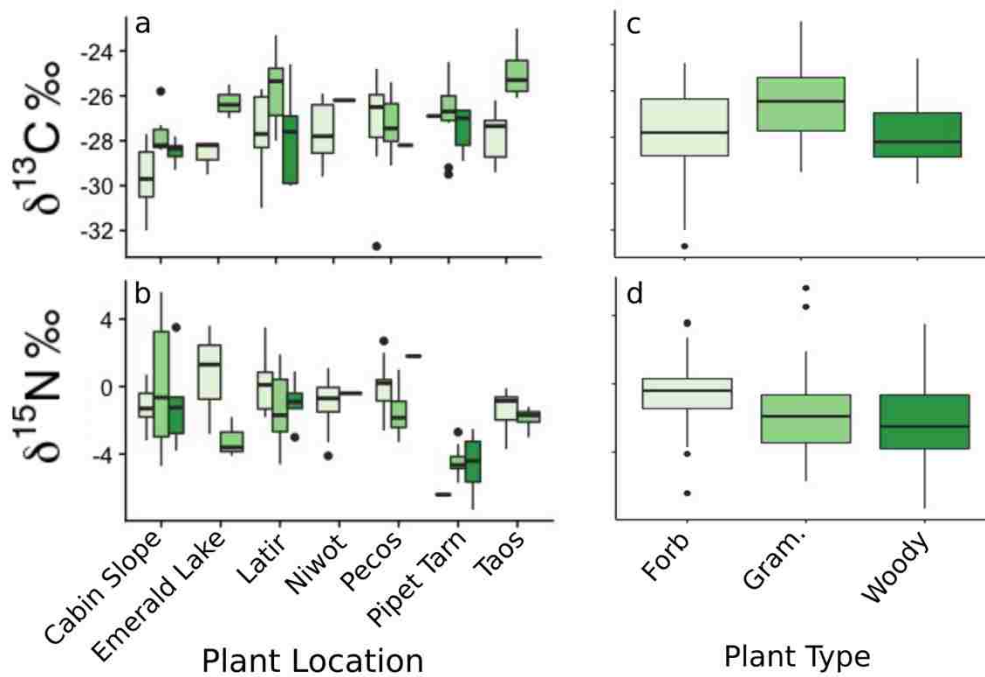Figure 3. Plant types and parts collected from New Mexico.

Figure 4. Mean isotope (δ^{13}C‰, δ^{15}N‰) values of plant functional types across and within geographic sites. A) Boxplots of δ^{13}C values for plant functional types by location. B) Boxplots of δ^{15}N values for plant functional types by location. C) Graminoids had significantly higher δ^{13}C values than forbs and woody vegetation. D) Forbs had significantly higher δ^{15}N than graminoids and woody vegetation.

Table 1. Mean isotope values and standard deviations for each population and tissue type analyzed. Bone collagen mean values across populations sampled were -23.3 ± 0.7‰ for $\delta^{13}C$ and 2.6 ± 1.1‰ for $\delta^{15}N$. Location data (latitude, longitude, elevation) used for estimating climate variables for each population is included. CWNA year is the year that most specimens for each population came from and was used to estimate climate data (http://www.climatewna.com/,Wang et al. 2016).

Population	Sample type	Mean $\delta^{15}N$	sd $\delta^{15}N$	Mean corrected $\delta^{13}C$	sd $\delta^{13}C$	SEA	State	Latitude	Longitude	Elev. (m)	CWNA year
Centennial 1987	Bone	1.8	0.7	-23.5	0.7	0.76	WY	41.3707	-106.2962	3288	1987
Cumbres 1913-1915	Bone	3.4	0.3	-24.6	0.7	3.57	CO	37.1999	-106.6640	2628	1913
Cumbres 1990	Bone	2.9	0.9	-23.6	0.5	0.96	CO	37.0206	-106.4500	3166	1990
Garfield 1987	Bone	2.3	0.5	-23.2	0.3	1.26	CO	38.5773	-106.3250	3328	1987
Grand 1912-1914	Bone	2.4	0.8	-24.0	0.5	1.92	CO	39.9330	-105.6832	3559	1912
Grand 1987	Bone	3.7	1.4	-23.0	0.4	1.36	CO	39.8917	-105.7631	2755	1987
Jemez 1985	Bone	3.6	1.9	-23.8	0.6	1.32	NM	35.8701	-106.5670	2542	1985
Ouray 1988	Bone	1.5	0.6	-23.1	0.4	0.78	CO	37.9793	-107.6163	3428	1988
Santa Fe 1987	Bone	2.0	0.8	-23.0	0.2	0.50	NM	35.7906	-105.7895	3318	1987
Taos 1925	Bone	3.2	0.7	-23.2	0.5	0.69	NM	36.6072	-105.4414	3338	1925
Taos 1985	Bone	2.6	0.8	-23.1	0.5	0.32	NM	36.5839	-105.4593	2868	1985
Trappers 1909-1912	Bone	2.9	0.7	-22.6	0.4	1.05	CO	40.1397	-107.3328	3123	1912
Trappers 1987	Bone	2.0	0.8	-23.0	0.4	0.77	CO	39.9755	-107.2444	2977	1987
Bodie 2014	Fall fur	5.1	1.1	-25.0	0.6	1.57	CA	38.2152	-119.0043	2669	2014
Centennial 1987	Fall fur	3.7	0.8	-25.4	0.4	1.49	WY	41.3707	-106.2962	3288	1987
Colorado 2010	Fall fur	3.6	0.7	-25.7	0.6	1.41	CO	40.0568	-105.5957	3612	2010
Colorado 2016	Fall fur	3.0	0.7	-27.0	0.8	1.77	CO	40.0568	-105.5957	3612	2016
Cumbres 1913-1915	Fall fur	3.4	1.7	-24.7	0.7	3.34	CO	37.1999	-106.6640	2628	1913
Cumbres 1990	Fall fur	4.2	1.0	-25.5	0.5	1.58	CO	37.0206	-106.4500	3166	1990
Garfield 1987	Fall fur	3.3	0.9	-25.9	0.6	2.33	CO	38.5773	-106.3250	3328	1987
Grand 1912-1914	Fall fur	3.8	0.5	-24.7	0.5	1.07	CO	39.9330	-105.6832	3559	1912
Grand 1987	Fall fur	2.4	0.5	-26.0	0.5	1.17	CO	39.8917	-105.7631	2755	1987
Jemez 1985	Fall fur	3.5	1.1	-26.3	0.8	2.70	NM	35.8701	-106.5670	2542	1985
Montana 2003	Fall fur	1.6	0.4	-26.3	0.6	0.51	MT	45.4071	-110.9400	2896	2003
Montana 2010	Fall fur	0.7	0.7	-26.4	0.7	1.54	MT	45.4071	-110.9400	2896	2010
Montana 2016	Fall fur	0.6	1.1	-26.9	0.6	1.79	MT	45.4071	-110.9400	2896	2016
Ouray 1988	Fall fur	2.6	0.9	-25.5	0.5	1.12	CO	37.9793	-107.6163	3428	1988
Pipet Tarn 2014	Fall fur	-0.1	1.0	-25.6	0.7	2.19	CA	37.9446	-119.2844	3187	2014
Santa Fe 1987	Fall fur	2.8	0.9	-25.9	0.6	1.59	NM	35.7906	-105.7895	3318	1987

Taos 1925	Fall fur	3.5	0.4	-25.4	0.3	0.49	NM	36.6072	-105.4414	3338	1925
Taos 1985	Fall fur	2.5	0.8	-25.8	0.7	1.42	NM	36.5839	-105.4593	2868	1985
Taos 2016	Fall fur	1.8	0.9	-26.7	0.7	2.05	NM	36.6163	-105.4998	3368	2016
Trappers 1909-1912	Fall fur	2.9	0.7	-25.0	0.5	0.95	CO	40.1397	-107.3328	3123	1912
Trappers 1987	Fall fur	2.3	0.9	-25.9	0.5	1.76	CO	39.9755	-107.2444	2977	1987
Centennial 1987	Summer fur	3.3	0.7	-24.4	0.3	1.49	WY	41.3707	-106.2962	3288	1987
Cumbres 1913-1915	Summer fur	2.8	1.5	-24.2	0.5	3.34	CO	37.1999	-106.6640	2628	1913
Cumbres 1990	Summer fur	4.0	0.6	-24.7	0.6	1.58	CO	37.0206	-106.4500	3166	1990
Garfield 1987	Summer fur	2.8	0.8	-24.5	0.5	2.33	CO	38.5773	-106.3250	3328	1987
Grand 1912-1914	Summer fur	3.9	0.5	-23.9	0.7	1.07	CO	39.9330	-105.6832	3559	1912
Grand 1987	Summer fur	1.9	0.6	-25.1	0.5	1.17	CO	39.8917	-105.7631	2755	1987
Jemez 1985	Summer fur	2.8	1.2	-25.6	0.4	2.70	NM	35.8701	-106.5670	2542	1985
Ouray 1988	Summer fur	2.3	0.9	-25.2	0.3	1.12	CO	37.9793	-107.6163	3428	1988
Santa Fe 1987	Summer fur	2.3	0.6	-24.9	0.5	1.59	NM	35.7906	-105.7895	3318	1987
Taos 1925	Summer fur	3.6	0.4	-25.1	0.4	0.49	NM	36.6072	-105.4414	3338	1925
Taos 1985	Summer fur	2.2	0.6	-25.3	0.6	1.42	NM	36.5839	-105.4593	2868	1985
Taos 2016	Summer fur	1.6	0.9	-25.8	0.6	2.05	NM	36.6163	-105.4998	3368	2016
Trappers 1909-1912	Summer fur	2.7	0.5	-24.5	0.4	0.95	CO	40.1397	-107.3328	3123	1912
Trappers 1987	Summer fur	1.4	0.8	-25.0	0.4	1.76	CO	39.9755	-107.2444	2977	1987

Table 2. Linear models testing climate and geographic influences on pika isotope values. The models are arranged from lowest AIC values for each isotope variable (e.g., fur, bone, seasonal difference, standard ellipse area). Expected relationships we drew from global trends reported in literature, resulting relationships we determined by constructing linear models of significant variables. Italicized font indicates significant results where the model variables are correlated at $r^2 > 0.5$ with another significant variable. Environmental variables with correlations of $r^2 > 0.5$ were not included in the same multiple linear models. Results that are the opposite of the expected trend are highlighted in gray.

Tissue	Isotope	Model	Expectation	Result	r^2	p	df	AIC
Fall onset fur[1]	$\delta^{13}C$	MAP_prev+ RH_prev	*Decrease*	*Decrease*	0.38	0.01	18	36.43
Fall onset fur	$\delta^{13}C$	RH_prev	*Decrease*	*Decrease*	0.32	0.00	19	37.39
Fall onset fur	$\delta^{13}C$	RH_sp_prev+ PPT_sp_prev	Decrease	Decrease	0.26	0.03	18	40.13
Fall onset fur	$\delta^{13}C$	MAP_prev	*Decrease*	*Decrease*	0.21	0.02	19	40.55
Fall onset fur	$\delta^{13}C$	RH_sm_prev+ PPT_sm_prev	*Decrease*	*Decrease*	0.21	0.05	19	41.50
Fall onset fur	$\delta^{13}C$	RH_sp_prev	Decrease	Decrease	0.17	0.03	19	41.55
Fall onset fur	$\delta^{13}C$	PPT_sp_prev	Decrease	Decrease	0.17	0.04	19	41.63
Fall onset fur	$\delta^{13}C$	RH_sm_prev	*Decrease*	*Decrease*	0.17	0.04	19	41.69
Fall onset fur	$\delta^{13}C$	PPT_sm_prev	Decrease	Decrease	0.14	0.05	19	42.45
Fall onset fur	$\delta^{13}C$	Latitude	Decrease	NS	0.07	0.13	19	44.04
Fall onset fur	$\delta^{13}C$	Tave_ sp_prev	Increase	NS	-0.04	0.58	19	46.29
Fall onset fur	$\delta^{13}C$	Tave_wt_prev	Decrease	NS	-0.05	0.78	19	46.54
Fall onset fur	$\delta^{13}C$	PPT_wt_prev	Decrease	NS	-0.05	0.90	19	46.61
Fall onset fur	$\delta^{13}C$	Elevation	Decrease	NS	-0.05	0.95	19	46.62
Fall onset fur	$\delta^{13}C$	Tave_sm_prev	Increase	NS	-0.05	0.96	19	46.63
Fall onset fur	$\delta^{13}C$	MAT_prev	Increase	NS	-0.05	0.97	19	46.63
Fall onset fur	$\delta^{15}N$	RH_sm_prev	Decrease	Decrease	0.35	0.00	19	64.33
Fall onset fur	$\delta^{15}N$	RH_prev	*Decrease*	*Decrease*	0.26	0.01	19	67.04
Fall onset fur	$\delta^{15}N$	RH_sp_prev	*Decrease*	*Decrease*	0.24	0.01	19	67.42
Fall onset fur	$\delta^{15}N$	RH_wt_prev	*Decrease*	*Increase*	0.17	0.03	19	69.25

Fall onset fur	$\delta^{15}N$	Latitude	Decrease	Decrease	0.17	0.04	19	69.33
Fall onset fur	$\delta^{15}N$	PPT_sp_prev	Decrease	NS	0.02	0.27	19	72.90
Fall onset fur	$\delta^{15}N$	PPT wt prev	Decrease	NS	0.00	0.34	19	73.28
Fall onset fur	$\delta^{15}N$	MAP_prev	Decrease	NS	-0.01	0.38	19	73.41
Fall onset fur	$\delta^{15}N$	Tave_sp_prev	Increase	NS	-0.01	0.40	19	73.49
Fall onset fur	$\delta^{15}N$	PPT_sm_prev	Decrease	NS	-0.04	0.62	19	74.03
Fall onset fur	$\delta^{15}N$	Tave_sm_prev	Increase	NS	-0.05	0.72	19	74.2
Fall onset fur	$\delta^{15}N$	MAT_prev	Increase	NS	-0.05	0.72	19	74.16
Fall onset fur	$\delta^{15}N$	Elevation	Decrease	NS	-0.05	0.75	19	74.19
Fall onset fur	$\delta^{15}N$	Tave_wt_prev	Increase	NS	-0.05	0.77	19	74.21
Summer onset fur[2]	$\delta^{13}C$	Tave_wt	Increase	Decrease	0.48	0.00	12	17.65
Summer onset fur	$\delta^{13}C$	Tave_sp	*Increase*	*Decrease*	0.39	0.01	12	19.85
Summer onset fur	$\delta^{13}C$	Tave_sm_prev	*Increase*	*Decrease*	0.33	0.02	12	21.15
Summer onset fur	$\delta^{13}C$	PPT_sm_prev	Decrease	NS	0.10	0.15	12	25.23
Summer onset fur	$\delta^{13}C$	PPT_wt	Decrease	NS	-0.01	0.38	12	26.85
Summer onset fur	$\delta^{13}C$	PPT_sp	Decrease	NS	-0.03	0.44	12	27.08
Summer onset fur	$\delta^{13}C$	RH_wt	Decrease	NS	-0.06	0.64	12	27.53
Summer onset fur	$\delta^{13}C$	RH_sp	Decrease	NS	-0.08	0.77	12	27.70
Summer onset fur	$\delta^{13}C$	RH_sm_prev	Decrease	NS	-0.08	0.90	12	27.78
Summer onset fur	$\delta^{15}N$	Tave_wt	Increase	NS	0.07	0.19	12	36.95
Summer onset fur	$\delta^{15}N$	PPT_sm_prev	Decrease	NS	0.03	0.25	12	37.45
Summer onset fur	$\delta^{15}N$	Tave_sm_prev	Increase	NS	0.00	0.34	12	37.94
Summer onset fur	$\delta^{15}N$	PPT_wt	Decrease	NS	-0.02	0.39	12	38.17
Summer onset fur	$\delta^{15}N$	RH_wt	Decrease	NS	-0.03	0.44	12	38.34
Summer onset fur	$\delta^{15}N$	RH_sp	Decrease	NS	-0.06	0.63	12	38.77
Summer onset fur	$\delta^{15}N$	Tave_sp	Increase	NS	-0.06	0.65	12	38.81
Summer onset fur	$\delta^{15}N$	RH_sm_prev	Decrease	NS	-0.07	0.69	12	38.87
Summer onset fur	$\delta^{15}N$	PPT_sp	Decrease	NS	-0.07	0.76	12	38.95
Fur seasonal difference[3]	$\delta^{13}C$	RH seasonality	Increase	NS	0.36	0.09	9	2.77
Fur seasonal difference	$\delta^{13}C$	Latitude	Increase	NS	-0.04	0.48	12	7.61
Fur seasonal difference	$\delta^{13}C$	Elevation	Increase	NS	-0.04	0.52	12	7.71

Fur seasonal difference	$\delta^{13}C$	Temp seasonality	Increase	NS	-0.08	0.85	12	8.18
Fur seasonal difference	$\delta^{13}C$	PPT seasonality	Increase	NS	-0.06	0.54	9	9.87
Fur seasonal difference	$\delta^{15}N$	Temp seasonality	Increase	NS	-0.02	0.42	12	-15.31
Fur seasonal difference	$\delta^{15}N$	PPT seasonality	Increase	NS	-0.03	0.48	10	-13.84
Fur seasonal difference	$\delta^{15}N$	RH seasonality	Increase	NS	0.09	0.30	10	-15.47
Fur seasonal difference	$\delta^{15}N$	Elevation	Increase	NS	-0.06	0.60	12	-14.85
Fur seasonal difference	$\delta^{15}N$	Latitude	Increase	NS	-0.06	0.63	12	-14.80
Fur	SEA[4]	RH seasonality	Increase	NS	0.06	0.28	12	47.30
Fur	SEA	Temp seasonality	Increase	NS	-0.03	0.55	12	47.49
Fur	SEA	PPT seasonality	Increase	NS	-0.13	0.88	12	51.11
Bone[5]	$\delta^{13}C$	MAP_prev	Decrease	NS	0.10	0.15	11	23.15
Bone	$\delta^{13}C$	MAP_avg	Decrease	NS	-0.06	0.58	11	25.29
Bone	$\delta^{13}C$	RH_prev	Decrease	NS	-0.08	0.76	11	25.56
Bone	$\delta^{13}C$	MAT_avg	Increase	NS	-0.09	0.81	11	25.61
Bone	$\delta^{13}C$	MAT_prev	Increase	NS	-0.09	0.88	11	25.65
Bone	$\delta^{13}C$	RH_avg	Decrease	NS	-0.09	0.94	11	25.67
Bone	$\delta^{15}N$	MAT_prev+ MAP_prev	+/-	+/+	0.70	0.00	10	17.07
Bone	$\delta^{15}N$	MAP_prev	Decrease	Increase	0.59	0.00	11	20.39
Bone	$\delta^{15}N$	MAP_avg	Decrease	Increase	0.46	0.01	11	23.87
Bone	$\delta^{15}N$	MAT_avg	Increase	Increase	0.43	0.01	11	24.58
Bone	$\delta^{15}N$	MAT_prev	Increase	Increase	0.35	0.02	11	26.23
Bone	$\delta^{15}N$	RH_prev	Decrease	NS	0.07	0.20	11	31.02
Bone	$\delta^{15}N$	RH_avg	Decrease	NS	0.05	0.23	11	31.30
Bone	SEA	Temp_seasonality	Increase	Increase	0.41	0.01	11	29.01
Bone	SEA	RH_seasonality	Increase	NS	-0.14	0.6831	8	39.04
Bone	SEA	Precip_seasonality	Increase	NS	-0.31	0.8764	8	41.33

[1]For fall-onset molt, we analyzed annual climate variables from the year prior to collection to reflect the climate of the year the fur was grown, as well as summer, spring and winter seasonal variables of relative humidity, precipitation, and mean temperature. Since we have the most populations represented by fall-onset fur, we examined the relationships of annual climate variables, seasonal climate variables and geographic variables to understand which environmental factors influence pika population $\delta^{13}C$ and $\delta^{15}N$ values across their range. [2]For summer-onset molt, we investigated winter and spring seasonal climate variables from the year of collection, as well as summer from the year prior to collection to include the weather when haypiles would have been cached. We tested the relationships of isotopes with the seasonal climate variables from the year collected (winter, spring) and prior to collection (summer) of summer-onset molts

as well as prior year's summer, spring and winter seasonal variables for fall-onset molts. [3]Fur seasonal difference is the absolute difference between fall-onset fur and summer-onset fur.[4]Standard ellipse area (a measure of isotopic dietary niche breadth). [5]Since bone collagen reflects isotopic diet over the individuals' lifetime, we tested climate values from year prior to collection as well as averages. Abbreviations are as follows: SEA= standard ellipse area, NS= not significant (p ≥ 0.05), avg= averaged climate values from the year of collection and the year prior to collection, prev= climate data from year prior to collection, RH= relative humidity (%), MAT= mean annual temperature (°C), MAP = mean annual precipitation (mm), PPT= precipitation (mm), at = autumn, wt = winter, sp = spring, sm = summer.

Table 3. Plant families analyzed from Cabin Slope CA, Pipet Tarn CA, Niwot Ridge CO, Emerald Lake MT, Santa Fe NM, Taos NM. See Appendix 1 Table 2 for species and locality information.

Family	Functional type	Frequency	Mean δ^{13}C	Mean δ^{15}N
Asteraceae	forb	14	-28.2	-1.3
Boraginaceae	forb	4	-27.3	0.6
Caryophyllaceae	forb	1	-26.5	1.0
Cyperaceae	gamminoid	21	-26.8	-2.3
Ericaceae	woody	13	-28.4	-2.9
Fabaceae	forb	6	-26.4	0.3
Unknown Fern	woody	2	-27.8	-0.6
Gentianaceae	forb	1	-28.1	3.6
Grossulariaceae	woody	4	-28.0	-0.4
Juncaceae	gramminoid	5	-27.4	-1.2
Lamiaceae	forb	1	-29.7	-0.7
Orobanchaceae	forb	1	-25.9	0.1
Poaceae	gramminoid	25	-24.8	-2.1
Polygonaceae	forb	2	-28.1	0.1
Ranunculaceae	forb	13	-28.1	-0.8
Rosaceae	woody	9	-26.8	-0.2
Salicaceae	woody	4	-28.5	-2.1
Woodsiaceae	woody	1	-28.3	0.4

Table 4. Sampled material for each *O. princeps* population. See Appendix 2 Table 1 for population isotope and climate values.

Pika Population	Unique specimens (n)	Winter Molt (n)	Summer Molt (n)	Bone (n)
Bodie 2014	9	9	NA	NA
Centennial 1987	18	13	16	12
Colorado 2010	16	16	NA	NA
Colorado 2016	12	12	NA	NA
Cumbres 1913-1915	17	15	16	25
Cumbres 1990	11	11	8	10
Garfield 1987	22	19	19	21
Grand 1912-1914	13	13	9	12
Grand 1987	17	17	17	13
Jemez 1985	12	12	8	18
Montana 2003	8	8	NA	NA
Montana 2010	9	9	NA	NA
Montana 2016	10	10	NA	NA
Ouray 1988	12	11	12	16
Pipet Tarn 2014	9	9	NA	NA
Santa Fe 1987	9	8	9	9
Taos 1925	15	14	15	16
Taos 1985	16	14	19	14
Taos 2016	18	18	17	NA
Trappers 1909-1912	15	15	15	15
Trappers 1987	26	25	23	14
Total samples	294	278	203	195

Table 5. Historical comparisons of fall onset fur isotope values for pika populations. Analyses are two-sample t tests assuming unequal variance. Population mean isotope values are reported in Appendix 1 Table 1.

Fall onset fur	Isotope	t	df	p	Significance
Cumbres 1913-1990	$\delta^{13}C$	2.95	23.92	0.007	**
	$\delta^{15}N$	-1.34	22.90	0.194	
Grand 1912-1987	$\delta^{13}C$	6.92	26.38	0.000	***
	$\delta^{15}N$	7.27	25.94	0.000	***
Montana 2003-2016	$\delta^{13}C$	2.06	15.19	0.057	
	$\delta^{15}N$	2.84	11.51	0.016	*
Taos 1925-2016	$\delta^{13}C$	6.61	25.08	0.000	***
	$\delta^{15}N$	7.65	25.67	0.000	***
Trappers 1909-1912	$\delta^{13}C$	5.55	29.10	0.000	***
	$\delta^{15}N$	2.60	34.22	0.014	*

APPENDIX 3

Table 1. Univariate logistic regression models we tested to predict current pika occupancy against all unoccupied sites (n=327) and formerly-occupied sites (n=275). We report the models in order of lowest AIC. We include the odds ratio, lower 95% confidence interval (L95%CI), upper 95% confidence interval (U95%CI), p value (Wald's test) and log likelihood.

Occupied vs not occupied (n=327) Variable name	AIC	Odds Ratio	L95%CI	U95%CI	p (Wald's)	Log likelihood
Winter moisture stress	405.76	0.54	0.45	0.65	< 0.001	-200.88
Chronic cold	407.58	0.66	0.58	0.75	< 0.001	-201.79
Sub-lethal cold	414.69	1.08	1.05	1.11	< 0.001	-205.35
Acute cold	415.14	1.05	1.03	1.07	< 0.001	-205.57
Sub-lethal heat	416.12	0.93	0.91	0.96	< 0.001	-206.06
Chronic heat	422.41	0.68	0.61	0.77	< 0.001	-209.21
Acute heat	426.05	0.93	0.91	0.96	< 0.001	-211.03
Patch size	426.59	1.03	1.01	1.04	< 0.001	-211.30
Mean grass	437.64	1.13	1.06	1.21	< 0.001	-216.82
Annual precip	443.78	1.00	1.00	1.00	< 0.001	-219.89
Forage	443.80	1.06	1.02	1.11	0.002	-219.90
Growing moisture stress	444.43	0.44	0.28	0.70	< 0.001	-220.21
Peak moisture stress	445.36	0.26	0.12	0.57	< 0.001	-220.68
Winter precip	445.64	1.01	1.00	1.01	< 0.001	-220.82
Chronic moisture stress	447.54	0.53	0.35	0.80	0.002	-221.77
Growing-season precip	450.39	1.00	1.00	1.01	0.01	-223.19
Monsoon precip	454.82	1.00	1.00	1.01	0.118	-225.41
Mean forbs	454.91	1.05	0.98	1.11	0.146	-225.46
Null model	455.32	1.00	1.00	1.00	0.956	-226.66
Potential solar insolation	457.27	1.05	0.69	1.60	0.823	-226.63
Forb:Grass ratio	472.49	1.00	0.99	1.01	0.804	-234.25
Occupied vs extirpated (n=275)						
Winter moisture stress	336.26	0.56	0.45	0.68	< 0.001	-166.13
Chronic cold	337.68	0.68	0.59	0.78	< 0.001	-166.84
Chronic heat	339.66	0.71	0.62	0.80	< 0.001	-167.83
Sub-lethal cold	342.62	1.07	1.04	1.10	< 0.001	-169.31
Sub-lethal heat	342.97	0.94	0.91	0.96	< 0.001	-169.48
Acute cold	344.73	1.04	1.03	1.06	< 0.001	-170.36
Acute heat	351.01	0.94	0.91	0.97	< 0.001	-173.50
Mean grass	354.83	1.15	1.05	1.25	0.002	-175.42
Forage	354.98	1.11	1.04	1.18	0.002	-175.49

Patch size	356.41	1.02	1.01	1.03	0.003	-176.21
Annual precip	363.40	1.00	1.00	1.00	0.005	-179.70
Winter precip	363.81	1.01	1.00	1.01	0.007	-179.90
Mean forbs	364.25	1.16	1.01	1.35	0.04	-180.12
Potential solar insolation	365.82	1.03	0.64	1.66	0.89	-180.91
Growing moisture stress	366.25	0.53	0.31	0.91	0.023	-181.12
Peak moisture stress	367.30	0.38	0.15	0.96	0.041	-181.65
Chronic moisture stress	368.25	0.64	0.39	1.04	0.07	-182.13
Growing-season precip	368.90	1.00	1.00	1.01	0.106	-182.45
Null model	369.59	1.00	1.00	1.00	< 0.001	-183.79
Monsoon precip	371.42	1.00	1.00	1.01	0.683	-183.71
Forb:Grass ratio	371.56	1.00	0.99	1.01	0.874	-183.78
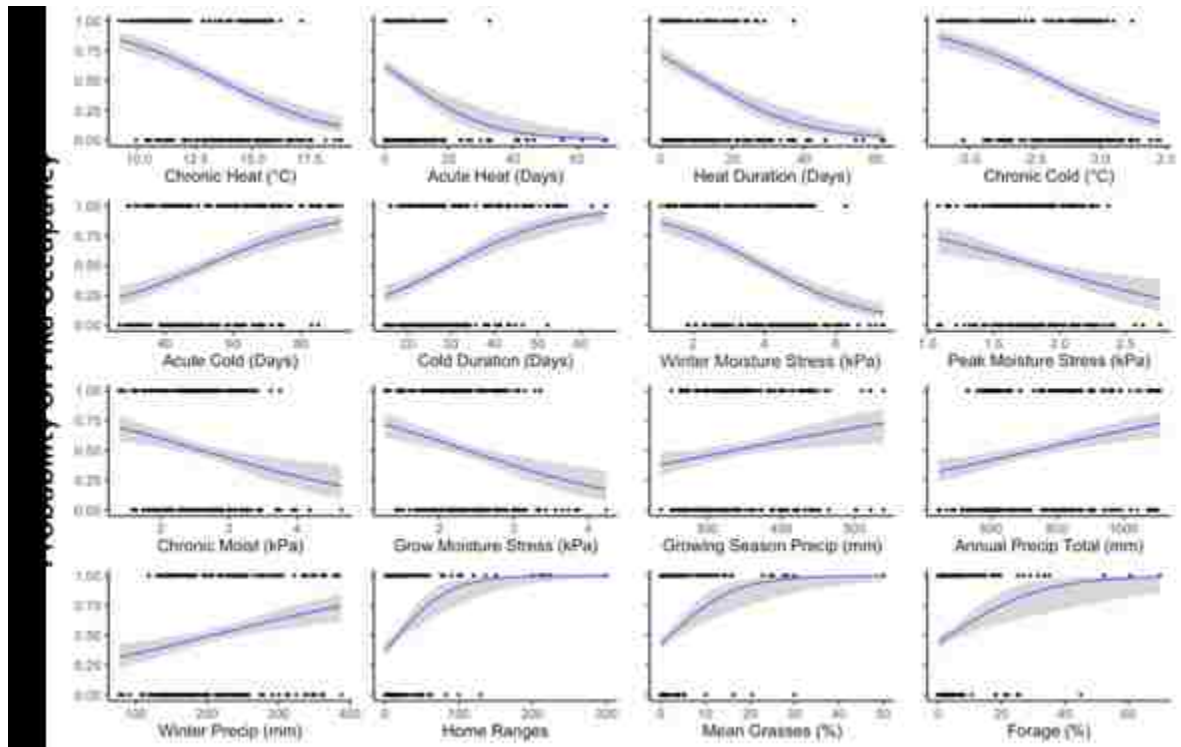
Figure 1. Logistic regressions of variables with significant influence on pika occupancy (p< 0.05, df = 326). p values and test statistics in SI Table 1.
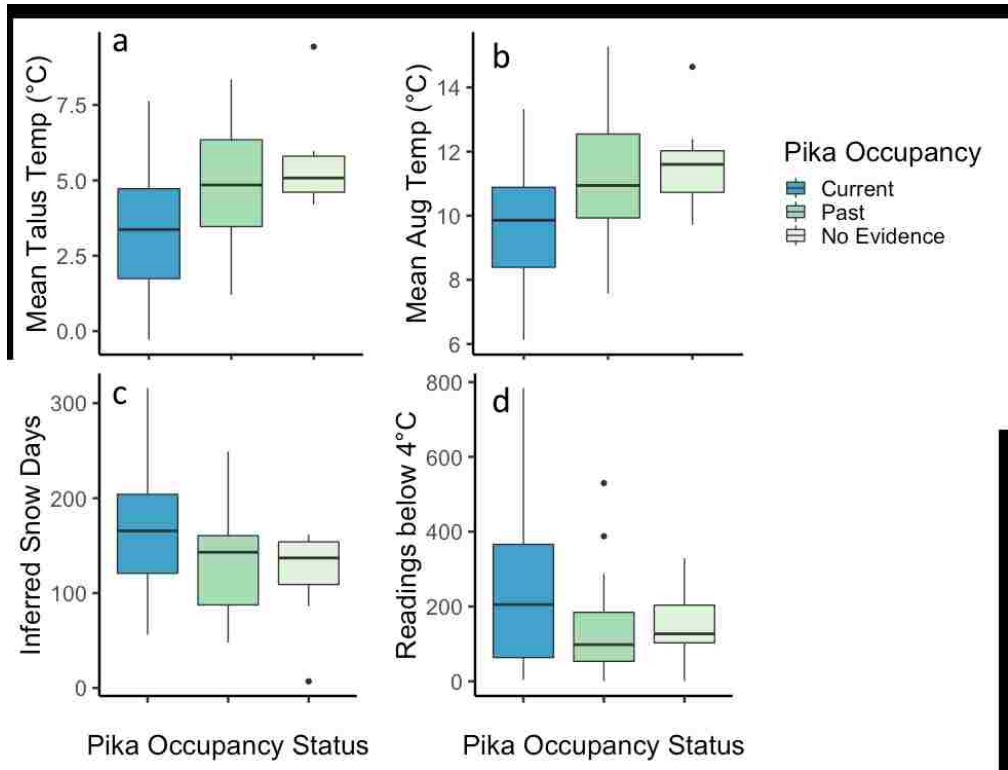
Figure 2. Boxplots indicating the mean variable values of currently occupied, previously occupied and sites with no pika evidence found. Climate variables (a,b,c,d,f) are derived from within-talus temperature sensors. Patch isolation, as measured by distance to nearest patch (e), we considered an alternative hypothesis to climate mechanisms influencing pika occupancy.
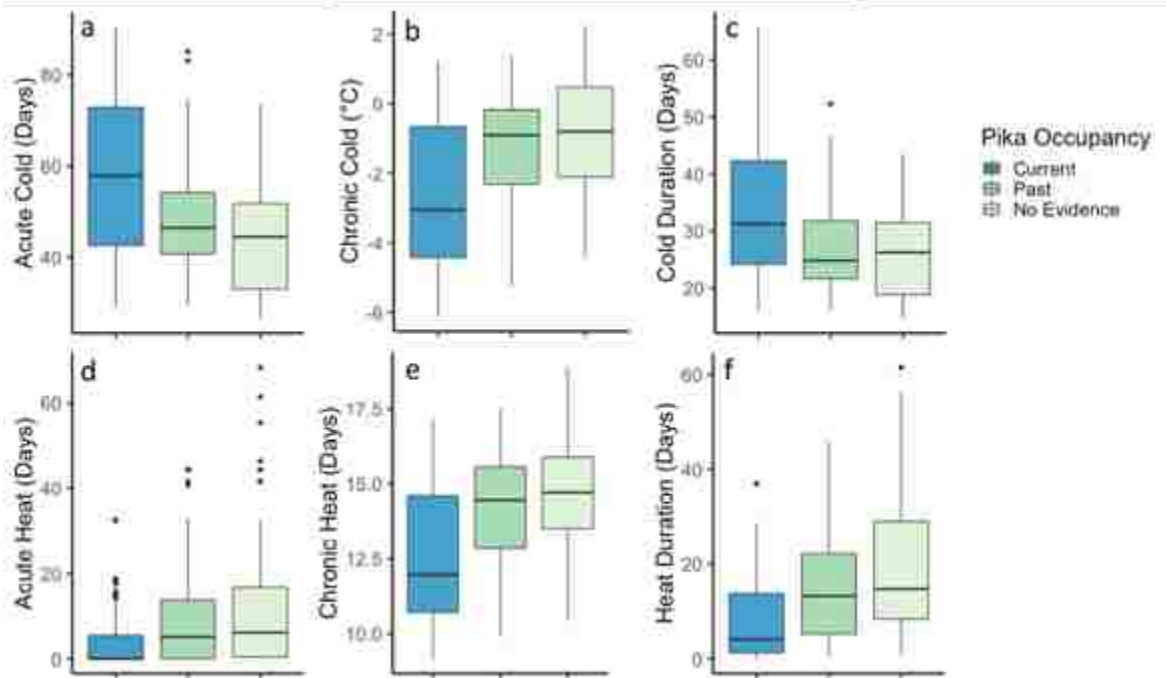
Figure 3. Pika occupancy status compared to mean PRISM near-surface temperature variables. Pikas were more likely to be found at sites with lower chronic cold temperatures (b), more acute cold days (a) and longer cold durations (c). Pikas were less likely to be found at sites with higher chronic temperatures (e), longer hot durations (f) and more days of acute heat (d).

SUPPLEMENTAL INFORMATION ON STUDY AREA

The lowest-latitude pika populations occur in the Jemez and Sangre de Cristo Mountains of northern New Mexico. Due to their position at the lowest latitudes of the pika's range, northern New Mexico pika populations may have an outsized importance on the study of pika distribution and ecology. The Sangre de Cristo Mountains are the southernmost reaches of the Rocky Mountains, extending southward from Colorado into northern New Mexico. The dominant vegetation types in the southern Rocky Mountains include alpine grasses and forbs, spruce-fir, aspen and ponderosa pines (Julyan 2006). The Sangre de Cristos are isolated by the Rio Grande Rift to the west and Raton Basin to the east (Julyan 2006). Much of the mountainous areas are administered by the Carson and Santa Fe National Forests, which contain the Pecos Wilderness, Latir Peak Wilderness, Columbine-Hondo Wilderness and Wheeler Peak Wilderness areas. The tallest mountains in New Mexico are found within the Sangre de Cristos, with Wheeler Peak (4011m) reaching the highest elevation (Julyan 2006). The Jemez Mountains are physically and geographically distinct from the Sangre de Cristos. The Jemez Mountains are volcanic in origin and separated by the Rio Grande Valley from the Sangre de Cristo and separated from the San Juan mountains by the Chama River (Bailey 1913) (Fig. 1a). The middle of the range is a large caldera, which creates a high elevation (~2600m) grassy valley. The tallest peaks in the Jemez are along the caldera rim or resurgent domes, which reach elevations above of 3,500m (Julyan 2006).

Pikas allow for efficient surveys and sampling as they are highly detectable, reliable study organisms. The majority of their habitat is in protected wilderness areas, which are less likely to be disturbed by anthropogenic habitat loss or modification. In addition, they are largely confined to broken rock talus slopes, which are easily identifiable both *in situ* and by satellite imagery (Hafner and Smith 2010). Pikas are highly detectable, with repeat surveys regularly (> 90%) resulting in the same detections across surveyors (Beever et al. 2010; Rodhouse et al. 2010; Moyer-Horner et al. 2012). Unlike most small mammals, they are active and conspicuous during daylight hours (Smith and Weston 1990). In addition, pikas vocally mark their territories, vocalize for conspecific attraction, communicate alarm to neighbors, and store conspicuous hay piles, all of which contribute to reliable detections (Smith and Weston 1990; Dearing 1997; Moyer-Horner et al. 2012). Compared to small mammals and other lagomorphs, pikas have relatively stable population sizes, making it more likely that surveys are reliable across years (Southwick et al. 1986).

Pikas have high body temperatures and can die if exposed to relatively low temperatures (25.5°C) when unable to behaviorally thermoregulate (MacArthur and Wang 1973, 1974). Talus habitat serves to protect pikas against both summer and winter temperature extremes, due to the insulating properties of rock and snow (e.g., Millar et al. 2016). Talus also protects pikas from larger predators such as birds of prey, but they are susceptible to weasels who can follow them into the talus interstices. Pikas are herbivorous, typically consuming a combination of grasses and

forbs from talus slopes and talus-adjacent meadows, as well as moss, shrubs and other vegetation to a lesser extent (Varner and Dearing 2014). Pikas do not hibernate, and store vegetation in hay piles to consume in the winter (Dearing 1997). Often, these hay piles are visible below large rocks in talus.

The naturalist Vernon Bailey described the historical extent of pikas in New Mexico in the early 20th century (Bailey 1931). In historical surveys, Bailey reported that pikas in the Pecos and Truchas mountains inhabited rock slides from 3353m to the tallest summits and in the Taos Mountains from 3475m to 4145m. In the Jemez Mountains, pikas were historically found from 2743m to the tops of the tallest peaks (Bailey, 1931). The pikas in the Jemez Mountains (goat peak pika, *O. princeps nigrescens*, Bailey 1913). were once considered a separate subspecies from the Sangre de Cristo pikas (*O. princeps incana,* Howell 1924), but revisions based on genetic studies place all populations in the Southern Rockies into the subspecies *O. princeps*

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