

ECOLOGY AND BEHAVIOR OF AMERICAN
PIKAS (*OCHOTONA PRINCEPS*) IN
ATYPICAL HABITATS

by

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ABSTRACT

Contemporary climate change is occurring at an unprecedented rate and is already dramatically affecting biodiversity worldwide. However, despite many well-documented changes, relatively little is known about specific mechanisms by which climate affects species. Investigating survival and recruitment in sub-optimal habitat can be as illuminating as population declines or extinctions, in terms of identifying mechanisms by which climate impacts species distributions. This dissertation incorporates aspects of global change ecology, disturbance ecology, and animal behavior to understand mechanisms of survival and recruitment of a climate-sensitive small mammal, the American pika (*Ochotona princeps*), in atypical habitats. I first elucidate mechanisms underlying low-elevation pika survival in the Columbia River Gorge, Oregon. This region is characterized by a high degree of moss cover, which appears to promote pika survival in two ways. First, by consuming the moss, which is available year-round, pikas are released from constructing large food caches for winter, a hallmark of their behavior in typical habitats. Second, the moss mediates the microclimates relevant to the species, in some cases completely decoupling ambient temperatures from those measured in the pikas' rocky habitat. Pikas in this habitat also exhibit a high degree of behavioral plasticity in foraging strategy and microhabitat selection. Finally, I had a unique opportunity to build upon these results by investigating how pikas recolonize habitat severely disturbed by wildfire. Pikas quickly recolonized seemingly barren habitat, but

animal abundance did not increase until after a threshold in vegetation availability was reached. Defining these habitat thresholds will significantly advance our understanding of pikas' resource requirements and their sensitivity to disturbance. These results will also inform practical conservation measures for this species and other small alpine animals.

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CHAPTER 1

INTRODUCTION

Contemporary climate change is occurring at an unprecedented rate, and it is now widely accepted that anthropogenic sources of greenhouse gases are a significant contributor to global warming (IPCC 2007). Rising temperatures and changes in precipitation patterns are affecting ranges, population dynamics, and timing of life-cycle events for many species (Walther et al. 2002, Parmesan 2006). It is unlikely that all species will be able to adapt quickly enough to tolerate these new environmental conditions, and as a result, many are becoming vulnerable to extinction (Davis et al. 2005). A recent study estimated that 15 - 37% of terrestrial species in a global sample will be “committed to extinction” by the year 2050 under a mid-range climate warming scenario (Thomas et al. 2004).

The changing climate will perhaps have the most pronounced effects in sensitive arctic and alpine ecosystems (Parmesan 2006). In addition to warmer temperatures, climate models project substantial decreases in alpine snowpack, which will translate to water shortages for many human, animal and plant communities that depend on snowmelt or glaciers (Hayhoe et al. 2004). Changes in temperature and precipitation patterns have already forced many species’ ranges poleward and upslope to maintain their climatic niches (Moritz et al. 2008), but some plants and animals are already at the upper limit of suitable habitat and will have nowhere to go.

This thesis seeks to understand how climate affects mammals by identifying critical aspects of habitat suitability. For my research, I chose to focus on the American pika (*Ochotona princeps*). Pikas are small, generalist mammalian herbivores (Order: *Lagomorpha*) whose habitat is mostly restricted to high-elevation talus (rock slides and boulder fields) in mountain ranges of the western United States. This species is ideal for investigating habitat suitability in the context of climate change because pikas are highly susceptible to heat stress when prevented from behaviorally thermoregulating (MacArthur and Wang 1973, 1974, Smith 1974). They also have strict habitat requirements and limited dispersal ability (Smith and Weston 1990). As a result of these constraints, localized extinctions have already been observed for this species in many parts of their range, linked to high summer temperatures and reduced winter snowpack (Beever et al. 2010, Beever et al. 2011, Erb et al. 2011, Stewart and Wright 2012, Erb et al. 2013, Stewart et al. 2015).

In my dissertation, I evaluate how habitat characteristics and behavioral modifications enable pikas to persist in atypical habitats that appear to be unsuitable in the context of climate change. I focus on pika populations in the Columbia River Gorge (CRG), where pikas persist at elevations as low as 46 m. In this habitat, nearly half of the summer growing season exceeds 25.5°C (Simpson 2009). For comparison, pikas in the Sierra Nevada died after a few hours at this temperature (Smith 1974).

A unique feature of pika habitat in the CRG is its high degree of moss cover (Simpson 2001). My thesis research suggests that moss serves a dual purpose for pikas in this unusual habitat. In Chapter 2, I report that pikas can consume large amounts of moss, which is abundantly available year-round and requires little energy to harvest. Although

it is low in nitrogen and high in fiber, pikas that consume moss are released from leaving the talus to forage and from constructing large winter food caches, which in turn may reduce their exposure to predation and high ambient temperatures. I also developed a technique to reconstruct pika diet from DNA recovered in feces and successfully used this technique to detect atypical food resources (e.g., bryophytes, ferns, pine needles) in the diet of CRG pikas (Appendix A).

In Chapter 3, I show that moss also insulates pikas in the CRG against warm summer temperatures by decoupling the talus microclimates that pikas actually experience from ambient conditions at the surface. Average summer temperatures at the talus surface in sites with high moss cover (>65% of surface area) were 5-10°C cooler than in sites with low moss cover (<40%). Furthermore, experimental moss removal raised surface temperatures by 5-7°C. The moss cover, extensive forest canopy cover, and high relative humidity also contribute to highly heterogeneous microclimate temperatures in the CRG, such that instantaneous measurements collected within the same patch of talus are not necessarily more correlated than those separated by several kilometers.

Finally, this spatial heterogeneity of microclimate provides pikas with ample opportunities to behaviorally thermoregulate. In Chapter 4, I describe differences in behavior between pikas living at low elevations in the CRG and at high elevations in more typical alpine habitat. Compared to high-elevation pikas, I show that low-elevation pikas are far less likely to invest in caching food for the winter and far more likely to be using off-talus forested habitat, particularly as a midday thermal refuge. Pikas also had far smaller home ranges in the CRG, potentially because mosses are so widely available

as a food resource (Chapter 2).

Climate change may also increase the impact of secondary disturbances like fire. Indeed, wildfires have increased in both frequency and severity due to warm temperatures and early spring snowmelt, particularly in western North America (Westerling et al. 2006, Dennison et al. 2014). Most large animals can move away from a fire, but small animals with limited dispersal ability may be threatened by altered fire regimes. I had an unexpected opportunity to investigate the impact of wildfire on habitat suitability when several of my instrumented study sites burned. In Chapter 5, I show that temperatures in talus interstices remained below 19°C during a severe fire, suggesting that animals could have survived *in situ*. Within three years of the fire, pikas were widely distributed throughout burned areas and did not appear to be physiologically stressed at severely burned sites. Furthermore, pika densities were better predicted by vegetation availability and topographic variables known to affect this species than by metrics of fire severity. This widespread distribution may reflect quick vegetation recovery and the fact that the fire did not alter the talus microclimates in the following years.

Taken together, the results in this dissertation highlight the value of talus as a thermal refuge for pikas and other small animals. They also underscore the importance of further study in individual species' persistence in atypical habitats. Finally, these results suggest that, if provided with suitable microclimates and sufficient food resources, pikas may be relatively resilient to future changes in climate and disturbance regimes.

References

- Beever, E. A., C. Ray, P. W. Mote, and J. L. Wilkening. 2010.** Testing alternative models of climate-mediated extirpations. *Ecol Appl* 20:164-178.
- Beever, E. A., C. Ray, J. L. Wilkening, P. F. Brussard, and P. W. Mote. 2011.**

Contemporary climate change alters the pace and drivers of extinction. *Glob Chang Biol* 17:2054-2070.

- Davis, M. B., R. G. Shaw, and J. R. Etterson. 2005.** Evolutionary responses to changing climate. *Ecology* 86:1704-1714.
- Dennison, P. E., S. C. Brewer, J. D. Arnold, and M. A. Moritz. 2014.** Large wildfire trends in the western United States, 1984–2011. *Geophysical Research Letters* 41:2928-2933.
- Erb, L. P., C. Ray, and R. Guralnick. 2011.** On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*). *Ecology* 92:1730-1735.
- Erb, L. P., C. Ray, and R. Guralnick. 2013.** Determinants of pika population density vs. occupancy in the Southern Rocky Mountains. *Ecol Appl* 24:429-435.
- Hayhoe, K., D. Cayan, C. B. Field, P. C. Frumhoff, E. P. Maurer, N. L. Miller, S. C. Moser, S. H. Schneider, K. N. Cahill, and E. E. Cleland. 2004.** Emissions pathways, climate change, and impacts on California. *Proceedings of the National Academy of Sciences of the United States of America* 101:12422.
- Intergovernmental Panel on Climate Change. 2007.** *Climate change 2007: The physical science basis.*
- MacArthur, R. A. and L. C. H. Wang. 1973.** Physiology of thermoregulation in the pika, *Ochotona princeps*. *Canadian Journal of Zoology* 51:11-16.
- MacArthur, R. A. and L. C. H. Wang. 1974.** Behavioral thermoregulation in the pika, *Ochotona princeps*: A field study using radiotelemetry. *Can J Zool* 52:353-358.
- Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008.** Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322:261-264.
- Parmesan, C. 2006.** Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* 37:637-669.
- Simpson, W. G. 2001.** Foraging activities of the pika (*Ochotona princeps*): A comparison of two populations. M.S. thesis, Portland State University, Portland.
- Simpson, W. G. 2009.** American pikas inhabit low-elevation sites outside the species' previously described bioclimatic envelope. *WNAN* 69:243-250.
- Smith, A. T. 1974.** The distribution and dispersal of pikas: Influences of behavior and climate. *Ecology* 55:1368-1376.
- Smith, A. T. and M. L. Weston. 1990.** *Ochotona princeps*. *Mammal Species* 352:1-8.

- Stewart, J. A. E., J. D. Perrine, L. B. Nichols, J. H. Thorne, C. I. Millar, K. E. Goehring, C. P. Massing, and D. H. Wright. 2015.** Revisiting the past to foretell the future: Summer temperature and habitat area predict pika extirpations in California. *Journal of Biogeography*: doi: 10.1111/jbi.12466.
- Stewart, J. A. E. and D. H. Wright. 2012.** Assessing persistence of the American pika at historic localities in California's northern Sierra Nevada. *Wild Soc Bull* 36:759-764.
- Thomas, C. D., C. A. R. Green, M. Bakkenes, and B. L.J. 2004.** Extinction risk from climate change. *Nature* 427:425-428.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002.** Ecological responses to recent climate change. *Nature* 416:389-395.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006.** Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940-943.

CHAPTER 2

DIETARY PLASTICITY IN PIKAS AS A STRATEGY FOR ATYPICAL RESOURCE LANDSCAPES

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Abstract

Mammalian habitat specialists are suffering notable population declines and localized extinctions in response to climate change. Plastic behavioral responses, especially in foraging, may be critical for specialists to tolerate changes in temperature, precipitation, and resource availability. Here, we investigate the foraging behavior of a mammalian alpine specialist living in atypical habitat. American pikas (*Ochotona princeps*) are typically limited to high elevations in western North America; however, they persist near sea level in the Columbia River Gorge, well outside of their previously assumed climatic niche. We hypothesized that utilizing unusual food resources contributes to pika persistence in this unusual climate. Moss comprised over 60% of the diet at 2 sites, more than observed for any mammalian herbivore in the wild. Moss is available year-round in this habitat; thus, by specializing on moss, pikas do not have to construct large food caches to survive winter. These results suggest a larger degree of behavioral and dietary plasticity than previously assumed for this species. Understanding a species' capacity to adapt its foraging strategies to new resource landscapes will be essential to assessing its vulnerability to future climate change and to developing conservation plans.

Introduction

Anthropogenic climate change is occurring at an unprecedented rate and is already dramatically affecting the abundance and diversity of species worldwide (Parmesan 2006). For mammals, rapid and pronounced responses have been documented in community structure (Rowe et al. 2011), phenology (Ozgul et al. 2010), population dynamics (Kausrud et al. 2008), and species distributions, including range retractions

(Moritz et al. 2008), population declines, and localized extinctions (Cahill et al. 2013). Across many taxa, habitat specialists are suffering particular declines (e.g., Warren et al. 2001; Jiguet et al. 2007; Rowe et al. 2011), presumably because they are less flexible than generalists in adapting to atypical climates or to the changing availability or quality of food resources. Indeed, altered food availability is the most common mechanism of climate-mediated extinctions or population declines (Cahill et al. 2013). Alpine and arctic specialists may be particularly vulnerable to climate change because, in addition to having restricted ranges, they are often also sensitive to warm temperatures (Parmesan 2006).

Understanding the adaptability of habitat specialists to new conditions will be critical for predicting their responses to further changes and for informing the development of viable conservation plans. One mechanism by which species adapt to atypical climates or resource landscapes is through behavioral plasticity. Flexible behaviors may allow habitat specialists to tolerate rapid environmental changes if the response improves fitness under the new conditions (Sih et al. 2012). One common plastic response to rapid environmental changes is inclusion of new food resources into the diet (Tuomainen and Candolin 2011). These could include food resources that move into the range of a species due to environmental change or an underutilized resource already present in the environment.

The American pika, *Ochotona princeps*, is an excellent system in which to investigate the role of behavioral plasticity in mammalian adaptation to atypical climates, particularly with respect to diet choice and foraging strategy. Pikas are habitat specialists in high-elevation talus (rockslides and boulder fields, generally over 2,500 m elevation)

in western North America (Smith 1974b; Smith and Weston 1990; Hafner 1993). Pikas are sensitive to warm temperatures when prevented from behaviorally thermoregulating (MacArthur and Wang 1974; Smith 1974b) and possess a limited ability to disperse between patches of habitat (Smith 1974a; Smith and Ivins 1983). As a result, this species may be imminently threatened by climate change (Smith et al. 2004; but see Millar and Westfall 2010). Localized extinctions linked to climate have been documented in parts of their range (Beever et al. 2011; Erb et al. 2011; Stewart and Wright 2012), although the effect of climate on pika distribution appears complex and locality-specific (Jeffress et al. 2013). Pikas must spend much of the short alpine summer collecting and storing food for winter (Conner 1983; Dearing 1997b). However, warm summer temperatures may preclude foraging, resulting in low quality food caches for winter. Furthermore, reduced snowpack also exposes the animals to more harsh winter temperatures (Tapper 1973; Smith 1978; Beever et al. 2010).

Despite an apparent reliance on cold climates (Hafner 1993) and a documented sensitivity to aspects of climate (Beever et al. 2011), pikas have existed near sea level in the Columbia River Gorge (CRG) in Oregon and Washington for over a century (Horsfall 1925; Simpson 2009). This population persists well outside of the previously assumed climatic niche for pikas, in terms of both temperature and precipitation patterns (Simpson 2009). Although the existence of pikas in the CRG was deemed “worthy of further study” 15 years ago (Verts and Carraway 1998), only 1 study to date has examined their persistence in this unusual habitat (Simpson 2009). This study documented that the CRG is well outside of the climate niche predicted by previous research (e.g., Hafner 1993), but it did not elucidate how pikas persist in this seemingly unsuitable climate.

A unique feature of pika habitat in the CRG is its high degree of moss cover (Simpson 2001). Moss is typically nutritionally deficient and is therefore not extensively consumed by herbivores (Richardson 1981; Prins 1982). However, in this habitat, moss could potentially be an abundant resource that requires little energy to harvest. Given the unusual distribution and abundance of food resources for pikas in this environment, we hypothesized that utilizing an atypical food resource (i.e., moss) may allow, at least in part, pika persistence in this climate, which is unusual relative to the geographic range of this species. Furthermore, if pikas could consume moss, we hypothesized that they would be released from constructing large winter food caches during the warmest times of year. Understanding the mechanisms that promote survival of a species in a highly atypical habitat may provide critical information about its capacity for behavioral plasticity in adapting to new resource landscapes and its vulnerability to future climate change.

Materials and Methods

Study organism. The American pika is a small mammalian herbivore in the order Lagomorpha. Although they are generalist herbivores, pikas have unique and specific diet selection criteria. Unlike many alpine mammals, pikas do not hibernate; instead, they spend short summers amassing large food caches called haypiles, which sustain them over winter (Dearing 1997b). The plants collected and stored in haypiles are different than those consumed fresh in summer. Pikas typically consume grasses, but they collect and cache forbs high in phenolic toxins, which enhance winter storage (Dearing 1996, 1997c). However, heat sensitivity limits the time for pikas to forage and construct haypiles. Captive pikas overheat and die after 2 hours at 25.5°C because they have a

limited capacity to physiologically regulate their body temperature (MacArthur and Wang 1973, 1974; Smith 1974a). Therefore, pikas must behaviorally thermoregulate by retreating to cool talus interstices during summer (MacArthur and Wang 1974; Smith 1974b).

Study sites and vegetation surveys. Foraging data were collected on the Oregon side of the Columbia River Gorge (CRG) near Wyeth at 2 large (ca. 15,000 m²) north-facing talus patches: Site 1 and Site 2, each of which had at least 8 resident pikas. The patches are separated by approximately 600 m of dense, old growth forest dominated by Douglas fir (*Pseudotsuga menziesii* ssp. *menziesii*), western redcedar (*Thuja plicata*), and bigleaf maple (*Acer macrophyllum*). These tree species also dominate the vegetation along the patch perimeter. Unlike typical high-elevation talus, both sites are covered in a thick layer of nearly continuous moss (5–15 cm thick, Supporting Information S1, DOI:). The moss also serves as a substrate for graminoids and forbs. Because the talus itself is covered in vegetation, there is no clear boundary between the rocks and the foraging arena (e.g., a meadow or patch of vegetation on the talus perimeter) as is typical in pika habitat. As a result, the foraging environment in the CRG is far more heterogeneous and spatially complex than typical high-elevation habitat because pikas can consume moss or herbaceous plants growing on the talus, as well as the leaves of large trees or shrubs that hang over the talus. Moreover, they can traverse the talus slope under the cover of moss, which likely reduces their predation risk (Morrison et al. 2004).

To quantify potential food resources for pikas at each site and across seasons, we conducted vegetation surveys in which we measured the relative cover of each vegetation growth form on the talus (modified from Wilkenning et al. 2011). Growth forms were

characterized as: none (bare rock), lichens, mosses, ferns/clubmosses, graminoids (grasses, sedges, and rushes), forbs (herbaceous flowering plants), or shrubs (woody plants without a central trunk). At 3 locations in each site, we recorded the dominant vegetation type every 10 cm along each of 3, parallel 5-m transects, spaced 5 m apart. This method generated a total of 459 plant cover data points per site. Because these surveys were conducted on the talus instead of in the forest, this method significantly underestimates shrubs and trees as a potential food source, though pikas consume leaves from low-hanging branches of shrubs and trees on the talus perimeter.

Diet and foraging behavior. We visited both sites in February, March, and May-October. In these visits, we found that both sites were continuously occupied, but pikas were most active above the talus between June and August. In fact, little surface activity was observed at any sites in February, March, May, or October, though the animals could be heard calling from within the talus. Because diet composition was directly estimated from observations of pika foraging behavior, we chose to sample extensively between June and August. We worked at Site 1 in 2011, and at both Site 1 and Site 2 in 2012. Congruent with previous observations, pikas did not appear disturbed by stationary observers (Conner 1983; Dearing 1996). Observers ($n = 3$ in 2011, $n = 5$ in 2012, 2 observers present in both years) used 10 x 40 binoculars to document foraging activity and were rigorously trained in plant identification prior to collecting any foraging data.

Individual pikas were trapped and marked with unique colored eartags or identified by unique scar patterns on the eyes or ears. As in previous work (Dearing 1996), each animal included in this analysis was observed consuming vegetation a minimum of 5 times. Although juveniles were observed at both sites in July and August

2012, only adult animals were included in the diet analysis. Observers recorded the amount of each plant species consumed. Diet biomasses were calculated by multiplying the average dry weight of the food item by the number of times each food item was consumed. Pikas were only observed when active in the open talus or forest periphery. Because of the dense understory vegetation, we were unable to observe pikas if they were active in the forest. All research on live animals followed ASM guidelines (Sikes et al. 2011) and was approved by the University of Utah institutional animal care and use committee.

Nutritional analyses. Several factors are known to impact pika diet selection, including nitrogen and water content (Morrison and Hik 2008), plant size and plant secondary compounds (Dearing 1996), and previous herbivory by insects (Barrio et al. 2013). Fiber content is also an important determinant of diet selection for many herbivores (Van Soest 1994). For each species in the diet, we collected the plant parts that pikas consumed. For mosses, we trimmed the top 2 cm of plant material as it would be grazed by pikas. For ferns, forbs, and shrubs, only leaves were collected. Grass leaves and seed heads were collected together because pikas consumed these items together. To minimize the effects of individual variation, several samples of each plant species in the diet were collected at both sites, dried at 40°C, and ground to pass through a 1 mm screen. Total fiber content (Neutral Detergent Fiber, NDF) and cellulose/lignin content (Acid Detergent Fiber, ADF) were measured in a fiber analyzer (ANKOM 200 Fiber Analyzer, ANKOM Technology, Macedon, New York). Nitrogen content was measured by combusting 5 mg plant material in an Elemental Combustion System (Costech Analytical Technologies, Valencia, California) coupled to a Delta Plus Advantage mass

spectrometer (Thermo Finnigan, San Jose, California) operating in the continuous flow mode.

Phenolics are an important determinant of pika caching selection (Dearing 1996); thus plants were also analyzed for total phenolic content using the Folin-Ciocalteu method (Waterman and Mole 1994). Although this method is unreliable in measuring absolute phenol content, it provides a consistent estimate of biological activity in ecological studies when activity depends on phenolic oxidation, as in plant-herbivore interactions (Appel et al. 2001). Plant samples were collected and stored on dry ice in the field, then transferred to a laboratory freezer (-80°C) until analysis. Phenolic contents of 0.2 g of fresh plant material were extracted into a solution of 95% methanol by grinding with a Polytron PT3100 Mixer (Kinematica, Lucerne, Switzerland) at 12,000 rpm for 30 s. Samples were then centrifuged for 5 min at 3,300 rpm, and the supernatant was used in the Folin-Ciocalteu reaction following the protocol of Ainsworth and Gillespie (2007). Gallic acid was used as the standard. Total phenolic activity is expressed as mg gallic acid equivalent/g dry weight of plant material.

Overall differences in nutritional quality of plants in the diet were assessed with multivariate analysis of variance (MANOVA), with fiber content (ADF and NDF), nitrogen content, and phenolic activity as dependent variables and plant growth form (i.e., moss, forb, fern, shrub) as the independent variable. Post-hoc Tukey's Honest Significant Difference tests were used to further examine differences between means within dependent variables ($\alpha = 0.05$). Phenolic activity data were log-transformed to meet the assumption of normality. Only 1 species each of fir and lichen were collected, and graminoids were not sorted to species. These growth forms are therefore excluded from

statistical analyses. All statistical analyses were performed in R 2.13.1 (R Development Core Team 2011).

We also estimated the total nutrient content of each diet, as in Dearing (1996). For each nutritional variable (i.e., ADF, NDF, nitrogen, and phenolics), the contribution of each food item to the diet of each animal (by % dry weight) was multiplied by the nutritional or phenolic value of that food item. We then summed the nutritional contribution of each food item in the diet of each animal and calculated averages and standard errors for pika diets at each site and year.

Haypile sampling. In September of 2011 and 2012, we excavated and weighed all haypiles that we observed pikas constructing at Site 1 and Site 2. To excavate haypiles, we temporarily removed rocks to access as much stored vegetation as possible. We then replaced all rocks and all but a small (50 g), well-mixed sample of the vegetation in the haypile. Haypile samples were dried at 40°C, and sorted to species. Haypile dry weight was calculated according to the following equation: $\text{dry weight} = \text{fresh weight} \times (100 - \% \text{ water})/100$, where haypile fresh weight was measured in the field, and water content was measured from the sample. Haypile composition was calculated by the dry weight of each plant species in the sample.

To increase our sample size of haypiles, we also exhaustively searched for haypiles in September at 2 additional sites: Site 3 (near Herman Creek) and Site 4 (near Wygant State Park), which are also north-facing talus patches on the Oregon side of the CRG that are similar in size to Sites 1 and 2 (ca. 18,000 m²). Only haypiles with fresh vegetation and fresh pika scat were sampled at these sites because bushy-tailed woodrats (*Neotoma cinerea*) also inhabit talus in the CRG and occasionally construct haypiles

(Smith 1997; Morton and Pereyra 2008); however, no data exist to suggest direct competition between pikas and woodrats (e.g., stealing from haypiles—Smith and Weston 1990). We recognize that these data were collected from a limited number of patches and that diet and caching behavior may vary in conjunction with moss cover and other habitat features across the CRG; however, this study provides an important, initial characterization of resource use and foraging strategy in this habitat, which is highly atypical for this species.

Pikas in the CRG experience fewer days of persistent snowpack or extreme weather events that may preclude foraging than pikas living in typical, high-elevation habitat. To determine whether pikas construct haypiles in proportion to the length of winter in the CRG, we quantified the number of days of persistent snowpack at each site in 2010–2011. We placed HOBO UA-001 temperature dataloggers (Onset Computer Corporation, Bourne, Massachusetts) near the surface of each rockslide. These loggers can be used to reliably estimate the duration of snowpack by counting the number of days in which surface temperature was near 0°C and diel temperature variation was less than 2°C (Lundquist and Lott 2008; Beever et al. 2010).

Results

Study sites and vegetation surveys. The talus at both sites had high vegetation cover (60–70%; Table 2.1, Supporting Information 2.S1). Although the total vegetation cover was similar, Site 2 had higher moss cover (68.6% versus 54.3%) than Site 1 and reduced cover in other growth forms (Table 2.1). Moss cover changed little with season at both sites (Table 2.1), although fern cover increased in late winter and early spring.

Diet and foraging behavior. Over both seasons and sites, we observed 220 h of

pika behavior. A total of 20 marked adult animals were observed for more than 5 foraging bouts each and were included in this analysis. At Site 1, we observed 4 individuals in 2011 and 7 individuals in 2012, 2 of which were observed in both years. At Site 2, we observed 11 animals in 2012. During the 2 summers of this study, we observed a total of 1,577 foraging bouts.

In total, we observed pikas consuming 31 different plant species, ranging from foliose lichens to Douglas fir needles. Moss represented over half of the feeding observations and comprised roughly 60% of the diet by dry weight (Fig. 2.1). This trend held across both sites and in both years. In particular, pikas appeared to prefer 2 species of moss: *Racomitrium lanuginosum* and *Pleurozium shreberi*. These 2 species alone comprised over 80% of moss consumed and thus nearly 50% of each diet by dry weight. We also observed pikas consuming shrubs, primarily vine maple (*Acer circinatum*), Oregon grape (*Mahonia aquifolium*, young leaves only), and thimbleberry (*Rubus parviflorus*). Pikas also occasionally consumed Douglas fir needles from low-hanging branches. These food resources are not commonly consumed in other habitats (Conner 1983; Huntly et al. 1986; Dearing 1996). In fact, “typical” food resources for pikas (graminoids and forbs) made up less than 25% of pika diet in the CRG at both sites and in both years (Fig. 2.1).

Nutritional analysis. Mosses differed significantly in nutritional quality from other growth forms (MANOVA: Pillai’s trace = 1.224, $F_{12,45} = 6.591$, $P = 0.01$). In the metrics that we measured, mosses do not appear to be a highly nutritious food resource (Fig. 2.2, Supporting Information 2.S2). On average, mosses contained twice as much fiber as forbs, ferns, or shrubs (Fig. 2.2a). Mosses also had roughly twice the

cellulose/lignin content of forbs, ferns, or shrubs (Fig. 2.2b). Reindeer lichen (*Cladina portentosa*) also had high total fiber, and Douglas fir also had high cellulose/lignin content, but these species were excluded from statistical analyses due to low sample sizes.

All mosses contained less than 1% nitrogen (Fig. 2.2c). In contrast, forbs, ferns, and shrubs all had significantly higher nitrogen content (Fig. 2.2c). Interestingly, pika caecal pellets (highly fermented digesta that are reingested) were nearly 6% nitrogen, far higher than any plant species that we tested (Supporting Information 2.S2).

Similar to other studies (Dearing 1996, 1997c), shrub, fern, and forb leaves had the highest phenolic activity, on average 1–3 orders of magnitude higher than mosses (Fig. 2.2d). Forbs had the greatest range in phenolic activity, ranging from 12.2–132.8 mg gallic acid equivalents/g (Supporting Information 2.S2). Douglas fir needles also had high levels of phenolic activity (Fig. 2.2d) and are also known to contain terpenes (Kepner and Maarse 1970), though we did not measure terpene content or activity.

In both sites and both years, the diet of CRG pikas was extremely low in nitrogen (< 1%) and high in fiber (70–80% total fiber [NDF]), ~ 30% cellulose and lignin [ADF; Table 2.2). However, because mosses had relatively low phenolic activity, the total phenolic activity in the diet was relatively low (5–12 mg/g).

Haypile frequency and contents. In contrast to the > 1500 cases of pikas consuming vegetation, we observed only 231 cases of pikas caching (carrying vegetation into the talus) across both years. Of the 20 marked animals that we observed in both years, 14 pikas made at least 1 haytrip ($\bar{X} \pm SE = 16.4 \pm 6.6$ observed haytrips per animal per year; range = 1–67). However, most of these trips were decentralized: animals carried

vegetation under the talus, but not to a conspicuous haypile, and in most cases, we never observed that animal carrying vegetation to that location again. Of the pikas that we observed haying, only 4 animals built a conspicuous haypile (20% of marked pikas; Table 2.3).

Across both years, we sampled 5 haypiles at Sites 1 and 2 and an additional 6 haypiles at Sites 3 and 4 (Table 2.3). Overall, haypiles ranged from 0.5–4.2 kg fresh weight ($\bar{X} \pm SE = 2.0 \pm 0.4$ kg). Haypile composition varied; however, Douglas fir was a top component of haypiles at most sites. In general, haypiles tended to contain primarily forbs, shrubs, and pine needles that were high in phenolic activity (Table 2.3, Supporting Information 2.S2). In contrast, moss made up a small portion of haypiles, though it was the primary component of the summer diet.

Although haypile size in the CRG was absolutely much smaller than haypile sizes reported in the literature from typical, high-elevation habitat (Smith and Ivins 1984; Dearing 1997b; Morrison et al. 2009), when standardized to the length of winter, haypile fresh weights were remarkably consistent (80–90 g fresh weight per day) between the CRG and high-elevation sites in Colorado (Table 2.4). However, when accounting for water weight in each haypile, pikas in the CRG actually stored relatively more food per day of winter than at high elevations (Table 2.4). At high elevations, a pika must collect roughly 22 g dry weight of vegetation per day of winter to sustain itself (Dearing 1997b). On average, CRG haypiles contained 56 g dry weight of vegetation per day, whereas haypiles at high elevations contained less than 35 g per day (Dearing 1997b).

Discussion

We investigated behavioral and dietary plasticity of an alpine habitat specialist, *O. princeps*, in an atypical, temperate rainforest climate. Pikas are dietary generalists (Dearing 1996): they typically consume a variety of graminoids and forbs present in alpine meadows (Huntly et al. 1986; Dearing 1996), and they are unable to specialize on a diet high in tannins (Dearing 1997a). Here, we demonstrate that some pikas are capable of incorporating large amounts of bryophytes into their diet in the low-elevation habitat of the Columbia River Gorge (CRG).

To our knowledge, this study represents the highest degree of voluntary moss consumption reported for a mammalian herbivore in the wild. Few herbivores consume mosses because mosses are high in fiber, low in nitrogen, and low in digestible energy (Richardson 1981; Prins 1982). Some mammals are known to incorporate moss into their winter diets, particularly in winter in the Arctic, when little other forage is available, but few to the degree that we observe in CRG pikas. Although wood lemmings (*Myopus schisticolor*) can survive on a diet of 100% moss in the lab, their natural diet includes substantial amounts of grasses and dwarf shrubs, and mosses are typically only consumed in winter (Andreassen and Bondrup-Nielsen 1991). In addition, wood lemming growth and reproduction were reduced when fed 100% moss, compared to a varied diet including grasses and shrubs (Andreassen and Bondrup-Nielsen 1991). Svalbard reindeer (*Rangifer tarandus*) are considered moss specialists and can consume up to 54% moss during winter (van der Wal 2006); however, most studies report that reindeer winter diet contains only 22–30% moss (Bjørkvoll et al. 2009; Heggberget et al. 2010). Brown lemmings (*Lemmus sibiricus*) can also consume up to 40% moss during arctic winters

(Batzli and Pitelka 1983). Other mammals reported to consume moss include the Norwegian lemming (*Lemmus lemmus*—Kalela et al. 1961), the collared lemming (*Dicrostonyx torquatus*) and tundra vole (*Microtus oeconomus*; both less than 10% of diet—Batzli and Jung 1980), and Soay sheep (*Ovis aries*; 20–30% of winter diet—Milner and Gwynne 1974).

Although pikas are known to exhibit source-sink population dynamics (Kreuzer and Huntly 2003), we believe that the CRG populations in this study are adapted to consuming moss, rather than population sinks consuming a low-quality starvation diet. First, Simpson (2009) conducted monthly occupancy surveys at 4 talus patches in the CRG, 2 of which were < 1 km from Sites 1 and 4. He reported that all 4 patches were continuously occupied from June 2000–June 2001. We too observed continuous occupancy at all 4 sites in this study for 2 years, with visits spread across the year. In addition, we observed juveniles in mid-summer at Sites 1 and 2, some of which established territories in their natal patches. Finally, 2 of the 4 individuals marked at Site 1 in 2011 were observed again in 2012. Taken together with the fact that pikas also occupied the CRG 100 years ago (Horsfall 1925), these observations suggest that the pika populations in this study are not simply population sinks for dispersing animals from higher elevation.

In a recent review on dietary specialization in mammals, a facultative specialist was defined as an animal that is fundamentally capable of consuming a broad variety of foods but can also specialize on “difficult” foods when “easier” foods are less abundant (Shipley et al. 2009). Here, we argue that pikas are facultative moss specialists in the CRG. Moss is typically considered a “difficult” food for herbivores because it contains

high fiber, low nitrogen, and low digestible energy, compared to other forage options (Richardson 1981). Indeed, the 60% moss diet consumed by pikas in the CRG is extremely high in fiber and $< 1\%$ nitrogen on average (Table 2.2), lower than that estimated for nonruminant herbivores to maintain nitrogen balance ($\sim 1.3\%$ —Karasov 1982). As a result of these nutritional challenges, few organisms are known to feed on moss (Richardson 1981; Prins 1982). However, moss is an abundant year-round resource in this region of the CRG (Table 2.1), and consuming moss appears to confer other benefits, such as the opportunity to forage from within the safety or thermal refuge of the talus and apparent release from constructing large food caches for winter survival during the hottest times of year. Although pikas consume different food resources (i.e., forbs and graminoids) in typical alpine habitat, they still appear capable of consuming a diet $< 1\%$ nitrogen (Dearing 1996).

Because lichens and mosses absorb nutrients through air and water, they may become enhanced in nitrogen when they are down-wind of nitrogen-rich pollution sources (Wolterbeek 2002). The prevailing air currents from the Portland metropolitan area flow from west to east through the CRG, which may enhance the nitrogen content of mosses and lichens in the area (Fenn et al. 2007). If they were enriched in nitrogen, mosses and lichens could become a more valuable food resource for herbivores. However, we found no support for this idea in our nutritional data. Even if they are enriched in nitrogen relative to other parts of their ranges, the mosses and lichens that we examined still had significantly lower nitrogen content than any other plants tested (Fig. 2.2c, Supporting Information 2.S2).

Moss consumption may enhance thermoregulation for arctic and alpine herbivores

during cold stress because moss can contain relatively high concentrations of essential fatty acids and lipids, especially arachidonic acid (Prins 1982). Although this hypothesis was proposed over 30 years ago, it remains largely untested. Thick moss in this habitat could cool the microclimates in the talus, decoupling them from the relatively warm macroclimate of the CRG, thereby necessitating enhanced thermoregulatory abilities. However, we hypothesize that pikas may harbor gut microbes that are extremely efficient at fermenting the fiber found in mosses. Like all lagomorphs, pikas are coprophagic, which allows reingestion of fermented fiber. Caecal pellets were by far the most nutritious food item tested in this study in terms of low fiber content and high nitrogen content (Supporting Information 2.S2). This mechanism may allow pikas to gain more nutritional value from mosses than other herbivores that do not reingest fecal material (e.g., Batzli and Pitelka 1983).

Although mosses have extraordinarily slow growth rates compared to vascular plants (Furness and Grime 1982), a rough calculation indicates that the amount of moss harvested by pikas is sustainable. The daily energy requirements of an adult (nonlactating) pika have been estimated at 54.8 kcal/day (Smith and Weston 1990). Mosses contain between 4.5–5.0 kcal/g (Pakarinen and Vitt 1974; Richardson 1981). Thus, if approximately 60% of their diet in the CRG is moss, then pikas consume roughly 7.31 g/day and 2.67 kg/year in moss. Given the dry mass of moss per area of talus in the CRG (12.4–15.8 kg/m², pers. obs.), and an estimate of pika home range size in the CRG (727 m², pers. obs.), a pika consumes roughly 0.002% of the moss in its home range each year. The most common species of moss in the diet (*R. lanuginosum*) has one of the slowest exponential growth rates: 0.005/day between 10–25°C (Furness and Grime

1982). Even with a conservative estimate of 3 months/year being suitable for moss growth in the CRG (i.e., appropriate temperature and relative humidity), the moss in a home range will grow 4 orders of magnitude faster than the rate at which pikas consume it. In addition, pikas may also facilitate moss growth by fertilization or spore dispersal via fecal pellets.

The only previous study to examine the foraging behavior of CRG pikas found no evidence that pikas store food or construct haypiles in the CRG (Simpson 2009); however, behavioral observations in that study were limited. In contrast, we provide evidence that at least some pikas construct haypiles in the area. Other pikas likely also construct haypiles; however, the structural complexity of the CRG talus makes it difficult to observe haying behavior and locate haypiles. In addition, pika haypiles are difficult to excavate because plant material may be located deep within the talus interstices; thus, our haypile sizes may underestimate stored plant material.

Moss and some evergreen plants (e.g., Douglas fir, Oregon grape) are available at the CRG sites year-round. To harvest these resources, pikas do not have to leave the safety and thermal refuge of the talus; however, foraging at the surface is likely extremely restricted under persistent snow cover, which lasts 15–50 days/year at each site. We therefore propose that CRG haypiles are likely to serve as a supplemental food resource for winter weather that may preclude foraging, such as persistent snow cover or ice storms. Both the rate at which pikas collected hay during August and September, and the size of the haypiles that we excavated were absolutely far smaller than values reported in the literature from typical habitat (e.g., Conner 1983; Smith and Ivins 1984; Huntly et al. 1986; Dearing 1997b). However, pikas in the CRG collected a remarkably

consistent 80–90 g of fresh weight for each day of persistent snowpack (Table 2.4), which is nearly identical to relative haypile sizes at Niwot Ridge, Colorado, where haypiles must sustain pikas for the long alpine winter (Dearing 1997b).

Furthermore, CRG pikas appear to cache more food per day in winter than pikas at high elevations: dry weight stored per day of winter in the CRG was consistently higher than values published in the literature from 2 sites in Colorado (Table 2.4). We suggest that the decomposition-promoting environment of the CRG necessitates slightly larger haypiles per day of winter, compared to alpine talus. Climate influences vegetation decay rates more than leaf chemistry, and leaves decay much faster in climates with warmer temperatures and high humidity (Aerts 1997). Thus, although pikas in the CRG collected plants high in phenolic activity, which may enhance their storage (Dearing 1997c), haypiles likely decay faster in the CRG than in typical alpine habitat.

It is interesting to note that Douglas fir comprised such a large part of haypiles, even though fresh needles are available all winter. This may be a behavioral mechanism to avoid the relatively high levels of phenolic activity (Fig. 2.2d, Supporting Information 2.S2) and terpenes (Kepner and Maarse 1970) present in fresh Douglas fir needles. Toxins break down during storage in a cache; thus, herbivores can avoid ingesting high levels of toxins by storing food for later consumption (Dearing 1997c; Torregrossa and Dearing 2009). In addition, long-term storage in haypiles can enhance the nitrogen content of pika winter diet (Dearing 1997c), which may be especially important for an herbivore consuming such a low nitrogen diet (Table 2.2).

Finally, we speculate that the moss covering CRG talus slopes may also impact many other aspects of pika ecology in the CRG, including thermoregulation, predation

pressure, space use, territoriality, and dispersal. We observed pikas travelling long distances below the moss cover, which may insulate them from warm summer surface temperatures and reduce predation pressure. In addition, pikas live at relatively high densities in this habitat (> 11 adults/15,000 m² at site 2), perhaps because moss is such an abundant and utilized food resource. Indeed, across the range of pikas, vegetation availability is a strong predictor of both occupancy (Wilkening et al. 2011; Jeffress et al. 2013) and density (Beever et al. 2013). The abundance of mosses in the CRG may also impact home range size, territorial behaviors, and juvenile dispersal versus philopatry (i.e., establishing territories in their natal patch, which we observed at both Sites 1 and 2).

Taken together, our results suggest that pikas may be more adaptable to unusual climates or habitats than previously thought. An expanding literature describes and predicts pika population declines, range contractions, and extirpations in response to climate change (Beever et al. 2011, 2013; Erb et al. 2011; Stewart and Wright 2012). Our results suggest that, in some cases, pikas may persist in warm climates if they can modify their foraging behavior to acquire adequate nutrition and avoid activity during temperature extremes. Indeed, different climatic factors appear to constrain the distribution of pikas across their range (Jeffress et al. 2013), and other populations of pikas persist in atypical habitats, including lava flows (Ray and Beever 2007; Rodhouse et al. 2010; Jeffress et al. 2013) and low elevations in the Great Basin and Sierra Nevada (Beever et al. 2008; Millar and Westfall 2010). However, with continued climate change, some habitats may simply become unsuitable for pikas if the availability of food resources and thermal refuges shift outside of the range of behavioral plasticity for the species. This study advances our understanding of the fundamental habitat requirements

of pikas and their capacity for behavioral and dietary plasticity, particularly with respect to foraging strategy.

In summary, we provide evidence that a habitat specialist has acclimated to an atypical habitat, at least in part, by incorporating unusual food sources into its diet. Pikas facultatively specialize on moss in the Columbia River Gorge, and as a result, they appear to be released from spending a significant amount of their summer constructing haypiles, which is a hallmark behavior of most species of pika (Dearing 1997c; Smith 2008; Morrison et al. 2009). Protecting mosses (e.g., from trampling by hikers or unsustainable harvest) may therefore be a tractable management priority for pika conservation in this region. Given the rapidly changing distribution and abundances of plants due to climate change, this ability to incorporate unusual resources into the diet may be a critical mechanism by which mammalian herbivores will adapt to climate change.

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Literature Cited

- Aerts, R. 1997.** Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. *Oikos* 79:439-449.
- Ainsworth, E. A., and K. M. Gillespie. 2007.** Estimation of total phenolic content and other oxidation substrates in plant tissues using Folin–Ciocalteu reagent. *Nature Protocols* 2:875-877.
- Andreassen, H., and S. Bondrup-Nielsen. 1991.** A comparison of the effects of a moss diet and a varied diet on the growth of juvenile wood lemmings, *Myopus schisticolor* (Lilljeb.). *Zeitschrift für Säugetierkunde* 56:378-379.
- Appel, H. M., H. L. Govenor, M. D'Ascenzo, E. Siska, and J. C. Schultz. 2001.** Limitations of Folin assays of foliar phenolics in ecological studies. *Journal of Chemical Ecology* 27:761-778.
- Barrio, I. C., D. S. Hik, K. Peck, and C. G. Bueno. 2013.** After the frass: Foraging pikas select patches previously grazed by caterpillars. *Biology Letters* 9:20130090.
- Batzli, G. O., and H.-J. G. Jung. 1980.** Nutritional ecology of microtine rodents: Resource utilization near Atkasook, Alaska. *Arctic and Alpine Research* 12:483-499.
- Batzli, G. O., and F. A. Pitelka. 1983.** Nutritional ecology of microtine rodents: Food habits of lemmings near Barrow, Alaska. *Journal of Mammalogy* 64:648-655.
- Beever, E. A., S. Z. Dobrowski, J. Long, A. R. Mynsberge, and N. B. Piekielek. 2013.** Understanding relationships among abundance, extirpation, and climate at ecoregional scales. *Ecology* 94: 1563-1571.
- Beever, E. A., C. Ray, P. W. Mote, and J. L. Wilkening. 2010.** Testing alternative models of climate-mediated extirpations. *Ecological Applications* 20:164-178.
- Beever, E. A., C. Ray, J. L. Wilkening, P. F. Brussard, and P. W. Mote. 2011.** Contemporary climate change alters the pace and drivers of extinction. *Global Change Biology* 17:2054-2070.
- Beever, E. A., J. L. Wilkening, D. E. McIvor, S. S. Weber, and P. E. Brussard. 2008.** American pikas (*Ochotona princeps*) in northwestern Nevada: A newly

discovered population at a low-elevation site. *Western North American Naturalist* 68:8-14.

- Bjørkvoll, E., B. Pedersen, H. Hytteborn, I. S. Jónsdóttir, and R. Langvatn. 2009.** Seasonal and interannual dietary variation during winter in female Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Arctic, Antarctic, and Alpine Research* 41:88-96.
- Cahill, A. E., et al. 2013.** How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences* 280:20121890.
- Conner, D. A. 1983.** Seasonal changes in activity patterns and the adaptive value of haying in pikas (*Ochotona princeps*). *Canadian Journal of Zoology* 61:411-416.
- Dearing, M. D. 1996.** Disparate determinants of summer and winter diet selection of a generalist herbivore, *Ochotona princeps*. *Oecologia* 108:467-478.
- Dearing, M. D. 1997a.** Effects of *Acomastylis rossii* tannins on a mammalian herbivore, the North American pika, *Ochotona princeps*. *Oecologia* 109:122-131.
- Dearing, M. D. 1997b.** The function of haypiles of pikas (*Ochotona princeps*). *Journal of Mammalogy* 78:1156-1163.
- Dearing, M. D. 1997c.** The manipulation of plant toxins by a food-hoarding herbivore, *Ochotona princeps*. *Ecology* 78:774-781.
- Erb, L. P., C. Ray, and R. Guralnick. 2011.** On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*). *Ecology* 92:1730-1735.
- Fenn, M., L. Geiser, R. Bachman, T. Blubaugh, and A. Bytnerowicz. 2007.** Atmospheric deposition inputs and effects on lichen chemistry and indicator species in the Columbia River Gorge, USA. *Environmental Pollution* 146:77-91.
- Furness, S., and J. Grime. 1982.** Growth rate and temperature responses in bryophytes: II. A comparative study of species of contrasted ecology. *The Journal of Ecology* 70:525-536.
- Hafner, D. J. 1993.** North American pika (*Ochotona princeps*) as a Late Quaternary biogeographic indicator species. *Quaternary Research* 39:373-380.
- Heggberget, T. M., E. Gaare, and J. P. Ball. 2010.** Reindeer (*Rangifer tarandus*) and climate change: Importance of winter forage. *Rangifer* 22:13-31.
- Horsfall, R. 1925.** The pika at sea level. *Journal of Mammalogy* 6:201-202.

- Huntly, N. J., A. T. Smith, and B. L. Ivins. 1986.** Foraging behavior of the pika (*Ochotona princeps*), with comparisons of grazing versus haying. *Journal of Mammalogy* 67:139-148.
- Jeffress, M. R., T. J. Rodhouse, C. Ray, S. Wolff, and C. Epps. 2013.** The idiosyncrasies of place: Geographic variation in the climate-distribution relationships of the American pika. *Ecological Applications* 4:864-878.
- Jiguet, F., A. S. Gadot, R. Julliard, S. E. Newson, and D. Couvet. 2007.** Climate envelope, life history traits and the resilience of birds facing global change. *Global Change Biology* 13:1672-1684.
- Kalela, O., T. Koponen, E. A. Lind, U. Skarén, and I. Tast. 1961.** Seasonal change of habitat in the Norwegian lemming, *Lemmus lemmus* (L.). *Annales Academiae Scientiarum Fennicae, Series A IV Biologica* 55:1-72.
- Karasov, W. H. 1982.** Energy assimilation, nitrogen requirement, and diet in free-living antelope ground squirrels, *Ammospermophilus leucurus*. *Physiological Zoology* 55:378-392.
- Kausrud, K. L., et al. 2008.** Linking climate change to lemming cycles. *Nature* 456:93-97.
- Kepner, R. E., and H. Maarse. 1970.** Changes in composition of volatile terpenes in Douglas fir needles during maturation. *Journal of Agricultural and Food Chemistry* 18:1095-1101.
- Kreuzer, M., and N. Huntly. 2003.** Habitat-specific demography: Evidence for source-sink population structure in a mammal, the pika. *Oecologia* 134:343-349.
- Lundquist, J. D., and F. Lott. 2008.** Using inexpensive temperature sensors to monitor the duration and heterogeneity of snow-covered areas. *Water Resources Research* 44:W00D16.
- MacArthur, R. A., and L. C. H. Wang. 1973.** Physiology of thermoregulation in the pika, *Ochotona princeps*. *Canadian Journal of Zoology* 51:11-16.
- MacArthur, R. A., and L. C. H. Wang. 1974.** Behavioral thermoregulation in the pika, *Ochotona princeps*: A field study using radiotelemetry. *Canadian Journal of Zoology* 52:353-358.
- Millar, C. I., and R. D. Westfall. 2010.** Distribution and climatic relationships of the American pika (*Ochotona princeps*) in the Sierra Nevada and western Great Basin, USA; Periglacial landforms as refugia in warming climates. *Arctic Antarctic and Alpine Research* 42:76-88.

- Milner, C., and D. Gwynne. 1974.** The Soay sheep and their food supply, Pp. 273-325 in *Island Survivors: The Ecology of the Soay Sheep of St. Kilda* (P. Jewell, C. Milner and J. Morton Boyd, eds.). The Athlone Press, London.
- Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008.** Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322:261-264.
- Morrison, S., L. Barton, P. Caputa, and D. S. Hik. 2004.** Forage selection by collared pikas, *Ochotona collaris*, under varying degrees of predation risk. *Canadian Journal of Zoology* 82:533-540.
- Morrison, S. F., and D. S. Hik. 2008.** Discrimination of intra-and inter-specific forage quality by collared pikas (*Ochotona collaris*). *Canadian Journal of Zoology* 86:456-461.
- Morrison, S. F., G. Pelchat, A. Donahue, and D. S. Hik. 2009.** Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. *Oecologia* 159:107-116.
- Morton, M. L., and M. E. Pereyra. 2008.** Haying behavior in a rodent, the bushy-tailed woodrat (*Neotoma cinerea*). *Northwestern Naturalist* 89:113-115.
- Ozgul, A., et al. 2010.** Coupled dynamics of body mass and population growth in response to environmental change. *Nature* 466:482-485.
- Pakarinen, P., and D. H. Vitt. 1974.** The major organic components and caloric contents of high arctic bryophytes. *Canadian Journal of Botany* 52:1151-1161.
- Parmesan, C. 2006.** Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637-669.
- Prins, H. H. 1982.** Why are mosses eaten in cold environments only? *Oikos* 38:374-380.
- R Development Core Team. 2011.** R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, www.R-project.org. Accessed 01 July 2011.
- Ray, C., and E. Beaver. 2007.** Distribution and abundance of the American pika (*Ochotona princeps*) within Lava Beds National Monument. U.S. Department of the Interior, National Park Service, Final Report.
- Richardson, D. 1981.** The biology of mosses. Halsted Press, New York.
- Rodhouse, T. J., et al. 2010.** Distribution of American pikas in a low-elevation lava landscape: Conservation implications from the range periphery. *Journal of*

- Mammalogy 91:1287-1299.
- Rowe, R. J., R. C. Terry, and E. A. Rickart. 2011.** Environmental change and declining resource availability for small-mammal communities in the Great Basin. *Ecology* 92:1366-1375.
- Shipley, L. A., J. S. Forbey, and B. D. Moore. 2009.** Revisiting the dietary niche: When is a mammalian herbivore a specialist? *Integrative and Comparative Biology* 49:274-290.
- Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012.** Ecological implications of behavioural syndromes. *Ecology Letters* 15:278-289.
- Sikes, R. S., W. L. Gannon, and The Animal Care and Use Committee of the American Society of Mammalogists. 2011.** Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235-253.
- Simpson, W. G. 2001.** Foraging activities of the pika (*Ochotona princeps*): A comparison of two populations. MS thesis, Portland State University, Portland.
- Simpson, W. G. 2009.** American pikas inhabit low-elevation sites outside the species' previously described bioclimatic envelope. *Western North American Naturalist* 69:243-250.
- Smith, A., L. Weidong, and D. Hik. 2004.** Pikas as harbingers of global warming. *Species* 41:4-5.
- Smith, A. T. 1974a.** The distribution and dispersal of pikas: Consequences of insular population structure. *Ecology* 55:1112-1119.
- Smith, A. T. 1974b.** The distribution and dispersal of pikas: Influences of behavior and climate. *Ecology* 55:1368-1376.
- Smith, A. T. 1978.** Comparative demography of pikas (*Ochotona*): Effect of spatial and temporal age-specific mortality. *Ecology* 59:133-139.
- Smith, A. T. 2008.** The world of pikas, Pp. 89-102 in *Lagomorph Biology* (P.C. Alves, N. Ferrand, and K. Hackländer, eds.). Springer Berlin Heidelberg, Berlin, Germany.
- Smith, A. T., and B. L. Ivins. 1983.** Colonization in a pika population: Dispersal vs philopatry. *Behavioral Ecology and Sociobiology* 13:37-47.
- Smith, A. T., and B. L. Ivins. 1984.** Spatial relationships and social organization in adult pikas: A facultatively monogamous mammal. *Zeitschrift für Tierpsychologie*

66:289-308.

- Smith, A. T., and M. L. Weston. 1990.** *Ochotona princeps*. Mammalian Species 352:1-8.
- Smith, F. A. 1997.** *Neotoma cinerea*. Mammalian Species 564:1-8.
- Stewart, J. A. E., and D. H. Wright. 2012.** Assessing persistence of the American pika at historic localities in California's Northern Sierra Nevada. Wildlife Society Bulletin 36:759-764.
- Tapper, S. C. 1973.** The spatial organisation of pikas, *Ochotona*, and its effect on population recruitment. Ph.D. dissertation. University of Alberta, Edmonton, Canada.
- Torregrossa, A. M., and M. D. Dearing. 2009.** Caching as a behavioral mechanism to reduce toxin intake. Journal of Mammalogy 90:803-810.
- Tuomainen, U., and U. Candolin. 2011.** Behavioural responses to human-induced environmental change. Biological Reviews 86:640-657.
- van der Wal, R. 2006.** Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. Oikos 114:177-186.
- Van Soest, P. J. 1994.** Nutritional ecology of the ruminant. Cornell University Press, Ithaca,.
- Verts, B., and Carraway, L. 1998.** Land mammals of Oregon. University of California Press, Berkeley.
- Walker, M. D., P. J. Webber, E. H. Arnold, and D. Ebert-May. 1994.** Effects of interannual climate variation on aboveground phytomass in alpine vegetation. Ecology 75:393-408.
- Warren, M., et al. 2001.** Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414:65-69.
- Waterman, P. G., and S. Mole. 1994.** Analysis of phenolic plant metabolites. Blackwell Scientific, Boston, Massachusetts.
- Wilkening, J. L., C. Ray, E. A. Beaver, and P. F. Brussard. 2011.** Modeling contemporary range retraction in Great Basin pikas (*Ochotona princeps*) using data on microclimate and microhabitat. Quaternary International 235:77-88.
- Wolterbeek, B. 2002.** Biomonitoring of trace element air pollution: Principles, possibilities and perspectives. Environmental Pollution 120:11-21

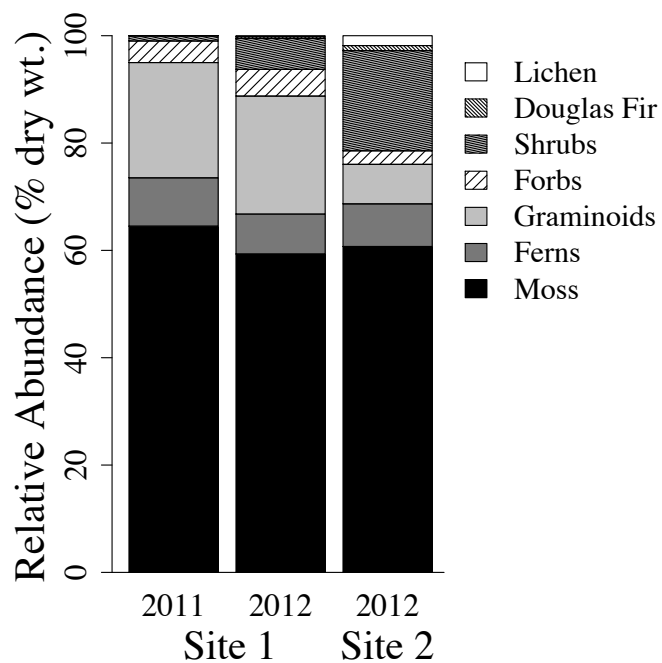


Fig. 2.1. American pika (*Ochotona princeps*) diet at 2 sites in the Columbia River Gorge. Relative frequency of different plant items in pika diet in 2011 ($n = 4$ animals at Site 1) and 2012 ($n = 7$ animals at Site 1, $n = 11$ animals at Site 2). Two animals were observed at Site 1 in both years. Moss comprised roughly 60% of the diet by dry weight at both sites in both years. Note: “Ferns” includes clubmosses in the genus *Selaginella*.

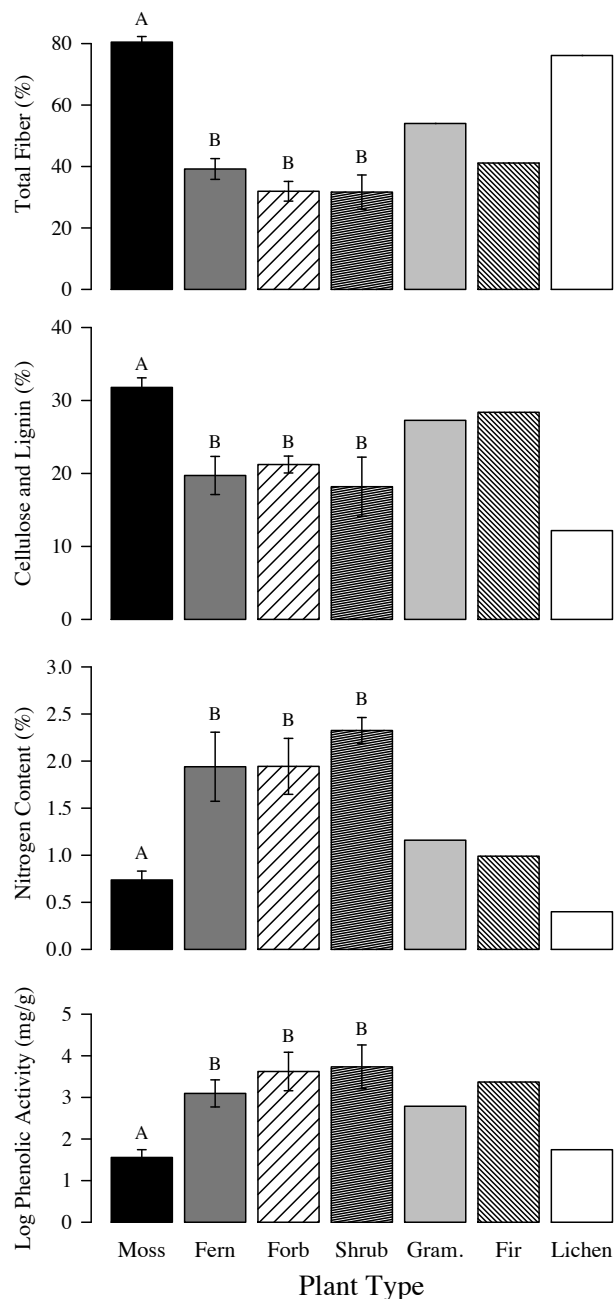


Fig. 2.2. Nutritional content of plants in pika diet. The dominant species in the diet were tested for (A) total fiber content (% dry weight), (B) cellulose and lignin content (% dry weight), (C) nitrogen content (% dry weight), and (D) phenolic activity (mg gallic acid equivalent/g dry weight). “Gram.” indicates graminoids, and “Ferns” includes clubmosses in the genus *Selaginella*. Bar shading is as in Fig. 1. Mean \pm SE between species in each growth form is shown. Letters indicate means that are significantly different at $P \leq 0.05$. Where error bars are absent, only a single species was tested, though the value represents the average of multiple biological replicates. Statistical analyses only include mosses, ferns, forbs, and shrubs because multiple species were tested.

Table 2.1. Percent vegetation cover at each site in summer (July) and winter (February). “Gram.” indicates graminoids, and “Fern” includes clubmosses in the genus *Selaginella*. Total vegetation cover (“*Total Veg.*”) did not include lichens because lichens were not usually foliose. Pikas (*Ochotona princeps*) were only observed consuming foliose lichens.

Cover Type	Site 1		Site 2	
	July	Feb.	July	Feb.
Bare rock	16.6	18.5	15.3	11.6
Lichen	21.5	22.0	13.4	17.0
Moss	54.3	51.2	68.6	63.4
Fern	2.4	5.9	2.0	7.6
Gram.	4.6	2.4	0.7	0.2
Forb	0.2	0	0	0.2
Shrub	0.4	0	0	0
<i>Total Veg.</i>	<i>61.9</i>	<i>59.5</i>	<i>71.3</i>	<i>71.4</i>

Table 2.2. Nutrient content of pika (*Octotona princeps*) summer diet. Mean (*SE*) nitrogen, total fiber, and cellulose/lignin are given in % dry weight. Phenolic activity is given in mg gallic acid equivalent/gram of dry weight of diet.

	Site 1		Site 2
	2011	2012	2012
Number of pikas	4	7	11
Total fiber (% NDF)	84.5 (4.4)	68.8 (1.3)	74.6 (3.6)
Cellulose/lignin (% ADF)	29.1 (0.2)	27.0 (0.4)	26.8 (0.8)
Nitrogen (%)	0.52 (0.09)	0.93 (0.02)	0.78 (0.11)
Phenolic activity (mg/g)	4.6 (2.0)	11.8 (1.1)	8.6 (1.1)

Table 2.3. Haypiles of pikas (*Ochotona princeps*) sampled in the Columbia River Gorge. Haypiles were excavated and weighed in September at 4 sites and haypile composition was calculated from a small, well-mixed sample.

Site	Elev. (m)	Year	<i>n</i>	Haypile size (kg)	Top components: % dry weight \bar{X} (SE) across all haypiles	
Site 1	144	2011	2	3.6	<i>Heuchera micracantha</i>	38.9 (9.4)
		2012	1	0.5	<i>Pseudotsuga menziesii</i>	32.0 (7.0)
					Gram.	8.5 (2.8)
					<i>Lupinus polyphyllus</i>	5.0 (2.6)
Site 2	150	2012	2	0.9	<i>Pseudotsuga menziesii</i>	14.4 (2.6)
					<i>Arnica spp.</i>	14.6 (14.6)
					<i>Rubus parviflorus</i>	14.5 (14.5)
Site 3	281	2011	2	1.2	<i>Cryptogamma crispa</i>	27.5 (6.5)
		2012	1	0.7	<i>Rosa gymnocarpa</i>	21.0 (11.0)
Site 4	91	2011	1	4.2	<i>Pseudotsuga menziesii</i>	68.5 (17.5)
		2012	2	2.8	<i>Acer macrophyllum</i>	19.8 (12.3)
					Caecal pellets	10.7 (5.3)

Table 2.4.—Haypile size of pikas (*Ochotona princeps*) in the Columbia River Gorge (CRG) compared to length of winter. Length of winter in the CRG was determined from temperature dataloggers, but at high-elevation habitat, it was estimated as the number of days without green vegetation (data from Smith and Ivins 1984; Walker et al. 1994). Haypile data from Niwot Ridge and Copper Creek, Colorado are reprinted from Dearing (1997b). Haypile data and length of winter from Yukon Territory are reprinted from simulations in Morrison et al. (2009). For CRG haypiles, dry weight was calculated from the water content of a small, well-mixed sample.

Site	<i>n</i>	Avg. fresh wt. (kg)	Avg. dry wt. (kg)	Length of winter (days)	Fresh wt./day (g)	Dry wt./day (g)
Site 1 (CRG)	2	3.6	2.31	41	88	56
Site 3 (CRG)	2	1.2	0.71	15	80	47
Site 4 (CRG)	1	4.2	3.48	47	89	74
Niwot Ridge, CO	10	25.2	6.86	295	85	23
Copper Creek, CO	NA	20.9	5.69	180	116	32
Yukon Territory	NA	NA	7.40	210	NA	35



Supporting Information 2.S1. Study sites in the Columbia River Gorge. (A) Site 1 and (B) Site 2. Both images were taken during the summer of 2012.

Supporting Information 2.S2. Nutritional content of common plants in the diet or environment at study sites. Means and standard deviations represent biological replicates. NDF: Neutral detergent fiber, or total fiber content. ADF: Acid detergent fiber, or cellulose and lignin content. Phenolic activity was measured in mg Gallic Acid Equivalents/g dry weight. %N: Percent Nitrogen.

	Scientific Name	Common Name	%NDF $\bar{X} \pm SE$	%ADF $\bar{X} \pm SE$	Phenolic Activity (mg GAEq/g)	%N
<i>Lic</i>	<i>Cladina portentosa</i>	Reindeer Lichen	76.1	12.2	5.72	0.4
<i>Moss</i>	<i>Pleurozium shreberi</i>	Big Red Stem Moss	83.6 ± 0.4	28.0 ± 1.7	4.30	0.6
	<i>Dicranum scoparium</i>	Broom Moss	74.5 ± 0.5	26.3 ± 1.2	6.13	0.9
	<i>Hypnum circinale</i>	Coiled Leaf Moss	81.5	31.0	3.45	1.0
	<i>Polytrichum piliferum</i>	Haircap Moss	73.7 ± 0.4	35.7 ± 1.5	11.66	1.2
	<i>Racomitrium lanuginosum</i>	Hoary Rock Moss	89.3 ± 0.3	29.1 ± 0.7	2.47	0.4
	<i>Rhytidiadelphus loreus</i>	Lanky Moss	77.5 ± 1.4	34.0 ± 2.5	2.98	0.7
	<i>Kindbergia oregana</i>	Oregon Beaked Moss	81.6 ± 0.6	34.2 ± 3.4	8.16	0.5
	<i>Hylocomium splendens</i>	Stair-Step Moss	82.3	36.1	4.03	0.6
	<i>Fern/ Clubmoss</i>	<i>Polypodium montense</i>	Pacific Polypody Fern	40.8 ± 8.4	23.2 ± 3.5	32.45
<i>Cryptogramma crispa</i>		Parsley Fern	32.7 ± 0.7	14.6 ± 0.7	28.80	2.6
<i>Selaginella spp.</i>		Selaginella (clubmoss)	44.1 ± 1.0	21.3 ± 1.0	11.57	1.8
<i>Gr.</i>	<i>Poaceae</i>	Graminoids	51.4 ± 5.9	25.9 ± 8.3	16.24	1.2
<i>Forb</i>	<i>Galium aparine</i>	Cleavers	30.5 ± 1.5	22.6 ± 1.2	92.01	2.9
	<i>Cerastium arvense</i>	Field Chickweed	43.6 ± 1.7	23.6 ± 0.8	12.19	2.2
	<i>Lupinus polyphyllus</i>	Large Leaved Lupine	29.0 ± 5.0	19.2 ± 3.7	26.60	1.9
	<i>Heuchera micracantha</i>	Small-flowered alumroot	24.2 ± 3.0	17.7 ± 2.1	132.80	1.3
	<i>Achillea millefolium</i>	Yarrow	32.3 ± 2.8	22.9 ± 1.5	18.57	1.5
<i>Shrub</i>	<i>Mahonia aquifolium</i> ^a	Oregon Grape	48.3 ± 8.8	30.2 ± 5.4	85.13	2.5
	<i>Rosa gymnocarpa</i>	Baldhip Rose	26.3	13.1	85.42	2.2
	<i>Rubus parviflorus</i>	Thimbleberry	27.0	16.0	9.18	2.6
	<i>Acer circinatum</i>	Vine Maple	25.1	13.4	46.03	2.0
<i>Tree</i>	<i>Pseudotsuga menziesii</i>	Douglas Fir	41.1 ± 1.0	28.4 ± 0.8	29.07	1.0
		Caecal Pellets	17.6 ± 2.3	8.8 ± 0.7	NA	5.8

^a: Data shown for young leaves of *M. aquifolium* because pikas showed a clear preference for young leaves of this plant. Mature leaves were higher in fiber content and lower in phenolic activity.

CHAPTER 3

THE IMPORTANCE OF BIOLOGICALLY RELEVANT MICROCLIMATES IN HABITAT SUITABILITY ASSESSMENTS

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The Importance of Biologically Relevant Microclimates in Habitat Suitability Assessments

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Abstract

Predicting habitat suitability under climate change is vital to conserving biodiversity. However, current species distribution models rely on coarse scale climate data, whereas fine scale microclimate data may be necessary to assess habitat suitability and generate predictive models. Here, we evaluate disparities between temperature data at the coarse scale from weather stations versus fine-scale data measured in microhabitats required for a climate-sensitive mammal, the American pika (*Ochotona princeps*). We collected two years of temperature data in occupied talus habitats predicted to be suitable (high elevation) and unsuitable (low elevation) by the bioclimatic envelope approach. At low elevations, talus surface and interstitial microclimates drastically differed from ambient temperatures measured on-site and at a nearby weather station. Interstitial talus temperatures were frequently decoupled from high ambient temperatures, resulting in instantaneous disparities of over 30°C between these two measurements. Microhabitat temperatures were also highly heterogeneous, such that temperature measurements within the same patch of talus were not more correlated than measurements at distant patches. An experimental manipulation revealed that vegetation cover may cool the talus surface by up to 10°C during the summer, which may contribute to this spatial heterogeneity. Finally, low elevation microclimates were milder and less variable than typical alpine habitat, suggesting that, counter to species distribution model predictions, these seemingly unsuitable habitats may actually be better refugia for this species under climate change. These results highlight the importance of fine-scale microhabitat data in habitat assessments and underscore the notion that some critical refugia may be counterintuitive.

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Introduction

Anthropogenic climate change has already profoundly affected range and community structure for many taxa [1–5]. Predicting future changes in species distributions and interactions is a challenge with great consequences for conserving biodiversity. However, realistic predictions and viable conservation plans depend on accurate forecasts of future habitat suitability.

Species distribution models (SDMs) are the most common approach to predicting habitat suitability under climate change. In this approach, a species' bioclimatic envelope is statistically determined from its present distribution, and suitable habitats are then predicted where similar climatic conditions will occur in the future [6]. Correlative SDMs have been criticized for failing to incorporate important factors like dispersal, biotic interactions, adaptation and behavioral plasticity [7]. However, the predictive power of these models is improved when used in conjunction with other approaches such as phylogenetics [8], mechanistic heat transfer models [9] or eco-physiological parameters [10].

In spite of recent criticism, few SDMs account for fine scale microhabitat features, which can profoundly influence microclimates and therefore habitat suitability [6,11,12]. In fact, a recent meta-analysis demonstrated that average climate grid lengths in

SDMs were 10,000-fold larger than the animals they study [13]. In addition, few studies explicitly incorporate data from the periphery of a species' range, though these populations may be particularly informative of climatic tolerance or critical habitat features [14].

The concept of refugia from climate change has received a great deal of recent attention in the literature [15–18]. Refugia are “safe-haven” habitats where species can persist in times of environmental change and may offer hope for *in situ* persistence, particularly for species with poor dispersal capacity [15]. A key feature of refugia is that their microclimates must be relatively stable and must buffer species against climate variability [17]. However, refugia can be difficult to identify, particularly when they are surrounded by areas of less suitable habitat [17]. Indeed, a key aim of conservation science is identifying and protecting habitat features that can serve as refugia through environmental changes.

In this study, we examined how micro-refugia may allow a climate-sensitive species to persist in habitat that appears unsuitable by the bioclimatic envelope approach. American pikas (*Ochotona princeps*) are small mammalian herbivores that have become widely considered indicators of climate change [19]. We hypothesized that vegetation features may create favorable

microclimates at low elevations by insulating against summer heat stress, which is known to affect pikas. Uncovering microhabitat variation in seemingly unsuitable climates provides important information about the thermal tolerance, capacity for plasticity and potential vulnerability of a species to future climate change. This information will therefore be vital for refining SDMs and targeting critical habitat refugia for conservation action.

Materials and Methods

Study organism

American pikas (*Ochotona princeps*; order *Lagomorpha*) are small mammalian herbivores that are typically distributed in high elevation mountains of western North America because they require short, cool summers and winters with extended snowpack [20]. Pikas are obligate talus specialists and are rarely found outside of rockslides and boulder fields that provide these suitable microclimates. In addition, pikas are extremely sensitive to high ambient temperatures [21,22] and possess a limited dispersal ability [23,24]. Unlike most alpine mammals, pikas do not hibernate during the winter but spend the short alpine summer amassing food caches called haypiles [25]. It has been hypothesized that warm summer temperatures may prevent pikas from constructing adequate haypiles, resulting in over-winter mortality [26]. This effect may be compounded by reduced snowpack, which exposes the animals to colder winter temperatures [27–29].

With climate change, parts of the pika's range are becoming unsuitable, resulting in upslope range retractions [27], population declines [28], and localized extinctions [27,30,31]. However, pikas persist in some regions with warm climates, including the Columbia River Gorge (CRG) in Oregon and Washington. Little study has been devoted to CRG pikas, though they exist over a thousand meters below the species' previously recognized bioclimatic envelope [20,32]. Given this species' demonstrated sensitivity to aspects of climate, marginal populations like the CRG have great potential to elucidate crucial features of micro-refugia and tractable conservation targets.

Study sites

We collected microhabitat data at four talus patches (ca. 15,000 m² each; hereafter, "sites") occupied by pikas in the CRG during June 2012–June 2014 (Table 1, Fig. S1). All sites were 32–35° in steepness, north to northwest facing and surrounded by a dense forest. One of the unique features of this region is a thick layer of moss that covers 25–80% of the surface of each rockslide. The moss also serves as a substrate for other plant cover, including graminoids, forbs and ferns. Sites ranged in elevation from 94 m to 437 m and varied in moss cover from over 65% ("high moss cover": sites 1 & 2) to less than 30% ("low moss cover": sites 3 & 4; Table 1, Fig. S1). Each of these sites is about a thousand meters lower in elevation than pikas are predicted to occur, based on the climate envelope approach [32].

We estimated potential solar exposure at each site using a previously-described insolation index [33]. The aspect and slope angle of each site were measured using a compass equipped with an inclinometer, and potential solar insolation was calculated as $\sin(\text{slope}) \times \cos(\text{aspect})$. This index ranges from -1 to 1 , where values of 1 indicate steeper north-facing slopes with little solar exposure, and values of -1 indicate steep south-facing slopes with high exposure [33].

We also sampled alpine microhabitats typical for pikas at two additional sites on the north face of Mt. Hood, approximately 30 km from sites 1–4 (Table 1). Clast size was similar across CRG and Mt. Hood sites, with most rocks at each talus site having

Table 1. Study sites in the CRG (elev. <500 m) and Mt. Hood (elev. >900 m).

Site	Latitude	Longitude	Elev. (m)	Veg. Cover (%) ^a	Moss Cover (%)	Avg. Clast Size (cm)	Aspect (deg.)	Slope (deg.)	Insolation ^b
Site 1	45°41'49"N	121°39'10"W	94	75.6	61.0	24.6	342	33	0.52
Site 2	45°41'16"N	121°47'45"W	194	71.2	68.6	40.1	2	32	0.53
Site 3	45°40'25"N	121°50'17"W	281	37.0	35.3	53.0	314	35	0.40
Site 4	45°33'50"N	122°09'14"W	437	35.7	25.5	48.7	313	33	0.37
Site 5	45°27'31"N	121°40'24"W	905	36.2	33.3	50.7	349	27	0.45
Site 6	45°24'41"N	121°41'59"W	1682	9.8	1.1	53.8	36	28	0.38

^aVegetation cover includes moss, ferns, grass, forbs and shrub cover on the talus.

^bInsolation = $\sin(\text{slope}) \times \cos(\text{aspect})$, from [33]. See Materials and Methods for interpretation of values.
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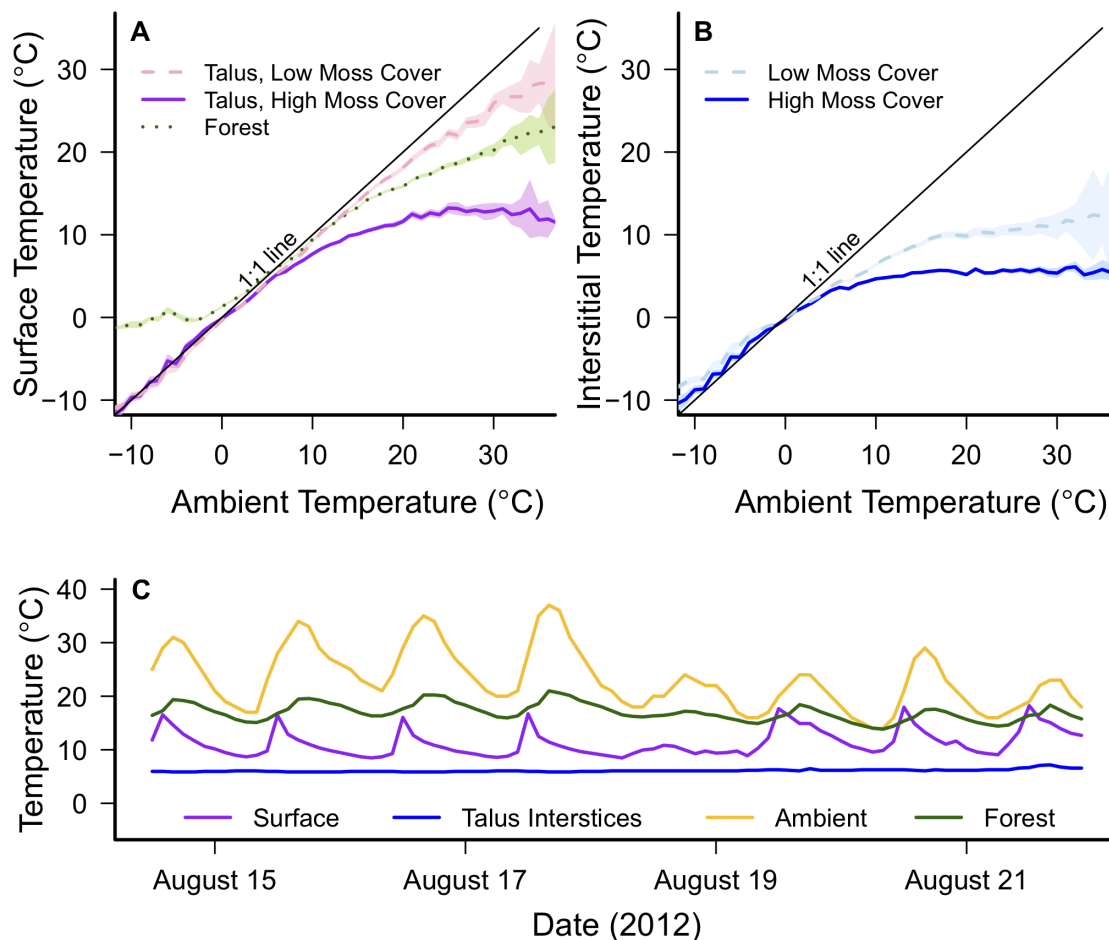


Figure 1. Pika microclimates compared to ambient temperatures. Temperature data were collected every two hours from June 2012 to June 2014 at four sites in the Columbia River Gorge. (A) Lines represent mean temperatures and shaded areas represent 95% confidence intervals. At high ambient temperatures, talus surface temperatures were lowest at sites with high moss cover. Forest surface temperatures were also cooler than ambient temperatures, but talus surface temperatures at sites with low moss cover closely tracked ambient temperatures. (B) Talus interstitial temperatures were functionally decoupled from variation in ambient temperature and remained a cool and constant 4–7°C at sites with high moss cover. (C) Time-trace of ambient, talus surface, forest surface, and talus interstitial temperatures measured at site 2 (high moss cover) during August 2012. doi:10.1371/journal.pone.0104648.g001

dimensions in the range of 20–100 cm, which is preferred for pikas (Table 1). All six sites were along publicly accessible trails on land owned by the United States Forest Service or Oregon Parks and Recreation Department. Appropriate permits for deploying dataloggers in Oregon State Parks were acquired from Oregon Parks and Recreation Department, permit no. 012-11.

Macroclimate temperature measurements

We downloaded ambient temperature data of the type used for SDMs from the Western Regional Climate Center (available: <http://www.raws.dri.edu/wraws/orF.html>) at the Cascades Locks station (45°40'10"N, 121°52'54"W, elevation 128 m). This weather station is centrally located in the CRG, 10.6 km from our four low elevation field sites, on average. It is closest (3.4 km) to site 3. To further characterize ambient temperatures at CRG sites, HOBO Pendant temperature dataloggers (model UA001-08;

Onset Computer, Bourne, MA) were suspended from a tree branch approximately 2 m above the ground and protected from solar radiation by a white plastic shield. All measurements labeled “ambient” reflect these 2 m shade air temperatures.

Microclimate temperature measurements

We measured temperatures in pika-relevant microhabitats with HOBO Pendant temperature dataloggers, which were housed in waterproof, plastic cases. At each site, we placed loggers at the talus surface in vegetated areas near the bottom of the talus slope where we had observed pikas foraging [34]. All surface loggers were shielded from direct solar radiation by moss. To characterize sub-surface temperatures, we threaded a second, paired sensor into the talus interstices to reach a final depth (i.e., vertical distance directly below the surface logger) of 80–100 cm. In some cases, small sub-surface rocks were removed for sensor insertion and

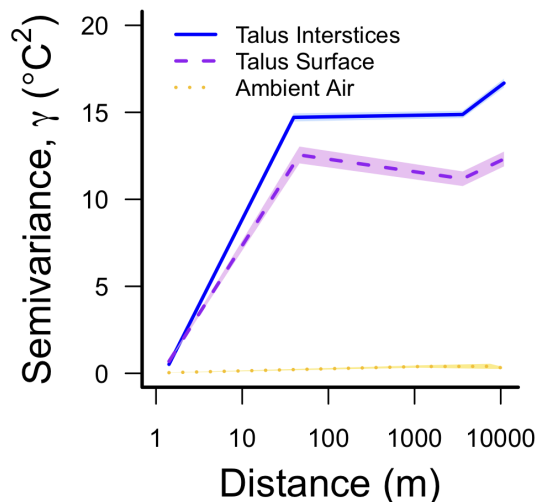


Figure 2. Spatial variation in pika-relevant microclimates and ambient temperatures. Thermal semivariance is shown as a function of distance between dataloggers at the 4 CRG sites during June–August 2013. Lines represent mean semivariance and shaded areas represent 95% confidence intervals. Temperatures in pika-relevant microclimates are far more heterogeneous and less spatially correlated than ambient shade temperatures measured 2 m above the ground. doi:10.1371/journal.pone.0104648.g002

immediately replaced, but vegetation cover at the surface was not disturbed. Finally, at sites 2 and 3, we deployed a third logger in the surrounding forest to characterize a potential midday thermal refuge. For consistency, these forest surface loggers were also shielded from solar radiation by moss.

Average summer temperature is known to impact pikas [27–29,33]. Furthermore, summer temperatures in the CRG are particularly unusual for this species [32]. To adequately capture average summer temperatures and to characterize spatial variation in summer temperatures, we deployed three additional surface-interstitial temperature logger pairs at each site during June–August 2013. To control for daily patterns of shade cover on the talus, one logger pair was placed near the top of the talus slope, and the other two logger pairs were placed approximately halfway up the talus on the east and west sides. Thus, at each site, we collected temperature measurements every two hours at four locations at the talus surface and four locations in the talus interstices during this time period. All datalogger locations were placed in areas of the talus where pikas were observed foraging, determined from behavioral observations [34].

Finally, to provide an initial characterization of humidity patterns between sites, we deployed HOBO relative humidity logger (model U12-011; one per site) at sites 2 and 3 during June 2012–August 2013. Loggers were placed in plastic housing with two mesh walls that permitted sufficient air exchange for accurate humidity readings but prevented the logger from direct contact with substrates or precipitation. This housing was then threaded approximately 80 cm into the talus interstices.

Spatial variation in temperature

To characterize thermal variation at very small scales, we deployed additional surface, interstitial and ambient loggers at site 2 and site 3 from July 14–August 30, 2013 in close proximity (1 m) to the sensor network described above. We then characterized

spatial variation in temperatures within and between sites with variograms, which are widely used in geostatistics to represent autocorrelation between measurements observed at different spatial locations. Variograms were recently recommended as a spatially explicit tool for examining thermal variance in microclimates as a function of distance between measurements [13]. The semivariance (γ) of temperature measurements at a given time point is half the average squared difference between logger-values (x), separated by a distance h , as given by:

$$\gamma(h) = \frac{1}{2N_h} \sum_{(i,j)|h_{ij}=h} (x_i - x_j)^2$$

where h is the number of logger pairs that are separated by this distance [35]. Lower semivariance therefore indicates higher autocorrelation between temperature measurements at a given separation distance. We computed semivariances with the *variogram* function in the R package *gstat* [36,37] for temperature measurements during June–August 2013. This function calculated semivariance at four average separation distances: 1 m (between closely placed loggers at sites 2 and 3), 39 m (between loggers within a site), 3,622 m (between loggers at nearby sites) and 10,908 m (between loggers at distant sites).

Vegetation cover and microclimate

To provide an initial test of the hypothesis that vegetation insulates against extreme surface temperatures, we manipulated vegetation cover at an additional talus patch (ca. 1 km from site 1). A patch of moss approximately 1 m in diameter was experimentally removed and relocated nearby where moss did not naturally grow (Fig. S2). We then measured temperatures every two hours from May 28–June 13, 2012 at four locations: under an unmanipulated patch of moss, under the transplanted moss, under a pile of bare control rocks that did not naturally have any moss, and under the pile of bare rocks where we removed moss (Fig. S2). The bare rocks in this experiment were approximately 15–20 cm in average dimension. All four locations were within 2 m of each other, and therefore should experience similar patterns of shade and sun exposure throughout the day. We compared daily average and maximum temperatures with two-way, repeated measures ANOVA, using treatment (i.e., manipulation vs. control) and cover (i.e., moss vs. rocks) as main effects and date as a repeated measure.

Microclimate and elevation

Temperature should decrease as elevation increases according to region-specific lapse rates, which may also vary by season [38]. In this region, previously reported lapse rates are $-2^\circ\text{C}/\text{m}$ for minimum temperatures and $-7^\circ\text{C}/\text{m}$ for maximum temperatures [39]. To investigate the impact of elevation on microclimate and calculate pika-relevant lapse rates, we placed paired surface-interstitial dataloggers at each high elevation site, which recorded temperatures at the same two-hour intervals as CRG loggers during June–August 2013. To test the effect of elevation on temperatures in pika-relevant microclimates, we computed Pearson correlation coefficients between elevation and average, maximum and minimum temperatures when all sites were free of snow.

Data deposition

The temperature and relative humidity measurements collected for this study are freely available in USPACE (<http://uspace.utah.edu>), the University of Utah's institutional repository. The accession number for these data is ark:/87278/s6b583mp

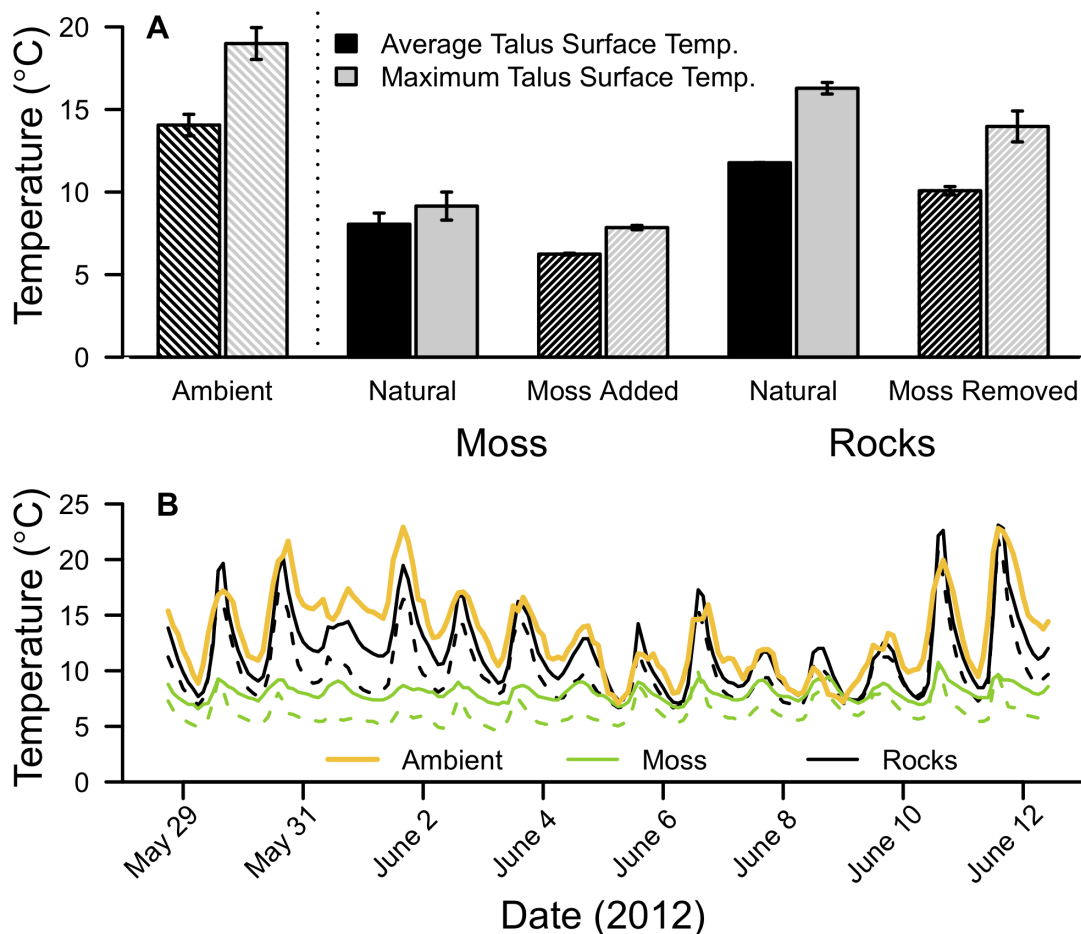


Figure 3. The effect of vegetation cover on summer surface temperatures. (A) Average and maximum summer surface temperatures were significantly cooler under moss, compared to rocks. Both types of surface temperature were cooler than ambient temperatures. (B) Time-trace of temperatures during this experiment. doi:10.1371/journal.pone.0104648.g003

(available: <http://content.lib.utah.edu/cdm/ref/collection/uspace/id/10610>).

Results

Macroclimate temperature measurements

We found no difference between 2 m shade ambient temperatures collected at sites 1–3 and temperatures measured at the Locks weather station for daily averages ($F_{3,1288} = 0.654$, $p = \text{NS}$), maxima ($F_{3,1288} = 2.162$, $p = \text{NS}$) or minima ($F_{3,1288} = 0.654$, $p = \text{NS}$) collected between October 2012 and August 2013. We therefore present data from our ambient loggers in future analyses because these data were collected at the same two-hour intervals as microclimate data.

Microclimate temperature measurements

We observed substantial divergence in microclimates relevant to pikas compared to 2 m shade ambient temperatures (Fig. 1). Although surface sensors were below moss cover at all sites,

patterns in talus surface temperature were dependent upon overall moss cover at the site. At sites with high moss cover (>65% coverage), talus surface temperatures rarely exceeded 20°C, even at ambient temperatures over 35°C (Fig. 1A, C). In contrast, at sites with low moss cover ($\leq 35\%$ coverage), talus surface temperatures were only a few degrees cooler than ambient temperatures, on average (Fig. 1A). Temperature at the forest floor was also 4–9°C cooler at high ambient temperatures, but rarely dipped below 0°C on very cold days (Fig. 1A).

At all sites, interstitial temperatures were strongly divergent from ambient temperatures (Fig. 1B). Even at ambient temperatures over 35°C, interstitial temperatures at sites with high moss cover remained a cool and constant 6–8°C, resulting in instantaneous disparities of up to 31.5°C between 2 m shade ambient temperatures (measured on-site) and microhabitats relevant to pikas (Fig. 1C). Daily variation in interstitial temperature was <1°C during the summer at sites with high moss cover, essentially decoupling interstitial temperatures from temperatures at the surface (Fig. 1B, C). At sites with low moss cover, interstitial

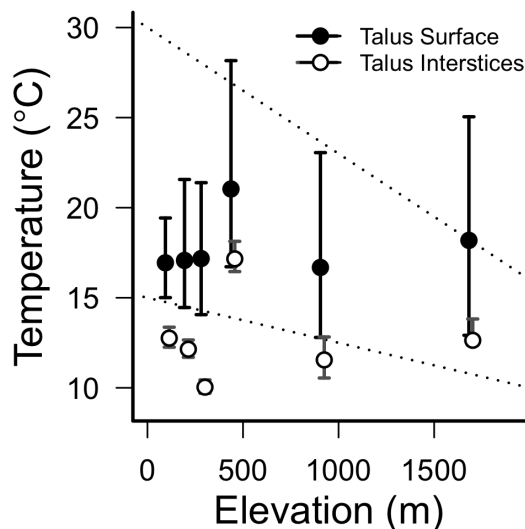


Figure 4. Average summer temperatures by elevation. Points represent mean summer temperatures at the talus surface (filled) and 1 m into talus interstices (open). Bars range from mean daily maxima to mean daily minima in each of these habitats. To show bars that overlap, interstitial points are shifted right by 20 m at some sites. Dotted lines represent previously-calculated lapse rates for the Pacific Northwest, from [39].

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temperatures were more variable but remained 5–11°C cooler on average than the talus surface.

Finally, relative humidity varied with ambient temperature (Fig. S3). At ambient temperatures below 10°C, both sites 2 and 3 had uniformly high relative humidity (>90%). At warmer ambient temperatures, relative humidity at both sites became more variable. However, site 2 (high moss cover) had consistently higher relative humidity (75–95%) than site 3 (low moss cover; 55–75% humidity).

Spatial variation in temperature

Semivariance, or the average squared difference in temperature measurements separated by a certain distance, remained very low ($<0.4^{\circ}\text{C}^2$) among ambient temperatures, indicating high autocorrelation between these measurements at all scales (Fig. 2). In contrast, spatial variation in pika-relevant microclimates far exceeded spatial variation in ambient temperatures at all scales (Fig. 2). At a 1 m separation distance, semivariances for temperatures recorded at the talus surface and in talus interstices were relatively low ($<1^{\circ}\text{C}^2$), indicating that temperature measurements separated by 1 m were highly correlated. However, at larger spatial scales, semivariance quickly increased to 12°C^2 for temperatures recorded at the talus surface and 16°C^2 for temperatures recorded in the talus interstices, indicating a very low degree of spatial autocorrelation. At separation distances larger than 1 m, microclimate temperatures recorded within the same site were not more similar to each other than temperatures recorded by sensors at the most distant sites.

Vegetation cover and microclimate

During the summer, average talus surface temperatures were 5–9°C cooler under both naturally occurring and transplanted moss, compared to bare rocks (Cover: $F_{(1,31)} = 239.2$, $p < 0.0001$;

Fig. 3A). Surprisingly, there was also a significant effect of treatment, such that unmanipulated moss and rocks were also 1–2°C warmer than manipulated moss and rocks (Treatment: $F_{(1,15)} = 118.6$, $p < 0.001$), but there was no interaction between cover and treatment. Maximum surface temperatures exhibited the same pattern (Cover: $F_{(1,31)} = 131.1$, $p < 0.0001$; Treatment: $F_{(1,15)} = 79.1$, $p < 0.001$; Fig. 3A). Over the duration of this experiment, both types of surface (moss and rocks) were cooler, on average, than ambient air temperature (Fig. 3A). However, surface measurements under rocks more closely tracked ambient temperatures; whereas surface measurements under moss were often up to 15°C cooler than ambient air temperature (Fig. 3B).

Microclimate and elevation

Summer temperatures in the CRG were substantially cooler than predicted by region-specific lapse rates ([39]; Fig. 4). In fact, elevation was not predictive of talus interstitial temperatures or surface temperatures. All Pearson correlation coefficients between elevation and average, minimum or maximum temperatures were ≤ 0.6 and non-significant ($p > 0.2$). The lowest elevation sites also had less than half the daily temperature range (i.e., daily maximum – daily minimum) of high elevation sites.

Discussion

We investigated the effects of vegetation and elevation on microclimates relevant to a sensitive species living in an atypical habitat. On the basis of climate envelope models alone, the Columbia River Gorge (CRG) appears to be unsuitable habitat for pikas because it does not have short, cool summers or long winters, which are commonly recognized as criteria for pika persistence [e.g., 20,32,40]. However, our results demonstrate that cool microclimates are available in the CRG and that these low elevation rockslides may actually be more suitable for pikas than the nearby alpine talus that is more typical for this species.

Interstitial temperatures in the talus typically depend on heat-transfer processes at the surface (i.e., convection, conduction, solar and long-wave thermal radiation). However, during the summer in the CRG, daily fluctuations in this microhabitat are frequently less than 0.2°C and instantaneous disparities with ambient temperatures may be up to 31.5°C (Fig. 1C), suggesting that, at some locations, the surface heat-transfer processes do not penetrate more than 1 m into the talus. As a result, interstitial microclimates are functionally decoupled from heat-transfer at the surface and are likely governed by other processes. CRG taluses have several features that are atypical for pika habitat, including a thick layer of vegetation covering the talus, high relative humidity, and reduced solar insolation (i.e., due to slope orientation and/or shade from the surrounding forest canopy). Each of these features may contribute to the significant disparities observed between the microclimate relevant to pikas and the macroclimate observed at weather stations.

Vegetation features, and moss cover in particular, appear to buffer against climate variability, differentiating talus microclimates at some sites from the surrounding macroclimate (Fig. 1). Our high moss cover sites likely experience more shade (Table 1) and higher humidity (Fig. S3). These features may facilitate moss growth because mosses are predisposed to grow in shady, humid conditions [41]. However, our experimental results suggest that mosses may also actively buffer talus microclimates from ambient temperature extremes (Fig. 3). In other ecosystems and urban environments, vegetation can similarly lower surface temperatures of dark substrates by 5–20°C [42,43]. This cooling effect may be caused by changes in diffuse reflectivity (albedo), which can

strongly affect surface temperatures. Specifically, mosses may raise the albedo of the dark basalt that makes up the talus in this region, increasing the amount of solar radiation that is reflected. The albedo of basalt is 0.1, whereas albedo estimates of moss and lichen-dominated surfaces are two to four times higher [0.2–0.4; 44]. For comparison, a change of albedo in 0.2 is capable of producing a 10°C change in midday surface temperatures [45]. In addition to increasing albedo, vegetation cover may also act as a layer of insulation [44], or it may have an evaporative cooling effect.

Relative humidity and/or precipitation may also play an important role in pika persistence and abundance in this habitat by maintaining high quality vegetation or water for evaporative cooling. During our study, the Locks weather station near our sites averaged ~150 mm of annual rainfall and 70–80% relative humidity. Similarly, relative humidity in the talus rarely dipped below 75% at our high moss cover sites (Fig. S3). Although differences in relative humidity may be responsible for the distribution of vegetation cover on talus in this region, the vegetation itself may also locally raise humidity through evapotranspiration. Although we did not explicitly measure their effects on microclimates, sub-surface water or ice may also influence microclimate temperatures in this region. Water availability is a strong determinant of pika persistence and abundance in other parts of their range [30,46], and we regularly experienced cold air flowing out of talus cavities, which may indicate subsurface rock-ice or water features [47].

These low elevation sites also experience relatively little solar radiation due to northerly slope orientations and daytime shade cover provided by the surrounding forest canopy. This reduced insolation likely has a large effect on both the magnitude and variability of temperatures in pika habitat. For example, although we did not directly measure solar radiation during this study, site 4 likely received more sunlight because its surrounding forest canopy is shorter than other sites due to a wildfire in 1991 (Fig. S1). Indeed, although they are similar in elevation, slope angle, aspect and moss cover, summer surface and interstitial temperatures were approximately 5°C warmer and much more variable at site 4, compared to site 3 (Fig. 4). Similarly, a shorter forest canopy and higher insolation indices at our high elevation sites may have also contributed to greater temperature variability, compared to the CRG (Fig. 4). Unlike high elevations, CRG microclimates rarely experienced temperature extremes beyond the best estimates of thresholds for acute heat stress (25.5°C) [22] or cold stress (−10°C) [27] in this species.

Shade and vegetation cover are also likely responsible for the mild surface temperatures that we observed in the forest at sites 2 and 3 (Fig. 1A). Consistent with our findings, forest surface temperatures in other studies are typically 5–8°C lower than ambient temperatures measured above the ground [48,49]. Forest surface temperatures were typically a few degrees warmer than talus surface temperatures at sites with high moss cover (Fig. 1A, C), but the forest may represent an important thermal refuge for pikas to remain active at midday at sites with low moss cover. Similarly, the forest may also serve as a winter refuge for CRG pikas, as forest temperatures also remained warmer than talus temperatures on the few very cold days in 2012–2014 (<−10°C; Fig. 1A). Finally, thick understory vegetation in the forest may also make pikas less visible to predators or serve as an additional food resource [34].

Regardless of mechanism, the temperature disparities that we observed between weather stations and talus interstices in the CRG far exceed those in the microclimate literature. Previous studies examining ambient temperatures and microclimates at or

below the soil surface report disparities up to 10°C between these measurements [12]. Similarly, burrow systems have a significant ability to buffer animals against temperature fluctuations, but instantaneous differences between ambient shade temperatures and internal burrow temperatures rarely exceed 10°C in the literature [50–55]. Rock-ice features in pika habitat in the Sierra Nevada range can also cool the average warm-season temperatures in talus interstices by 3.8°C, compared with the surface. In contrast, we observed differences of up to 11°C between average surface and interstitial microclimates in the warm season, and instantaneous disparities up to 31.5°C between talus interstitial temperatures and ambient temperature measured on site. For comparison, this disparity is roughly equivalent to 4500 m of elevation change (according to lapse rates for this region) and far exceeds the magnitude of observed and predicted directional climate change.

CRG microhabitats were also highly heterogeneous. A lack of spatial autocorrelation between temperature measurements (even between loggers at the same site, Fig. 2) suggests that spatially uncorrelated noise exceeds deterministic trends in temperature at scales over ~10 m in these microhabitats. This result may be due to the patchy nature of moss and vegetation cover on the talus or to the movement of shade cover across the talus throughout the day. Interestingly, strong correlations were observed in the Great Basin between interstitial temperatures in montane pika habitat and ambient temperatures measured at valley weather stations 40–60 km away [29]. The temperature disparities and spatial heterogeneity that we report here highlight the uniqueness of habitats with high vegetation cover, and more generally, the refugial value of places where surface conditions can partially decouple ambient temperatures from sub-surface microclimates. Importantly, high spatial heterogeneity in a habitat may also allow animals to behaviorally mitigate the impacts of directional climate change by shuttling between different areas within a habitat [12].

Taken together, these results suggest that the low elevation habitat in the CRG may actually be a better refuge from stresses caused by climate change than typical, high elevation habitat and that CRG pika populations have the potential to be relatively resilient to future environmental change. These results are a notable example of an unexpected or counter-intuitive thermal refuge, since the CRG was predicted to be unsuitable based on SDM results alone [e.g., 20,32,40]. Our results also suggest tractable conservation priorities for pikas and other thermally sensitive species in this region. Specifically, land managers could focus on protecting habitat features that contribute to the unique microclimates, including moss (e.g., from trampling by hikers or unsustainable harvest for the horticulture trade) and forest canopy cover (e.g., from logging or severe wildfires).

An ecologically similar species that is likely to be directly affected by talus microclimates in this region is the bushy-tailed woodrat, *Neotoma cinerea*. Like pikas, these woodrats inhabit exclusively rocky habitats in montane forests and are sensitive to high ambient temperatures [56]. This species has experienced localized extinctions in response to past climate change [57] and appears to be suffering a range collapse in response to contemporary climate change [1]. However, we have observed fresh woodrat sign at many talus patches in the CRG and speculate that cool microclimates and high vegetation availability also facilitate woodrat persistence at this unusually low elevation.

Course-scale SDMs should not be discarded as a predictive tool, but climate data and their resolution must be selected with great care. We echo calls from Potter et al. [13] that the ideal spatial resolution for climate data in SDMs must be related to the body size of the species of interest. However, we also suggest that

heterogeneity of microclimate features and the spatial or temporal extent to which an organism samples these features should also inform selection of appropriate climate data in SDMs. For example, larger, less-mobile organisms are more likely to experience macroclimates observed at greater spatial grid lengths. Conversely, our results demonstrate that ambient temperature data collected at distant locations may have relatively little relevance for small, mobile species that can rapidly shuttle between complex microhabitats, particularly in environments or seasons when surface features such as snow or vegetation decouple macro- and microclimates. Finally, the timing, frequency and amount of precipitation are rarely part of habitat suitability analyses, though they should be considered.

Microhabitat data will be critical for developing and validating spatial statistics to understand the relationship between climate change and microclimate stability [13]. Relatively little is known about the degree to which microclimates will respond to macroclimatic changes or the time-scale on which these changes will occur. Collecting organism-relevant microhabitat data at finer spatial resolutions and longer time scales will be critical for bridging this gap and for determining the resiliency of microclimate refugia to continued changes in broad-scale temperature and precipitation patterns. Such studies are becoming increasingly feasible, given the availability of relatively inexpensive and small temperature dataloggers with long battery lives.

Our results highlight the need for fine-scale temperature measurements in microhabitats that are relevant to a focal species. When identifying refugia from climate change for conservation action, we can learn much from fine-scale observations of populations in seemingly marginal climates. Indeed, the conservation value of refugia lies in promoting species' ability to persist even under unfavorable climates [16].

References

- Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, et al. (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322: 261–264.
- Rowe RJ, Terry RC, Rickart EA (2011) Environmental change and declining resource availability for small-mammal communities in the Great Basin. *Ecology* 92: 1366–1375.
- Sheldon KS, Yang S, Tewksbury JJ (2011) Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. *Ecol Lett* 14: 1191–1200.
- Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science* 333: 1024–1026.
- Şekercioğlu ÇH, Primack RB, Wormworth J (2012) The effects of climate change on tropical birds. *Biol Cons* 148: 1–18.
- Austin MP, Van Niel KP (2011) Improving species distribution models for climate change studies: variable selection and scale. *J Biogeogr* 38: 1–8.
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob Ecol Biogeogr* 12: 361–371.
- Buckley LB, Kingsolver JG (2012) Functional and Phylogenetic Approaches to Forecasting Species' Responses to Climate Change. *Annu Rev Ecol Evol Syst* 43: 205–226.
- Kearney MR, Wintle BA, Porter WP (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Cons Lett* 3: 203–213.
- Sinervo B, Méndez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, et al. (2010) Erosion of Lizard Diversity by Climate Change and Altered Thermal Niches. *Science* 328: 894–899.
- Suggitt AJ, Gillingham PK, Hill JK, Huntley B, Kunin WE, et al. (2011) Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* 120: 1–8.
- Graae BJ, De Frenne P, Kolb A, Brunet J, Chabrierie O, et al. (2012) On the use of weather data in ecological studies along altitudinal and latitudinal gradients. *Oikos* 121: 3–19.
- Potter KA, Woods HA, Pincebourde S (2013) Microclimatic challenges in global change biology. *Glob Chang Biol* 19: 2932–2939.
- Channell R, Lomolino MV (2000) Dynamic biogeography and conservation of endangered species. *Nature* 403: 84–86.
- Keppel G, Wardell-Johnson GW (2012) Refugia: keys to climate change management. *Glob Chang Biol* 18: 2389–2391.
- Ashcroft MB (2010) Identifying refugia from climate change. *J Biogeogr* 37: 1407–1413.
- Ashcroft MB, Gollan JR, Warton DI, Ramp D (2012) A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Glob Chang Biol* 18: 1866–1879.
- Dobrowski SZ (2011) A climatic basis for microrefugia: the influence of terrain on climate. *Glob Chang Biol* 17: 1022–1035.
- Smith A, Weidong L, Hik D (2004) Pikas as harbingers of global warming. *Species* 41: 4–5.
- Hafner DJ (1993) North American pika (*Ochotona princeps*) as a Late Quaternary biogeographic indicator species. *Quat Res* 39: 373–380.
- MacArthur RA, Wang LCH (1974) Behavioral thermoregulation in the pika, *Ochotona princeps*: a field study using radiotelemetry. *Can J Zool* 52: 353–358.
- Smith AT (1974) The distribution and dispersal of pikas: influences of behavior and climate. *Ecology* 55: 1368–1376.
- Smith AT (1974) The distribution and dispersal of pikas: consequences of insular population structure. *Ecology* 55: 1112–1119.
- Smith AT, Weston ML (1990) *Ochotona princeps*. *Mammal Species* 352: 1–8.
- Dearing MD (1997) The function of haypiles of pikas (*Ochotona princeps*). *J Mammal* 78: 1156–1163.
- Ray C, Wilkening JL, Sweazea K (2009) Signs of demographic change and physiological stress in Rocky Mountain pikas. *North American Pika Conference*, Jackson, WY.
- Beever EA, Ray C, Wilkening JL, Brussard PF, Mote PW (2011) Contemporary climate change alters the pace and drivers of extinction. *Glob Chang Biol* 17: 2054–2070.
- Beever EA, Dobrowski SZ, Long J, Mynsberge AR, Piekielek NB (2013) Understanding relationships among abundance, extirpation, and climate at ecoregional scales. *Ecology* 94: 1563–1571.
- Beever EA, Ray C, Mote PW, Wilkening JL (2010) Testing alternative models of climate-mediated extirpations. *Ecol Appl* 20: 164–178.

Supporting Information

Figure S1 Comparison of moss cover at four sites in the Columbia River Gorge. For reference, pikas are also shown at sites of high (E) and low moss cover (F). *Photo credits:* (A–E) J. Varner, (F) J. J. Horns. (TIFF)

Figure S2 Moss transplant experiment. (A) In an area of the site where moss did not naturally grow, temperatures were measured under rocks and transplanted moss. (B) In an area of the site naturally covered with moss, temperatures were measured under rocks where moss was removed and a patch of unmanipulated moss. Arrows indicate datalogger locations. (TIFF)

Figure S3 Relative humidity compared to ambient temperature. Relative humidity measurements were collected every 2 hours in the talus interstices at sites 2 and 3 during June 2012–August 2013. Ambient temperatures (2 m height, shaded) were collected at site 3 at the same temperature intervals. Lines represent mean temperatures and shaded areas represent 95% confidence intervals. (TIFF)

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Author Contributions

Conceived and designed the experiments: JV MDD. Performed the experiments: JV. Analyzed the data: JV. Wrote the paper: JV MDD.

30. Erb LP, Ray C, Guralnick R (2011) On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*). *Ecology* 92: 1730–1735.
31. Stewart JAE, Wright DH (2012) Assessing persistence of the American pika at historic localities in California's northern Sierra Nevada. *Wild Soc Bull* 36: 759–764.
32. Simpson WG (2009) American pikas inhabit low-elevation sites outside the species' previously described bioclimatic envelope. *WVAN* 69: 243–250.
33. Jeffress MR, Rodhouse TJ, Ray C, Wolff S, Epps C (2013) The idiosyncrasies of place: geographic variation in the climate-distribution relationships of the American pika. In press. *Ecol Appl*.
34. Varner J, Dearing MD (2013) Dietary plasticity in pikas as a strategy for atypical resource landscapes. *J Mammal* 94: 72–81.
35. Janis MJ, Robeson SM (2004) Determining the spatial representativeness of air-temperature records using variogram-nugget time series. *Phys Geog* 25: 513–530.
36. Pebesma E (2004) Multivariable geostatistics in S: the gstat package. *Comput Geosci* 30: 683–691.
37. R Core Development Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
38. Stone PH, Carlson JH (1979) Atmospheric lapse rate regimes and their parameterization. *J Atmos Sci* 36: 415–423.
39. Mote PW, Lundquist JD, Minder J (2009) Surface and free-air lapse rates in the Cascade Mountains of Washington. 21st Conference on Climate Variability and Change. Phoenix, AZ: American Meteorological Society.
40. Galbreath KE, Hafner DJ, Zamudio KR (2009) When Cold is Better: Climate-Driven Elevation Shifts Yield Complex Patterns of Diversification and Demography in an Alpine Specialist (American Pika, *Ochotona princeps*). *Evolution* 63: 2848–2863.
41. Zechmeister HG (1995) Growth rates of five pleurocarpous moss species under various climatic conditions. *J Bryol* 18: 455–468.
42. Qiu G, Li H, Zhang Q, Chen W, Liang X, et al. (2013) Effects of Evapotranspiration on Mitigation of Urban Temperature by Vegetation and Urban Agriculture. *J Integr Agric* 12: 1307–1315.
43. Yang X, Zhao L, Bruse M, Meng Q (2013) Evaluation of a microclimate model for predicting the thermal behavior of different ground surfaces. *Build Environ* 60: 93–104.
44. Beringer J, Lynch AH, Chapin FS, Mack M, Bonan GB (2001) The representation of arctic soils in the land surface model: the importance of mosses. *J Clim* 14: 3324–3335.
45. Li H, Harvey J, Kendall A (2013) Field measurement of albedo for different land cover materials and effects on thermal performance. *Build Environ* 59: 536–546.
46. Erb LP, Ray C, Guralnick R (2013) Determinants of pika population density vs. occupancy in the Southern Rocky Mountains. *Ecol Appl* 24: 429–435.
47. Millar CI, Westfall RD (2010) Distribution and climatic relationships of the American pika (*Ochotona princeps*) in the Sierra Nevada and western Great Basin, USA; periglacial landforms as refugia in warming climates. *Arct Antarct Alp Res* 42: 76–88.
48. Parker GG, Lowman M, Nadkarni N (1995) Structure and microclimate of forest canopies. In: Lowman M, Nadkarni N, editors. *Forest canopies*. San Diego, CA: Academic Press. 73–106.
49. Rambo TR, North MP (2008) Spatial and Temporal Variability of Canopy Microclimate in a Sierra Nevada Riparian Forest. *Northwest Sci* 82: 259–268.
50. Johnson SR (1970) The thermal regulation, microclimate, and distribution of the mountain beaver, *Aplodontia rufa pacifica* Merriam: Oregon State University. Available: <http://hdl.handle.net/1957/9420>. Accessed 20 June 2014.
51. Shenbrot G, Krasnov B, Khokhlova I, Demidova T, Fielden L (2002) Habitat-dependent differences in architecture and microclimate of the burrows of Sundevall's jird (*Meriones crassus*) (*Rodentia: Gerbillinae*) in the Negev Desert, Israel. *J Arid Environ* 51: 265–279.
52. Šumbera R, Chitaukali W, Elichová M, Kubová J, Burda H (2004) Microclimatic stability in burrows of an Afrotropical solitary bathyergid rodent, the silvery mole-rat (*Heliophobius argenteocinereus*). *J Zool* 263: 409–416.
53. Du Plessis A, Kerley GI, Winter PD (1992) Refuge microclimates of rodents: a surface nesting *Otomys unisulcatus* and a burrowing *Parotomys brantsii*. *Acta Theriol* 37: 351–351.
54. Pike D, Mitchell J (2013) Burrow-dwelling ecosystem engineers provide thermal refugia throughout the landscape. *Anim Conserv* 16: 694–703.
55. Stark HE (1963) Nesting habits of the California vole, *Microtus californicus*, and microclimatic factors affecting its nests. *Ecology* 663–669.
56. Smith FA (1997) *Neotoma cinerea*. *Mammal Species* 564: 1–8.
57. Grayson DK, Madsen DB (2000) Biogeographic implications of recent low-elevation recolonization by *Neotoma cinerea* in the Great Basin. *J Mammal* 81: 1100–1105.

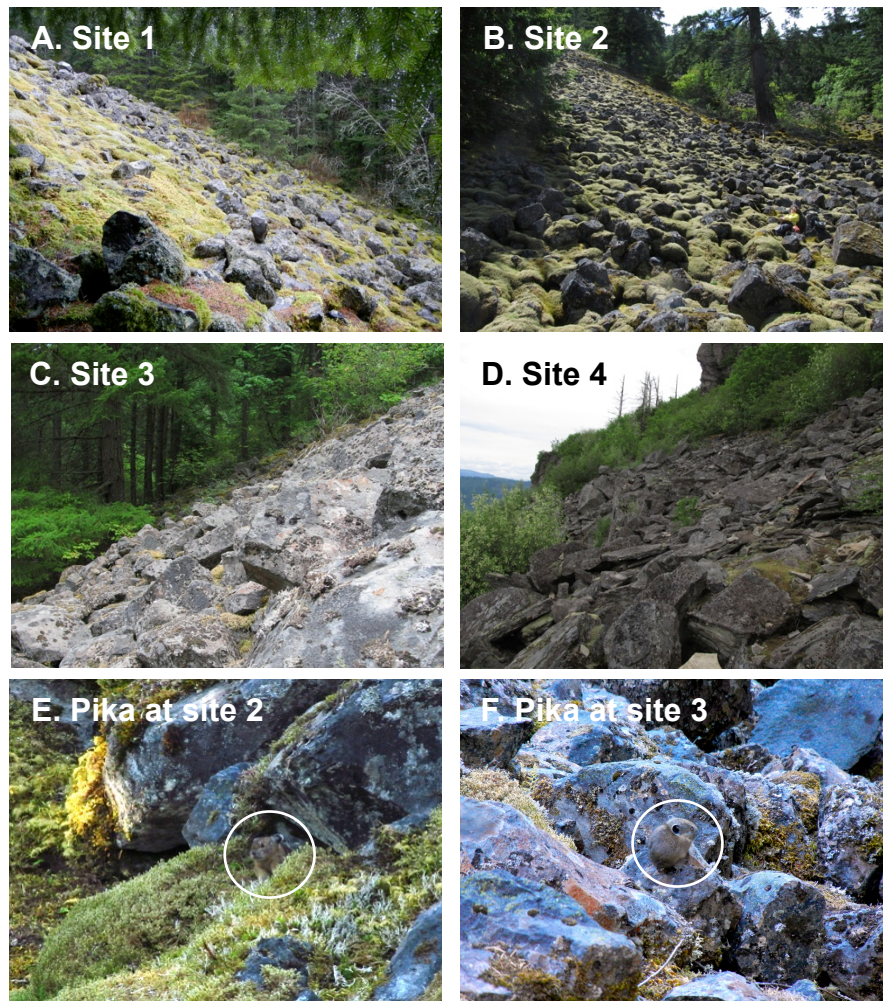


Figure S1. Comparison of moss cover at four sites in the Columbia River Gorge. For reference, pikas are also shown at sites of high (E) and low moss cover (F). *Photo credits:* (A-E) J. Varner, (F) J. J. Horns.

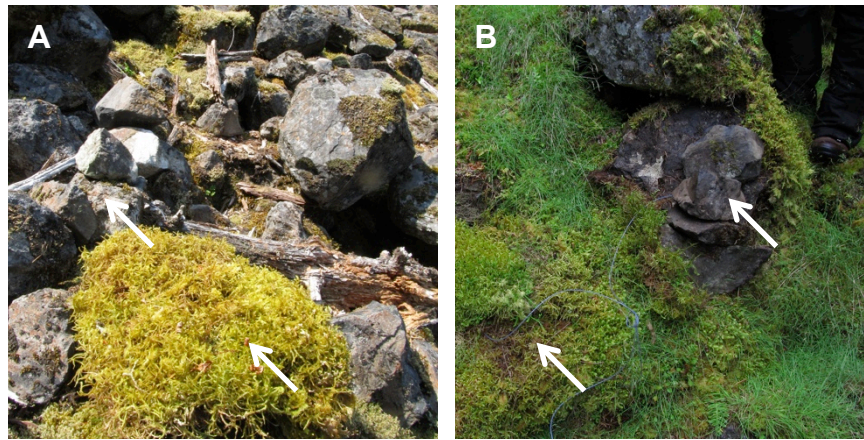


Figure S2. Moss transplant experiment. (A) In an area of the site where moss did not naturally grow, temperatures were measured under rocks and transplanted moss. (B) In an area of the site naturally covered with moss, temperatures were measured under rocks where moss was removed and a patch of unmanipulated moss. Arrows indicate datalogger locations.

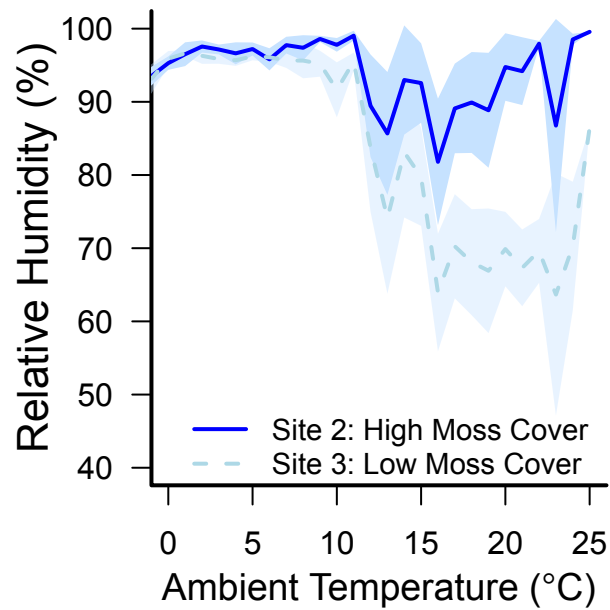


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CHAPTER 4

PLASTIC PIKAS: BEHAVIORAL FLEXIBILITY IN LOW- ELEVATION PIKAS (*OCHOTONA PRINCEPS*)

Abstract

Behavior is an important mechanism for accommodating rapid environmental changes. Understanding a species' capacity for behavioral plasticity is therefore a key, but understudied, aspect of developing tractable conservation and management plans under climate change scenarios. Here, we quantified behavioral differences between American pikas (*Ochotona princeps*) living in an atypical, low-elevation habitat versus more typical, alpine habitat. With respect to foraging strategy, low-elevation pikas spent more time consuming vegetation and less time caching food for winter, compared to high-elevation pikas. Low-elevation pikas were also far more likely to be detected in forested microhabitats off the talus than their high-elevation counterparts, particularly at midday. Finally, pikas living in the atypical habitat had extremely small home range sizes compared to those in typical habitat or any previously published home range sizes for this species. Although behavioral flexibility likely allows pikas to accommodate some extreme conditions in this habitat, they may still rely on critical habitat factors such as suitable microclimate refugia. Further study will be necessary to determine the capacity of pikas in other habitats to behaviorally mitigate the ongoing effects of climate change.

Introduction

Globally, climate change is occurring at an ever accelerating rate and has already caused changes in population dynamics (Kausrud et al. 2008), distribution and range shifts (Moritz et al. 2008), and localized extinctions of many species (Cahill et al. 2013). One rapid mechanism by which individuals of a species can respond to changes in climate is through behavioral plasticity (Sih et al. 2012). Changing behavior operates on a much faster time scale than distribution or range shifts, particularly for species with low vagility (Huey et al. 2012). Many behavioral responses have already been documented in response to changing environmental conditions, including shifts in phenology, reproduction, or use of food resources (Tuomainen and Candolin 2011). In addition, many species can tolerate changes in temperature or precipitation patterns by selecting microhabitats that moderate extreme climates and/or restricting activity to favorable time periods (e.g., Sinervo et al. 2010, Murray and Smith 2012).

In many cases, studying behavioral flexibility and variation at a range edge or marginal habitat can provide information about habitat features that are crucial for persistence under times of unfavorable conditions (Ashcroft 2010, Keppel and Wardell-Johnson 2012). Similarly, marginal habitats may also elucidate a species' capacity for plasticity in response to environmental stressors (Channell and Lomolino 2000). In this study, we use the term "plasticity" in the sense of "developmental behavioral plasticity," defined by Snell-Rood (2013) as the ability of a population to adopt different behaviors in different environments (as opposed to "activational plasticity," or the ability of an individual to express different behavioral syndromes throughout its lifetime; Snell-Rood 2013). Understanding a species' ability to modify its behavior is critical for identifying

potentially vulnerable populations and for developing future conservation and management plans.

The American pika is a small, generalist, mammalian herbivore (Order: *Lagomorpha*) that is largely a habitat specialist in high-elevation talus (rock slides and boulder fields) in western North America. Pikas are an ideal species for investigating behavioral plasticity for several reasons. First, they are diurnal and easily observed when active on the surface (Beever et al. 2008). They also exhibit a range of thermoregulatory and foraging behaviors that vary between habitats (Smith 1974). Since they do not hibernate, pikas spend the short alpine growing season collecting and storing vegetation in food caches called haypiles, which sustain them over the winter (Dearing 1997).

Pikas appear to be imminently threatened by climate change in many parts of their range (Beever et al. 2011, Beever et al. 2013, Stewart et al. 2015), and it is thought that warmer summer temperatures may preclude foraging, resulting in low-quality food caches for winter. Furthermore, reduced snowpack may expose the animals to more extreme winter temperatures (Tapper 1973, Smith 1978, Beever et al. 2010). However, the effect of climate on pikas appears complex and locality-specific (Jeffress et al. 2013). Furthermore, the persistence of many low-elevation populations in anthropogenic or seemingly marginal habitats (e.g., Beever et al. 2008, Simpson 2009, Rodhouse et al. 2010, Manning and Hagar 2011, Millar et al. 2013) suggests that pikas may possess a wider range of behavioral and habitat plasticity than is commonly thought.

The Columbia River Gorge (CRG) in Oregon, USA, provides an ideal opportunity for investigating the behavioral plasticity of this species in response to both atypical resource availability and climate. The 50 km stretch of the CRG in which pikas are

distributed is characterized by dense Douglas fir forest, and talus patches in this region are often covered in a thick carpet of moss. Pikas persist in this habitat as low as 46 m (the lowest elevation at which this species has ever been detected; E. Beever, pers. obs.) in a climate that appears to be unsuitable due to the long, warm summers and short winters without extended snowpack (Hafner 1993, Simpson 2009). However, the microclimates in this habitat are highly spatially heterogeneous, in part because the moss cover adds a unique microclimate that insulates talus microclimates from ambient temperature extremes (Varner and Dearing 2014b). Specifically, microclimates in talus interstices may vary by 3-5°C within a few meters in this habitat, which provides pikas with a unique opportunity to adjust their thermoregulatory behavior. This region also contains many vegetation resources that are unusual for this species. Specifically, pikas in this habitat demonstrate some plasticity in their diet by facultatively specializing on moss (Varner and Dearing 2014a). Moss is also available year-round at low elevations, which may release pikas from spending the warm summers caching food for winter.

Although pikas exhibit a range of variable behaviors, their capacity for behavioral flexibility in the context of warmer climates is still not well understood. In this study, we observed the behavior of pikas living in the atypical, low-elevation habitats of the CRG. We then compared the behavior of CRG pikas to those in high-elevation habitat on nearby Mt. Hood. Because food resources (e.g., mosses, evergreen shrubs, and ferns) are available year-round at low elevations, we hypothesized that pikas at low elevations would be under less pressure to cache food for winter and would instead spend more time in summer grazing (i.e., actively consuming vegetation).

We also sought to document microhabitat selection at high and low elevations.

First, we systematically investigated the use of off-talus forest microhabitats as a potential midday thermal refuge. We also measured home range sizes in the CRG and Mt. Hood as an indicator of space use. We hypothesized that, due to increased resource availability at low elevations, CRG pikas would have smaller home range sizes and reduced territorial behaviors, compared to high-elevation pikas. Understanding behavior modifications in a highly atypical habitat may provide critical information about a species' capacity for behavioral plasticity in adapting to new environmental conditions and, by extension, its vulnerability to future changes.

Methods

Study area and sites. Behavioral observations in the CRG were conducted at four north-facing talus patches (ca. 15,000 m² each; hereafter, “sites”) occupied by pikas. All sites were 32–35° in steepness, north to northwest facing, and surrounded by a dense forest dominated by Douglas fir (*Pseudotsuga menziesii menziesii*), western redcedar (*Thuja plicata*), and bigleaf maple (*Acer macrophyllum*). One of the notable features of talus in this region is a thick layer of mosses (typically comprised of > 3 species) that covers the surface of each rockslide (Varner and Dearing 2014a, b). Low-elevation sites ranged in elevation from 194 m to 437 m and varied in moss cover from over 65% (“high moss cover”: Sites 1 & 2) to less than 30% (“low moss cover”: Sites 3 & 4). Importantly, each of these sites is approximately 1,000 m lower in elevation than pikas are predicted to occur, based on their previously described bioclimatic envelope (Hafner 1993).

Pikas also live in more typical, high-elevation habitat on nearby Mt. Hood. Pika populations on Mt. Hood are separated from those in the CRG by less than 50 km, but

they differ in elevation by 900 - 2,000 m and thus experience vastly different climate regimes and resource availability. For comparison, we also conducted behavioral surveys at two sites (Sites 5 & 6) in alpine habitats typical for pikas on the north face of Mt. Hood. These sites were 905 and 1,682 m elevation, respectively, also faced north, and were 27-28 degrees in steepness. Although neither high-elevation site had considerable moss cover, both sites were located in dense forest dominated by Douglas fir, western redcedar, and western hemlock (*Tsuga heterophylla*).

Foraging behavior surveys. Foraging observations were primarily conducted in July of 2012 and 2013, although a few foraging observations were collected in July 2011 at Sites 5 and 6 ($n = 2$ observers in 2011). Upon arrival at a site, observers ($n = 5$ in 2012, $n = 4$ in 2013, 3 observers common to both years) selected a high vantage point near the edge of the talus and used 10 x 40 binoculars to document foraging activity and microhabitat use. As in previous studies, pikas habituated rapidly to observers on the talus (Conner 1983, Smith and Ivins 1984, Dearing 1996); however, activities were not recorded for the first 5 minutes of observer presence. Each observer recorded activities in nonoverlapping focal areas of the site, and surveys were limited to 3 hours to reduce observer fatigue. Following Moyer-Horner (2011) and Henry et al. (2012), survey start times were either in the morning (06:00 – 08:30), midday (12:00 – 15:00), or evening (17:00 – 19:30). Observers also recorded ambient temperatures with a handheld thermometer at the beginning and end of each survey.

Unique pika detections were defined as continuous surface activities separated by > 30 s of sub-surface inactivity (following Moyer-Horner 2011). Each detection was then classified into a behavior category, as defined by Smith and Weston (1990) (Fig. 4.S1).

Foraging behaviors included grazing (consuming vegetation) or haying (caching vegetation or carrying a plant clipping below a rock). Territorial behaviors included cheek rubbing (making territorial markings with apocrine glands on their cheeks) and aggression (active chases and contact encounters - i.e., fights). Other behaviors not specifically analyzed in this study included surveying (perching on a prominent rock), running, grooming, coprophagy, and vocalizing.

All detections were also noted as to whether they occurred in the open talus or under forest canopy cover. In some cases, these detections included calls heard from the forest although the animals were not seen due to dense understory vegetation. When possible, individual animals were identified by colored ear tags placed for a previous study (Varner and Dearing 2014a) or by distinctive scars on the ears or eyes.

Foraging behavior analysis. To assess the effect of region (i.e., CRG vs. Mt. Hood) on foraging behavior, we used a generalized linear mixed model (GLMM) to predict the probability of haying versus grazing behavior for all marked individuals ($n = 38$). All GLMMs were fit in R using the *glmer* function of the lme4 library (Bates et al. 2014, R Core Team 2014). Because all foraging detections were classified as either haying or grazing, we used a model assuming a binomial distribution with a logit link. Region was treated as a fixed effect, and individual pikas were nested within sites. Both individuals and sites were modeled as random effects to control for repeated measures and their intrinsic variation.

Forest microhabitat analyses. We conducted two analyses to explore variation in the use of off-talus forest microhabitats. In the first analysis, we assessed the effect of Region (i.e., CRG vs. Mt. Hood) on forest microhabitat use. We used a GLMM to predict

the probability of a detection occurring under forest canopy cover versus in open talus. Because all pika detections were classified as either occurring in the forest or on the talus, we used a model assuming a binomial distribution with a logit link. An observation was defined as when a single observer at a specific site monitored pika activity for up to 3 hours (total $n = 117$ observations). Although observations vary in total time and number of pika detections, these discrepancies are accounted for by pairing the count of forest detections directly to the count of talus detections in each observation. Region was treated as a fixed effect and date, observer, and site were modeled as random effects to control for repeated measures and variation due to these factors.

In the second analysis, we assessed the effect of ambient temperature, moss cover, and time of day on forest microhabitat use at low elevations, where large variations in ambient temperature and moss cover were present. We used a GLMM to predict the probability of a detection occurring under forest canopy cover versus in open talus. Ambient temperature, moss cover (high vs. low), and time of day (morning, midday, evening) were modeled as fixed effects. Date, observer, and site were modeled as random effects to control for repeated measures and introduced variation. The model intercept was set at 25.5°C, which is our best estimate of a threshold for acute heat stress in this species (MacArthur and Wang 1974, Smith 1974). Several candidate models were generated including and excluding interaction terms between the fixed effects, and model selection was based upon the Akaike information criterion (Burnham and Anderson 2002).

Home range size and aggressive behavior. In 2013, additional data were collected on space and microhabitat use at Sites 1 and 2 (CRG, high moss cover) and Site 5 (high

elevation). For marked animals at these sites, observers recorded the location at the beginning of each detection on an aerial satellite image of the site. These maps with pika observations were then scanned, and relative locations of observations within a site were scaled and digitized using Image J (Schneider et al. 2012). Only adult animals that could be reliably identified between observers were included in home range analysis (Site 1: $n=3$; Site 2: $n=6$; Site 5: $n=3$). The number of observations per animal ranged from 11 – 64 (mean = 36.6, median = 34), but did not differ between CRG sites and Mt. Hood (t-test, $t = 0.48$, $df = 2.68$, $p = 0.67$).

Pika home ranges in the CRG (Sites 1 and 2) and Mt. Hood (Site 5) were calculated in several ways. For comparison with previous pika home range studies, we calculated the 100% minimum convex polygon (Kawamichi 1982) and the modified bivariate home range model described by Koepl et al. (1975). We also divided the talus into 5 m x 5 m quadrats and tallied the area of quadrats where pikas were observed; this is a more conservative measure of home range because it does not include quadrats within the spatial distribution of pika detections, as do other procedures (Kawamichi 1982, Smith and Ivins 1984). Finally, we also used a bivariate normal kernel density estimator (*kernelUD* in R package *adehabitat3*) to estimate the 95% kernel utilization distribution using the reference bandwidth (Worton 1989, Calenge et al. 2011). Although many previous studies of pika home range and territorial behaviors have estimated nearest neighbor distances, we chose not to calculate this metric because we could not reliably identify all individuals at each site.

Home range sizes of pikas from the CRG and Mt. Hood were compared to each other as well as to published data from two high-elevation populations in Colorado using

one-way ANOVA and Tukey's multiple comparisons tests. A separate ANOVA was employed for each home range estimator.

Finally, to determine whether aggressive behaviors differed between the CRG and Mt. Hood, we used a GLMM in the same manner as forest microhabitat use described above, with the exception that the number of aggressive detections versus nonaggressive detections replaced the response variable of microhabitat type. As above, an observation was defined as a single observer at a specific site, monitoring pika activity for up to 3 hours (total $n = 112$ observations)

Results

Foraging behavior. In total, we collected 417 observer-hours of behavioral data across our 6 sites. In 2012, we observed 3,034 pika detections in 223 observer-hours. In 2013, we observed 2,216 pika detections in 194 observer-hours. Foraging behaviors were equally frequent between regions, as a percent of total detections (CRG: 15.0% in 2012, 14.3% in 2013; Mt Hood: 15.3% in 2012, 15.3% in 2013). However, the proportion of grazing versus haying behaviors differed significantly between regions (GLMM; $Z = 3.38, p < 0.001$; Table 4.1, Fig. 4.1). Specifically, CRG pikas were observed haying in 11.7% (SEM: + 6.79 – 4.53) of foraging detections and grazing the remainder, whereas Mt. Hood pikas were observed haying in 45.0% (SEM: +10.20 – 9.79) of foraging detections and grazing the remainder.

Forest microhabitat use. Low-elevation pikas in the CRG were far more likely to be detected in forest microhabitats than high-elevation pikas on Mt. Hood (GLMM; $Z = 2.18, p = 0.029$; Table 4.2, Fig. 4.2A). Specifically, CRG pikas were detected in forest microhabitats (i.e., off the main talus slope) 20.9% (SEM: +27.25 – 13.93) of the time,

whereas Mt. Hood pikas were only detected in the forest 1.7% (SEM: +3.12 –1.11) of the time.

Within the low-elevation sites of the CRG, we evaluated multiple factors to determine their influence on forest microhabitat use, including ambient temperature, moss cover (i.e., high vs. low), and time of day (i.e., morning vs. midday vs. evening). Only time of day was found to have a significant effect on forest microhabitat use in the CRG, with the highest levels of detections in the forest at midday (28.9% of all detections, SEM: +12.44 –9.91; Fig. 4.2B). Forest use in the morning was significantly lower than midday (19.2% of detections, SEM: +7.04 –5.49, GLMM; $Z = -2.70$, $p = 0.007$). Forest use in the evening was also significantly lower than midday (12.5% of detections, SEM: +4.25 –3.30, GLMM; $Z = -3.05$, $p = 0.002$).

Home range size and territorial behavior. Across all estimators of home range size, pika home ranges were significantly smaller in the CRG than any previously published estimates of pika home range size (ANOVA with Tukey post-hoc test, all comparisons across all metrics: $p < 0.001$; Table 4.3). Home ranges on Mt. Hood were significantly larger than those in the CRG according to the minimum convex polygon estimator (ANOVA with Tukey post-hoc test: $p < 0.01$). Although we did not detect significant differences between home range size in the CRG vs. Mt. Hood in the other three estimators (quadrat, kernel density estimator, or bivariate), the largest home range for a CRG pika was still smaller than the smallest home range on Mt. Hood by any estimator of home range size. The inconsistent nature of these findings is likely due to the small sample ($n = 3$) of pikas observed at Mt. Hood.

The frequency of territorial behaviors (aggression or cheek rubbing) was low in

our study (less than 1 act per 10 hours of observation and < 1% of total detections). Despite having small home ranges and living at high densities, pikas did not exhibit more frequent aggressive behaviors in the CRG than on Mt. Hood, as a proportion of total detections: both groups engaged in these activities at a frequency of 0.062% of total detections (GLMM; $Z = 0.275$, $p = 0.783$; Table 4.4).

Discussion

Here, we document substantial behavioral differences between pika populations living in atypical, low-elevation habitat in the Columbia River Gorge (CRG) and those in typical alpine habitat on nearby Mt. Hood. Specifically, we showed that low-elevation pikas do not invest as heavily in caching food for winter (Fig. 4.1). Pikas in low-elevation habitats were also significantly more likely to use forested areas off the talus than those living at high elevations. The pattern of off-talus detections (Fig. 4.2) suggests that the forest may serve as a thermal refuge at midday. Although pikas in the CRG are living at high densities with smaller home ranges, they do not exhibit increased territorial behaviors, perhaps because food resources are abundant and because they are not defending large winter food caches against kleptoparasitism (Varner and Dearing 2014a).

In our study, approximately 45% of foraging detections on Mt. Hood were haying (as opposed to grazing), which is comparable to previous studies in alpine habitat, in which pikas were observed haying 25-50% of foraging time (Huntly et al. 1986). Previous studies have also reported haying in typical habitats to represent 20-50% of a pika's surface activity in July (Conner 1983, Dearing 1997). However, pikas in the CRG were observed haying less than 12% of foraging time. Because foraging represented approximately 15% of detections across sites and years, CRG pikas spent approximately

2% of their activity budgets haying.

In a previous study, pika haypile size corresponded closely to the duration of winter across several habitat types (ca. 80 g vegetation per day of winter; Varner and Dearing 2014a). Unlike other populations, pikas in the CRG do not need to invest in winter food caches (a hallmark of their behavior in other habitats; Dearing 1997, Smith 2008, Morrison et al. 2009) because winters are short (ca. 2 weeks of persistent snow cover), and food resources such as evergreen trees and shrubs or mosses are available year-round (Varner and Dearing 2014a). Taken together with the current study, these results suggest that pikas have a large degree of behavioral plasticity with respect to foraging behaviors, such that they can adapt their grazing and haying behaviors to suit climatic conditions.

The high degree of resource availability in the CRG may also affect microhabitat selection in this habitat. Indeed, the pikas at our CRG sites also utilized significantly smaller home ranges than previously reported values in the literature (Table 4.3). Pika home ranges in the CRG were also smaller than those on Mt. Hood, although the limited number of marked animals on Mt. Hood ($n = 3$) limited our ability to detect statistical differences between these regions. However, despite higher densities and smaller home ranges, aggressive or territorial acts were not more frequent in this habitat, compared to typical alpine habitat on Mt. Hood. In fact, aggression in the CRG (1 act per 10 hours observation) was much lower than values reported in the literature (2.8 acts per 10 hours observation; calculated from data in Smith and Ivins 1983). Notably, Smith and Ivins only collected data during parts of the day when pikas were most likely to be active; however, when we removed midday observations from our dataset (i.e., to include only

observations when pikas were most likely to be active), we still observed fewer than 1 aggressive act per 10 hours of observation in the CRG.

Pikas are known to exhibit plasticity in other aspects of their behavior. For example, pikas are known to thermoregulate primarily by restricting surface activity to times when weather is favorable (MacArthur and Wang 1973, 1974, Smith 1974, Bhattacharyya et al. 2014). Favorable weather patterns also vary with elevation; thus, at cooler latitudes and elevations, pikas tend to be most active in the middle of the day, whereas in warmer climates, they exhibit more crepuscular activity patterns (E. Beever, E. Hall, pers. obs.). In addition, although pikas are considered to have an obligate relationship to broken rock features, they have also recently been detected in unusual, nontalus habitats in northeastern Wyoming, including downed logs and slash piles up to 100 m from the nearest talus (E. Hall, pers. obs.). The existence of haypiles in these locations suggests that pikas are extensively using these unusual habitats. Furthermore, temperatures measured inside haypiles in downed logs were up to 1.7°C warmer in winter than those measured in the nearest talus (over 100 m away; E. Hall, unpubl. data), suggesting that these nontalus habitats may buffer pikas against extreme winter temperatures. Similarly, in our study, we observed pikas using the coniferous forest off of the talus most frequently in the CRG at midday, when ambient temperatures are highest. Temperatures previously measured at the forest surface in this habitat suggest that this off-talus habitat may also be an important thermal refuge, particularly at sites with lower moss cover (Varner and Dearing 2014b).

Behavioral flexibility may have been adaptive during the biogeographic history of pikas. The genus *Ochotona* includes 30 currently recognized species of pikas, all of

which are distributed across Asia except for two species in North America (*O. princeps* and its ecologically-similar sister species *O. collaris*), which are thought to have dispersed across the Bering land bridge during the Pleistocene (Niu et al. 2004). Unlike American pikas, approximately half of Asian species are highly social and live at high densities in burrows (Smith 2008). This burrowing, meadow-dwelling ecotype is thought to be the ancestral form of the genus, given biogeographic and phylogenetic evidence (Reese et al. 2013). Substantial behavioral plasticity may have been adaptive for pikas to cope with new environmental conditions while dispersing across the continents. Indeed, some populations of the Asian talus-dwelling pikas also inhabit nontalus habitats, including woodpiles (Northern pika, *Ochotona hyperborea*) or old rock walls (Glover's pika, *Ochotona gloveri*) (Smith 2008), suggesting a higher degree of habitat plasticity within the genus than may be commonly assumed.

Future research will be necessary to understand how behavior can be used flexibly to accommodate changes in climate for pikas and other species. Pikas can clearly use behavior flexibly to accommodate changes in resource availability (e.g., Varner and Dearing 2014a); however, the species may require certain habitat features to persist, such as a suitable microclimate refuge (Henry et al. 2012, Varner and Dearing 2014b). Furthermore, pikas may be less behaviorally flexible in other ecoregions, where habitat quality has been degraded as a result of grazing or loss of suitable microclimates. In other habitats, pikas may simply not have access to spatially variable microclimates or microhabitats that provide behavioral opportunities (e.g., pikas inhabiting alpine areas above tree line will not have access to the dense forests observed in our study region). In addition, although pikas appear able to reduce investment in caching food for winter in

habitats where winters are short, and resources are widely available, restricting haying behavior (i.e., due to warm summer temperatures) may still be maladaptive in other habitats where large food caches are necessary to survive winter.

Our results contribute to a growing body of literature about variation in behavior between populations of pikas, and are an important first step to understanding pika foraging behavior and microhabitat use in atypical habitats. Further research will be needed to determine whether pikas, as a species, collectively have the “developmental plasticity” to accommodate climate change, even if individuals are not “activationally plastic” within their lifetimes (Snell-Rood 2013). A better mechanistic understanding of the linkages between climate change and variation in the behaviors of a species will be necessary to inform conservation management and planning to address climate change.

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References

- Ashcroft, M. B. 2010.** Identifying refugia from climate change. *Journal of Biogeography* 37:1407-1413.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014.** lme4: Linear mixed-effects models using eigen and S4. R Package Version 1.1-7. <http://CRAN.R-project.org/package=lme4>.
- Beever, E. A., S. Z. Dobrowski, J. Long, A. R. Mynsberge, and N. B. Piekielek. 2013.** Understanding relationships among abundance, extirpation, and climate at ecoregional scales. *Ecology* 94:1563-1571.
- Beever, E. A., C. Ray, P. W. Mote, and J. L. Wilkening. 2010.** Testing alternative models of climate-mediated extirpations. *Ecological Applications* 20:164-178.
- Beever, E. A., C. Ray, J. L. Wilkening, P. F. Brussard, and P. W. Mote. 2011.** Contemporary climate change alters the pace and drivers of extinction. *Global Change Biology* 17:2054-2070.
- Beever, E. A., J. L. Wilkening, D. E. McIvor, S. S. Weber, and P. E. Brussard. 2008.** American pikas (*Ochotona princeps*) in northwestern Nevada: A newly discovered population at a low-elevation site. *Western North American Naturalist* 68:8-14.
- Bhattacharyya, S., B. S. Adhikari, and G. S. Rawat. 2014.** Influence of microclimate on the activity of Royle's pika in the western Himalaya, India. *Zoological Studies* 53:73.
- Burnham, K. P. and D. R. Anderson. 2002.** Model selection and multimodel inference: A practical information-theoretic approach. Springer, New York, NY.
- Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Y. Ryu, G. C. Sbeglia, F. Spagnolo, J. B. Waldron, and O. Warsi. 2013.** How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences* 280:20121890.
- Calenge, C., M. Basille, S. Dray, and S. Fortmann-Roe. 2011.** adehabitat: Analysis of habitat selection by animals. R Package Version 1.8.15. <http://CRAN.R-project.org/package=adehabitat>.
- Channell, R. and M. V. Lomolino. 2000.** Dynamic biogeography and conservation of endangered species. *Nature* 403:84-86.

- Conner, D. A. 1983.** Seasonal changes in activity patterns and the adaptive value of haying in pikas (*Ochotona princeps*). *Canadian Journal of Zoology* 61:411-416.
- Dearing, M. D. 1996.** Disparate determinants of summer and winter diet selection of a generalist herbivore, *Ochotona princeps*. *Oecologia* 108:467-478.
- Dearing, M. D. 1997.** The function of haypiles of pikas (*Ochotona princeps*). *Journal of Mammalogy* 78:1156-1163.
- Hafner, D. J. 1993.** North American pika (*Ochotona princeps*) as a late quaternary biogeographic indicator species. *Quaternary Research* 39:373-380.
- Henry, P., A. Henry, and M. A. Russello. 2012.** Variation in habitat characteristics of American pikas along an elevation gradient at their northern range margin. *Northwest Science* 86:346-350.
- Huey, R. B., M. R. Kearney, A. Krockenberger, J. A. M. Holtum, M. Jess, and S. E. Williams. 2012.** Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology, and adaptation. *Philosophical Transactions of the Royal Society of London: B Biological Science*. 367:1665-79.
- Huntly, N. J., A. T. Smith, and B. L. Ivins. 1986.** Foraging behavior of the pika (*Ochotona princeps*), with comparisons of grazing versus haying. *Journal of Mammalogy* 67:139-148.
- Jeffress, M. R., T. J. Rodhouse, C. Ray, S. Wolff, and C. Epps. 2013.** The idiosyncrasies of place: Geographic variation in the climate-distribution relationships of the American pika. *Ecological Applications* 23:864–878.
- Kausrud, K. L., A. Mysterud, H. Steen, J. O. Vik, E. Østbye, B. Cazelles, E. Framstad, A. M. Eikeset, I. Mysterud, and T. Solhøy. 2008.** Linking climate change to lemming cycles. *Nature* 456:93-97.
- Kawamichi, T. 1982.** Factors affecting size of home range and territory in pikas, *Ochotona princeps*. *Japanese Journal of Ecology* 32:21-28.
- Keppel, G. and G. W. Wardell-Johnson. 2012.** Refugia: Keys to climate change management. *Global Change Biology* 18:2389-2391.
- Koepl, J., N. Slade, and R. Hoffmann. 1975.** A bivariate home range model with possible application to ethological data analysis. *Journal of Mammalogy*:81-90.
- MacArthur, R. A. and L. C. H. Wang. 1973.** Physiology of thermoregulation in the pika, *Ochotona princeps*. *Canadian Journal of Zoology* 51:11-16.
- MacArthur, R. A. and L. C. H. Wang. 1974.** Behavioral thermoregulation in the pika,

- Ochotona princeps*: A field study using radiotelemetry. Canadian Journal of Zoology 52:353-358.
- Manning, T. and J. C. Hagar. 2011.** Use of nonalpine anthropogenic habitats by American pikas (*Ochotona princeps*) in western Oregon. Western North American Naturalist 71:106-112.
- Millar, C. I., R. D. Westfall, and D. L. Delany. 2013.** New records of marginal locations for American pika (*Ochotona princeps*) in the western Great Basin. Western North American Naturalist 73:457-476.
- Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008.** Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science 322:261-264.
- Morrison, S. F., G. Pelchat, A. Donahue, and D. S. Hik. 2009.** Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. Oecologia 159:107-116.
- Moyer-Horner, L. 2011.** American pika distribution, behavior, and observer variability. Ph.D. Thesis; University of Wisconsin-Madison.
- Murray, I. W. and F. A. Smith. 2012.** Estimating the influence of the thermal environment on activity patterns of the desert woodrat (*Neotoma lepida*) using temperature chronologies. Canadian Journal of Zoology 90:1171-1180.
- Niu, Y., F. Wei, M. Li, X. Liu, and Z. Feng. 2004.** Phylogeny of pikas (lagomorpha, *Ochotona*) inferred from mitochondrial cytochrome B sequences. Folia Zoologica 53:141-156.
- R Core Team. 2014.** R: A language and environment for statistical computing. R Foundation for Statistical Computing. <http://www.R-project.org/>. Accessed 20 March 2015.
- Reese, A. T., H. C. Lanier, and E. J. Sargis. 2013.** Skeletal indicators of ecological specialization in pika (Mammalia, *Ochotonidae*). Journal of Morphology 274:585-602.
- Rodhouse, T. J., E. A. Beever, L. K. Garrett, K. M. Irvine, M. R. Jeffress, M. Munts, and C. Ray. 2010.** Distribution of American pikas in a low-elevation lava landscape: Conservation implications from the range periphery. Journal of Mammalogy 91:1287-1299.
- Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012.** NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9:671-675.

- Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012.** Ecological implications of behavioural syndromes. *Ecology Letters* 15:278–289.
- Simpson, W. G. 2009.** American pikas inhabit low-elevation sites outside the species' previously described bioclimatic envelope. *Western North American Naturalist* 69:243-250.
- Sinervo, B., F. Méndez-de-la-Cruz, D. B. Miles, B. Heulin, E. Bastiaans, M. Villagrán-Santa Cruz, R. Lara-Resendiz, N. Martínez-Méndez, M. L. Calderón-Espinosa, R. N. Meza-Lázaro, H. Gadsden, L. J. Avila, M. Morando, I. J. De la Riva, P. V. Sepulveda, C. F. D. Rocha, N. Iburgüengoytía, C. A. Puntriano, M. Massot, V. Lepetz, T. A. Oksanen, D. G. Chapple, A. M. Bauer, W. R. Branch, J. Clobert, and J. W. Sites. 2010.** Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328:894-899.
- Smith, A. T. 1974.** The distribution and dispersal of pikas: Influences of behavior and climate. *Ecology* 55:1368-1376.
- Smith, A. T. 1978.** Comparative demography of pikas (*Ochotona*): Effect of spatial and temporal age-specific mortality. *Ecology* 59:133-139.
- Smith, A. T. 2008.** The world of pikas. Pages 89-102 in A. PC, F. N, and K. Hackländer, editors. *Lagomorph biology*. Springer Berlin Heidelberg, Berlin, Germany.
- Smith, A. T. and B. L. Ivins. 1983.** Colonization in a pika population: Dispersal vs. philopatry. *Behavioral Ecology and Sociobiology* 13:37-47.
- Smith, A. T. and B. L. Ivins. 1984.** Spatial relationships and social organization in adult pikas: A facultatively monogamous mammal. *Zeitschrift für Tierpsychologie* 66:289-308.
- Smith, A. T. and M. L. Weston. 1990.** *Ochotona princeps*. *Mammal Species* 352:1-8.
- Snell-Rood, E. C. 2013.** An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour* 85:1004-1011.
- Stewart, J. A. E., J. D. Perrine, L. B. Nichols, J. H. Thorne, C. I. Millar, K. E. Goehring, C. P. Massing, and D. H. Wright. 2015.** Revisiting the past to foretell the future: Summer temperature and habitat area predict pika extirpations in California. *Journal of Biogeography*: doi: 10.1111/jbi.12466.
- Tapper, S. C. 1973.** The Spatial organisation of pikas, *Ochotona*, and its effect on population recruitment. Ph.D. Dissertation. University of Alberta, Edmonton, Alberta, Canada.

- Tuomainen, U. and U. Candolin. 2011.** Behavioural responses to human-induced environmental change. *Biological Reviews* 86:640-657.
- Varner, J. and M. D. Dearing. 2014a.** Dietary plasticity in pikas as a strategy for atypical resource landscapes. *Journal of Mammalogy* 94:72-81.
- Varner, J. and M. D. Dearing. 2014b.** The importance of biologically relevant microclimates in habitat suitability assessments. *PloS ONE* 9:e104648.
- Worton, B. 1989.** Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-168.

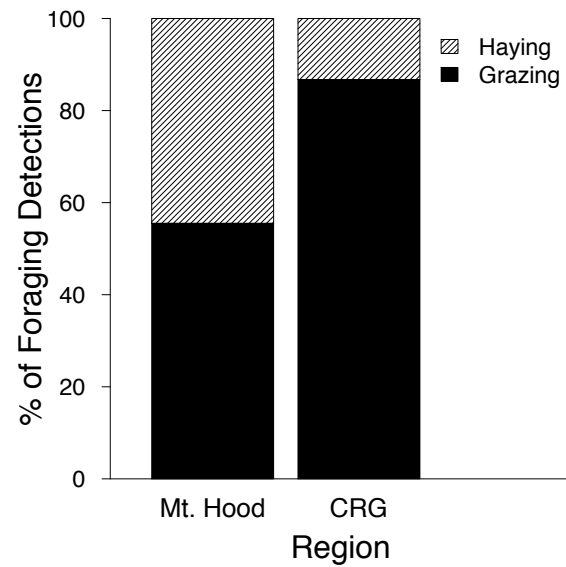


Fig. 4.1. Haying and grazing behaviors as a proportion of all foraging detections in the CRG vs. Mt. Hood. Detections are pooled across all animals and all years. As a proportion of total detections, foraging detections did not vary between regions or across years.

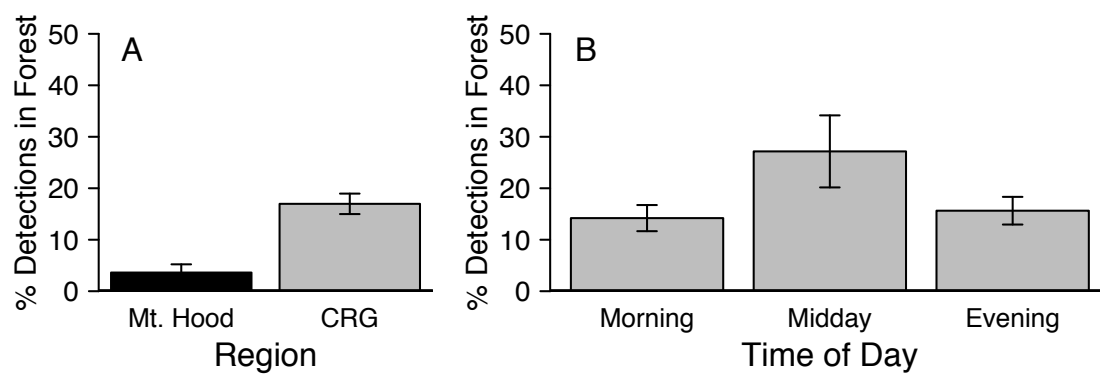


Fig. 4.2. Use of forested habitat in 2013. Detections are pooled across all animals. (A) Animals were detected in the forest habitat more frequently in the CRG versus Mt. Hood. (B) In the CRG, animals were detected in the forest significantly more frequently at midday versus morning or evening.

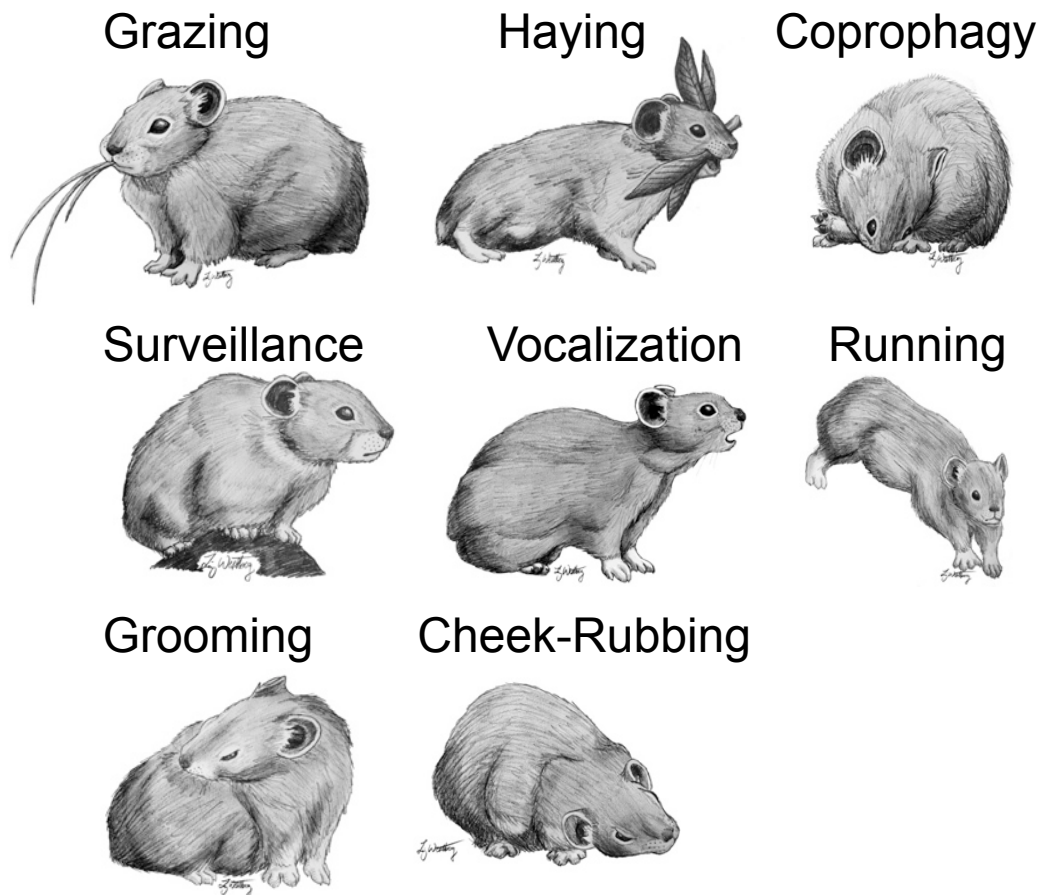


Fig. 4.S1. Ethogram of pika behavior. Pika detections were classified as one of these behaviors. Aggression and Social Tolerance are not depicted. Sketches by Elizabeth Westberg.

Table 4.1. Summary of mixed model results for foraging behavior.

Foraging Behavior (Haying vs. Grazing) by Region		GLMM with binomial distribution and logit link (groups: Individuals = 36, Sites = 6; observations = 38)			
<i>Random effects</i>		<i>Variance</i>	<i>Std. Deviation</i>		
Individual		1.211	1.100		
Site		0.000	0.000		
<i>Fixed effects</i>		<i>Estimate</i>	<i>Std. Error</i>	<i>Z value</i>	<i>Pr(> z)</i>
Intercept		-0.1998	0.4092	-0.488	0.6253
Region (CRG)		-1.8179	0.5372	-3.384	0.0007***

*** Indicates $p < 0.001$.

Table 4.2. Summary of mixed model results for forest microhabitat use.

Forest Use by Region	GLMM with binomial distribution and logit link (groups: date = 20, observers = 6 sites = 8; observations = 117)			
<i>Random effects</i>	<i>Variance</i>	<i>Std. Deviation</i>		
Date	0.2305	0.4801		
Observer	0.1163	0.3410		
Site	1.3696	1.1703		
<i>Fixed effects</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>Z value</i>	<i>Pr(> z)</i>
Intercept	-4.064	1.078	1.078	0.0002***
Region (CRG)	2.736	2.736	2.178	0.0294*
Forest Use in the CRG, by Temperature, Moss Cover, and Time of Day.	GLMM with binomial distribution and logit link (Intercept at 25.5°C; groups: dates = 18, observers = 6, sites = 5; observations = 81)			
<i>Random effects</i>	<i>Variance</i>	<i>Std. Deviation</i>		
Date	0.1851	0.4302		
Observer	0.0872	0.2953		
Site	0.4886	0.6990		
<i>Fixed effects</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>Z value</i>	<i>Pr(> z)</i>
Intercept (High Moss at MIDDAY)	-0.8983	0.5499	-1.634	0.1024
Ambient Temperature	-0.0271	0.0290	-0.935	0.3497
Site Type (Low Moss)	0.8235	0.8425	0.978	0.3283
Time (Morning)	-1.0877	0.4029	-2.700	0.0069**
Time (Evening)	-1.0441	0.3421	-3.052	0.0023**

* Indicates $p < 0.05$, ** < 0.01 , *** < 0.001 .

Table 4.3. Summary of home range analyses in the CRG, Mt. Hood, and the literature. Home ranges were compared across sites

within an estimator using ANOVA and Post-hoc Tukey's multiple comparisons tests. Letters indicate means within a home range estimator that significantly differ between sites at an α of 0.05.

Region	No. Animals	Date	Home range Estimate (Mean \pm SD, m ²)		
			Quadrat	Bivariate	Kernel Density
CRG	9	July 2013	327 \pm 112.8 (a)	111.2 \pm 70.7 (a)	289.9 \pm 188.3 (a) 675.5 \pm 426.3 (a)
Mt. Hood	3	July 2013	550 \pm 263.4 (a,b)	647.1 \pm 224.4 (a)	1712.3 \pm 187.4 (b) 11721.9 \pm 13653.2 (a)
Gothic, CO ¹	25	July 1981	1106 \pm 112	3918.5 \pm 676.5 (b)	NA NA
Loveland Pass, CO ²	18	Sept. – Nov. 1972	1840 \pm 768 (c)	NA	1367.4 \pm 763.7 (b) NA

¹: Data from Rocky Mountain Biological Lab, Smith & Ivins 1984

²: Data from Kawamichi 1982

Table 4.4. Summary of mixed model results for territorial behavior.

Territorial Behavior by	GLMM with binomial distribution and logit link			
Region	(groups: date = 18, observers = 4 sites = 7; observations = 112)			
<i>Random effects</i>				
	<i>Variance</i>	<i>Std. Deviation</i>		
Date	0.04397	0.2097		
Observer	0.24241	0.4924		
Site	0.00000	0.0000		
<i>Fixed effects</i>				
	<i>Estimate</i>	<i>Std. Error</i>	<i>Z value</i>	<i>Pr(> z)</i>
Intercept	-5.0861	0.6793	-7.488	<0.0001***
Region (CRG)	0.1994	0.7247	0.275c	0.783

*** Indicates $p < 0.001$

CHAPTER 5

TOO HOT TO TROT? EVALUATING THE EFFECTS OF WILDFIRE ON PATTERNS OF OCCUPANCY AND ABUNDANCE FOR A CLIMATE-SENSITIVE HABITAT SPECIALIST

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Too hot to trot? Evaluating the effects of wildfire on patterns of occupancy and abundance for a climate-sensitive habitat specialist

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Abstract. Wildfires are increasing in frequency and severity as a result of climate change in many ecosystems; however, effects of altered disturbance regimes on wildlife remain poorly quantified. Here, we leverage an unexpected opportunity to investigate how fire affects the occupancy and abundance of a climate-sensitive habitat specialist, the American pika (*Ochotona princeps*). We determine the effects of a fire on microclimates within talus and explore habitat factors promoting persistence and abundance in fire-affected habitat. During the fire, temperatures in talus interstices remained below 19°C, suggesting that animals could have survived *in situ*. Within 2 years, pikas were widely distributed throughout burned areas and did not appear to be physiologically stressed at severely burned sites. Furthermore, pika densities were better predicted by topographic variables known to affect this species than by metrics of fire severity. This widespread distribution may reflect quick vegetation recovery and the fact that the fire did not alter the talus microclimates in the following years. Together, these results highlight the value of talus as a thermal refuge for small animals during and after fire. They also underscore the importance of further study in individual species' responses to typical and altered disturbance regimes.

Additional keywords: *Ochotona*, pika, talus, thermal refuge, wildlife.

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Introduction

Climate change has already profoundly affected species distributions in terrestrial ecosystems (Parmesan 2006), but evidence suggests that indirect effects of climate change, such as changes in interspecific interactions (Mason *et al.* 2014), food availability (Cahill *et al.* 2012) or invasion of exotic species (Mooney and Hobbs 2000) may be more frequent drivers of distribution shifts than the direct effects of climate change (e.g. altered temperature and precipitation). One aspect of climate change that is particularly under-studied with regard to effects on species distributions is altered fire regimes. Globally, wildfires have increased in both frequency and severity in recent decades (Williams *et al.* 2001; Westerling *et al.* 2006; Flannigan *et al.* 2009). These trends are likely due to more severe fire weather (i.e. warmer, drier summers) and earlier snowmelt, and they appear to be particularly significant in mountainous

ecoregions (Dale *et al.* 2001; Dennison *et al.* 2014; Stavros *et al.* 2014).

Severe fires profoundly alter habitat for wildlife through changes in resource availability (e.g. via soil nutrients or plant communities) and local microclimates (e.g. through changes in albedo and loss of forest canopy cover; Agee 1996). However, relatively little evidence exists regarding the potential synergistic effects of altered fire regimes and climate change on species distributions (Driscoll *et al.* 2010). Indeed, it is difficult to directly study how fire affects animal distributions in the context of climate change due to logistical and ethical constraints and because these effects are complex (Roberts *et al.* 2008; Engstrom 2010). Furthermore, large, severe fires predicted under climate change may also increase landscape heterogeneity, complicating analyses of habitat suitability (Cansler and McKenzie 2014).

It is difficult to make generalisations about wildlife responses to fire because these responses depend on both the degree of specialisation of the species in diet or habitat preferences and on the characteristics of the fire (i.e. intensity, size or season in which the fire occurs; Smucker *et al.* 2005; Wiebe 2014). Trade-offs between habitat requirements and the functional traits or diet requirements of a species may further complicate responses to fire. For example, cavity-nesting birds often benefit from the habitat structure created by high-severity fire, but the invertebrates upon which these species depend for food are more widely available after low-severity fire or in unburned areas (Nappi *et al.* 2010; Azeria *et al.* 2011). A species may also respond differently to fires in different seasons as a result of its reproductive phenology or other short-term vulnerabilities (Engstrom 2010).

Despite these difficulties, a few generalisations have emerged from the literature. For example, evidence suggests that species that prefer open habitat are likely to have positive responses to fire (i.e. higher abundance in burned areas compared with unburned reference areas; Fontaine and Kennedy 2012). Some species that rely on short-term sources of food caused by fire (e.g. early colonising herbaceous species or conifer seeds; Engstrom 2010) are also likely to exhibit positive responses, including cavity-nesting birds that depend on dead or dying trees (Smucker *et al.* 2005; Wiebe 2014). Similarly, some bats may benefit from open habitat and abundant flying insects (Perry 2011). In contrast, species that prefer mesic, closed-canopy conditions tend to exhibit negative responses to fire (i.e. higher abundance in unburned reference areas compared with burned areas; Fontaine and Kennedy 2012). For example, fire may be driving declines in small mammal populations of Australian savanna habitat because ground cover removal increases predation risk (Oakwood 2000; Radford 2012).

High-severity fires also appear to favour species with generalist habitat preferences in both Argentina (Albanesi *et al.* 2014) and North America (Fontaine and Kennedy 2012). Similarly, negative responses correlate with high-elevation distributions and poor dispersal abilities (Panzer 2002). As a result, altered disturbance regimes may be particularly deleterious for high-elevation habitat specialists, which necessarily have strict requirements and may already be more susceptible to climate change than lowland generalist species (Rowe *et al.* 2011).

Here, we leverage an unexpected opportunity to investigate the effect of a severe wildfire on a climate-sensitive, mammalian habitat specialist, namely the American pika (*Ochotona princeps* Richardson). Pikas are ideal for investigating responses to climate change and disturbance because they are typically restricted to high-elevation talus (i.e. rock slides and boulder fields) and lava flows in mountain ranges of western North America (although several populations persist near sea level, particularly along the Pacific coast; e.g. Henry *et al.* 2012a; Varner and Dearing 2014a). This distribution is thought to be limited by susceptibility to heat stress (due to a narrow margin between resting body temperature and lethal body temperature; MacArthur and Wang 1974; Smith 1974b) and a limited ability to disperse between patches of talus (Smith 1974a; Smith and Ivens 1983; Henry *et al.* 2012b), especially in warm, dry contexts (Castillo *et al.* 2014).

The factors that limit pika distribution may also render them susceptible to climate change (Smith *et al.* 2004). Indeed, localised extinctions linked to climate have already been documented in many parts of the species' range (Beever *et al.* 2011; Erb *et al.* 2011; Stewart and Wright 2012; Stewart *et al.* 2015), although the effects of climate on pika distribution appear to be complex and locality specific (Millar and Westfall 2010; Jeffress *et al.* 2013). Finally, the foraging strategy of pikas may affect their vulnerability. Because they do not hibernate, pikas spend the short alpine growing season collecting and storing vegetation in food caches called haypiles, which sustain them over the winter (Dearing 1997). Warmer summer temperatures due to climate change may limit foraging, resulting in low-quality food caches for winter (Ray *et al.* 2009). Furthermore, because snow provides pikas with essential insulation against winter temperature minima, reduced snowpack may expose the animals to more extreme winter temperatures (Smith 1978; Beever *et al.* 2010) and affect vegetation availability or quality (Wilkening *et al.* 2011).

Despite widespread recent interest in climate-mediated pika extirpations, very little is known about how this species responds to disturbances like wildfire or whether altered disturbance regimes will heighten the species' susceptibility to climate change. Much of our knowledge about habitat recolonisation comes from meta-population studies where pikas were experimentally removed but resource availability was not manipulated (e.g. Tapper 1973). In contrast, pika recolonisation of Mt St Helens in the years following its 1980 eruption has also been documented (MacMahon *et al.* 1989; Crisafulli *et al.* 2005); however, this extreme event provides little information about responses to more common and less severe disturbances. A better understanding of how this species will respond to disturbance is particularly timely because the current distribution of pikas in western North America overlaps strikingly with areas that are predicted to experience more frequent and severe wildfires as a result of climate change (see fig. 4 in Westerling *et al.* 2006).

We had a unique opportunity to investigate the effect of a wildfire on microclimate refugia and the response of this species to disturbance when a severe forest fire burned many of the instrumented study sites (i.e. talus patches) where we had recently conducted occupancy surveys for *O. princeps* in the Mt Hood National Forest of western North America. In the present study, we addressed three aims. First, we determined how fire affected biologically relevant microclimates during and after the disturbance. We hypothesised that severely burned sites would experience more thermally stressful temperatures than unburned sites. Second, we explored habitat factors that permit populations to rebound in disturbed habitat. Specifically, we examined trends in pika abundance at 24 study sites over 3 years following the fire. We also used a non-invasive measure of physiological stress to assess the health of individual animals. We used abundance and physiological stress as more sensitive predictors of habitat suitability than occupancy because they provide a more detailed and mechanistic understanding of how this species is affected by the disturbance (Millsbaugh and Washburn 2004; Beever *et al.* 2013). Finally, to assess how fire affects pika population sizes in this region, we used an information theoretic framework to evaluate competing hypotheses

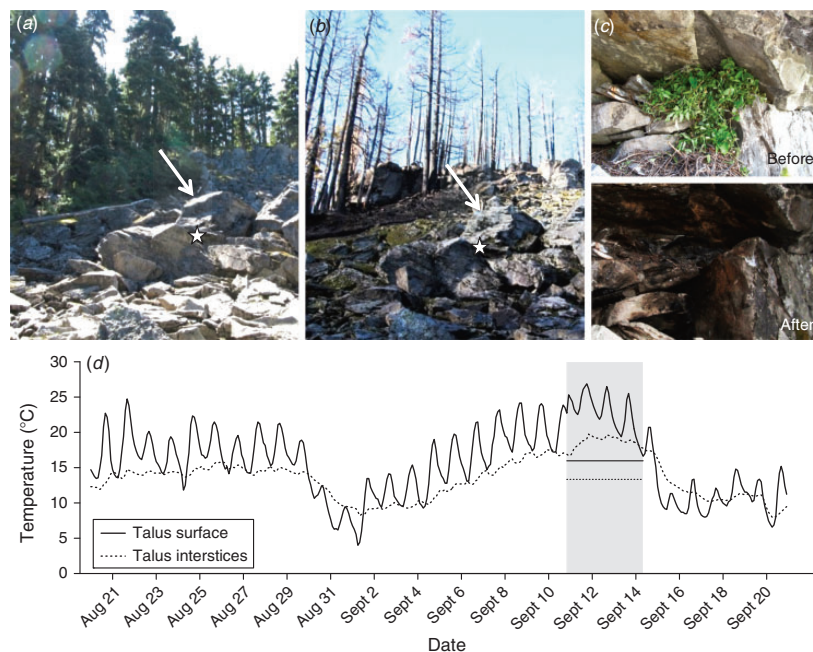


Fig. 1. Fire impacts at a severely burned site. Photographs taken in July (a) 2011 and (b) 2012. Arrows mark temperature datalogger location. Stars mark a pika haypile shown in (c) that burned in the fire. (d) Temperatures before, during and after the fire, recorded by the dataloggers in (a) and (b). Solid lines represent surface temperatures and dotted lines represent temperatures approximately 1 m down into the talus interstices. The grey shaded area indicates fire duration at this site, determined from infrared heat source images. Within this shaded area, horizontal lines represent average temperatures before the fire at the talus surface (solid) and talus interstices (dashed).

regarding whether pika densities are mediated more strongly by topographic factors known to affect this species or by metrics of fire severity and resource availability.

Methods

Study area and the Dollar Lake fire

In August 2011, before the fire, we collected data on pika behaviour and habitat on the north face of Mt Hood (OR, USA). Our aim was to compare talus microclimates and thermoregulatory behaviour with nearby low-elevation habitat in the Columbia River Gorge; thus, vegetation data collected before the fire are limited. In mid-August 2011, we searched for pikas at nine patches of talus (hereafter 'sites'), each separated from other sites by at least 25 m. Sites ranged in elevation from 900 m in a mixed-conifer forest dominated by western red cedar, Douglas fir and western hemlock to nearly 1700 m in a subalpine forest dominated by several species of huckleberry, Sitka mountain ash and subalpine fir. At each of three sites, two temperature dataloggers (HOBO UA-001-08 Pendant; Onset Computer Corporation, Bourne, MA, USA) were deployed to measure pika-relevant microclimates. One datalogger was placed near the surface, protected from direct solar radiation by multiple rocks. A second datalogger was threaded into the talus

interstices approximately 1 m below the surface logger. Each datalogger recorded temperatures every 2 h. Finally, at one site, we trapped and tagged four adult pikas, collected fresh faecal samples and observed the behaviour of the pikas.

One week after completing fieldwork in 2011, a lightning strike ignited the Dollar Lake Fire. From 26 August to 16 September 2011, this fire burned approximately 2430 ha across the north face of Mt Hood and was typical for the fire regime of the western Cascade region. In this area, wildfires are infrequent (approximately every 300–400 years), high severity and stand replacing; however, as these fires reach the subalpine zone, they become highly patchy in nature (due to the variable nature of interfaces between the forest and rocks, meadows and patches of persistent snow; Agee 1996). Within this mosaic of burned habitat, the fire reached four of the nine sites where we had previously surveyed for pikas, including two of three sites where we had placed temperature loggers (Fig. 1a–c). Therefore, these sensors measured temperatures at the talus surface and interstitial space every 2 h before, during and after the fire.

We learned of the fire in June 2012, approximately 9 months after the disturbance. In early August 2012, we surveyed 18 sites for pika abundance, including the nine sites that we visited before the fire (Table 1). Although we could not determine whether the nine new sites were occupied before the fire, all sites

Table 1. Pika occupancy and abundance, before and in the 3 years following the Dollar Lake Fire
NA, not applicable

	2011 pre-fire	2012 summer	2013 spring	2013 autumn	2014 spring	2014 autumn
Years since fire	0	1	2	2	3	3
No. sites sampled	9	18	24	24	23	24
Unburned	9	5	8	8	7	8
Moderate burn	NA	6	8	8	8	8
Severe burn	NA	7	8	8	8	8
Occupancy ^A	89%	83%	83%	96%	83%	96%
Unburned	89%	100%	100%	100%	85.7%	87.5%
Moderate burn	NA	100%	100%	100%	100%	100%
Severe burn	NA	57.1%	50%	87.5%	62.5%	100%
Abundance ^B	3.2 ± 1.2	3.5 ± 0.6	2.7 ± 0.4	3.9 ± 0.6	2.2 ± 0.3	4.0 ± 0.5
Unburned	3.2 ± 1.2	3.8 ± 1.2	3.0 ± 0.5	4.1 ± 1.1	2.3 ± 0.7	3.9 ± 0.9
Moderate burn	NA	4.7 ± 0.8	3.1 ± 0.6	5.8 ± 0.9	2.8 ± 0.3	6.1 ± 0.6
Severe burn	NA	1.3 ± 0.3	1.0 ± 0.0	1.4 ± 0.3	1.5 ± 0.5	2.1 ± 0.4

^AAll unoccupied sites had evidence of past occupancy (e.g. old haypiles or scat).

^BMean ± s.e. abundance of pikas at occupied sites.

had evidence of pikas (i.e. characteristic faecal pellets, haypiles or both), suggesting recent occupancy. However, at this time we could not distinguish between sites where pikas survived the fire *in situ* versus sites that were recolonised during the summer of 2012. To monitor this discontinuous recovery process, we sampled each site twice in each of 2013 and 2014. We also added six additional sites in 2013 for a total of 24 sites (Table 1). At each site, our ‘spring’ sampling period took place at an ecologically equivalent time for the species: as soon as possible after snowmelt, which varied between late May at low elevations to mid-July at high elevations. In contrast, our ‘autumn’ sampling period took place at all sites on equivalent Julian dates: 19–27 August 2013 and 17–27 August 2014.

Classification of burn severity

Fire severity was assessed in 2012 at 10 locations along the perimeter of the talus at each site using a rubric that assesses severity in four ecosystem components: substrate (soil and litter), herbaceous plants (non-woody plants such as graminoids and forbs), shrubs (woody plants without a central trunk) and trees (woody plants with a central trunk; Keane 2007). We then averaged these four metrics to capture overall severity. We also used a laser rangefinder to estimate the percentage of the linear patch perimeter that was burned (i.e. where we found evidence of burned vegetation within 1 m of the talus boundary). Finally, we recorded the presence and extent of white ashes along the burned perimeter, which indicate high fire temperatures (>500°C; Keeley 2009). We used this information to classify sites into three categories of burn severity: severely burned, moderately burned and unburned (see Fig. S1 available as Supplementary Material to this paper). Importantly, average patch size did not differ between these burn severity categories (ANOVA: $F_{1,22} = 0.6$, $P = 0.46$), indicating that the fire did not differentially burn smaller talus patches.

Effects of fire on microclimates

During the fire, temperatures at the talus surface and in talus interstices were recorded by dataloggers placed at three sites in 2011. None of these sensors malfunctioned during the fire.

The dates at which the fire reached each site were determined from fire progression maps and infrared heat maps available online (InciWeb Incident Management System 2011), which indicated zones of intense and scattered heat throughout the fire. To determine temperatures that pikas may have experienced during the fire, we inspected temperature data during the period in which our instrumented sites were zones of intense heat.

After the fire, we hypothesised that pika-relevant microclimates would be most thermally stressful at severely burned sites, either through loss of canopy cover (and therefore shade) or through alterations in surface reflectivity (i.e. darker rocks and soil that would absorb more heat). Alternatively, the fire could have preferentially burned the sites that were naturally the hottest and driest, which may also result in warmer temperatures at the most severely burned sites. To test our hypotheses, we deployed a temperature datalogger (HOBO UA-008; Onset Computer Corporation) in the top 20 cm of the talus at each site in the sampling season in which that site was first surveyed. The sensor was shielded from direct sunlight by multiple rocks (following Varner and Dearing 2014b) and was always placed within 5 m of the lower talus margin, which typically experiences cold air pooling (Millar and Westfall 2010) and therefore often has higher pika densities (Tapper 1973). These sensors were programmed to record temperatures every 2 h. For the purpose of temperature analyses, we combined unburned and moderately burned sites because moderately burned sites did not experience significant changes in either canopy cover or surface reflectivity. Furthermore, moderate-intensity fires typically do not have significant effects on post-fire soil microclimates (Agee 1996).

Habitat suitability for pikas and other talus-dwelling animals may be affected by both heat stress and cold stress, and these stresses can each act acutely or chronically (Beever *et al.* 2010, 2011). Thus, at each site, we calculated several previously validated metrics of thermal stress for pikas. First, we assessed chronic cold stress by estimating snowpack duration and average winter minimum temperatures at each site. Reduced snowpack (extent and duration) can result in lower winter minimum temperatures (Smith 1978; Beever *et al.* 2011). Snowpack

duration was calculated as the number of days in which diel surface temperature fluctuations were $<2^{\circ}\text{C}$ (Lundquist and Lott 2008). We also quantified acute cold stress by counting the number of days during winter in which minimum temperatures were less than -5°C (Beever *et al.* 2010).

Snowpack persisted at the highest elevation sites until mid-July. To avoid confounding the effects of persistent snowpack on summer temperatures, we indexed chronic summer heat stress as the average August temperature, which is biologically relevant for pikas because it is: (1) the only month that was snow free at all sites; (2) the hottest month of the year; and (3) the time at which pikas are most active constructing their winter food caches (Smith 1974b; Dearing 1997). We indexed acute heat stress by the number of days each year that surface temperatures exceeded 28°C . Finally, we quantified the August diel temperature range (i.e. daily maximum–daily minimum), which is an indicator of both acute and chronic heat stress. This variable has only recently been considered in analyses related to pikas and climate change (Wilkening *et al.* 2015); however, both climate change (Braganza *et al.* 2004) and wildfire (Agee 1996) are known to affect diel temperature range, and other species appear to be responding to this increased temperature variability (Walther *et al.* 2002).

Because the fire burned most severely at intermediate elevations, severely burned sites are non-randomly associated with elevation. To control for the inevitable effects of elevation and interannual variation on microclimate temperatures, each of our response variables was modelled as a function of elevation, year and burn status (i.e. severely burned vs moderately burned and unburned) using multiple linear regression. We then used the *step* function in R (v.3.0.2 for Mac OSX) to eliminate non-significant main effects and interactions (R Core Team 2014).

Trends in pika occupancy and abundance

In each sampling season (Table 1), we comprehensively searched each site for pika sign along line transects. Transects followed elevational contours and were spaced 15 m apart. To enumerate individuals, we recorded locations of unequivocal evidence of pikas (e.g. sightings, vocalisations or active hay-piles). Multiple pieces of evidence separated by <20 m were considered to be the same individual unless two animals were calling or visible at the same time. Surveys were conducted in the morning (0600–1000 hours) when temperatures are cool and pikas are most active. At sites where no fresh pika sign was found, we exhaustively resurveyed with greater sampling density (i.e. spacing transects 5–7 m apart) to confirm lack of occupancy (following Beever *et al.* 2011; Erb *et al.* 2011). The amount of talus habitat with rock diameters suitable for pikas (0.2–1.0 m; Tyser 1980) was quantified with a laser rangefinder in the field and pika density was defined as the number of individuals detected per 20-m diameter home range of appropriate habitat. Although we did not explicitly conduct detectability surveys, detectability for this species is reliably high (>0.9) when sampling occurs at appropriate times of day and season (Beever *et al.* 2008, 2011, 2013; Rodhouse *et al.* 2010; Erb *et al.* 2011; Jeffress *et al.* 2013).

To estimate forage availability for pikas, we quantified aboveground edible biomass and species richness of herbaceous plant material in five 1-m² quadrats per site, which were marked

with rebar for repeated sampling. For forbs, shrubs and trees, we counted the number of stems or branches of each plant that would be accessible to pikas (i.e. within 15 cm of the ground). For graminoids, mosses and cushion plants, we estimated the percentage cover of that species within the quadrat. The average biomass of each species was determined from samples ($n = 4–10$) collected in the same way that the abundance of that species was counted (i.e. by the stem for herbaceous plants, branch for shrubs and trees or area of cover for graminoids, mosses and cushion plants). Samples were also collected in the same way that a pika would consume the vegetation, as determined by previous behavioural observations (e.g. only leaves were collected from shrubs and trees; Varner and Dearing 2014a). To allow repeated sampling of quadrats and avoid influencing vegetation recovery at burned sites, we harvested plant samples from outside of quadrats, primarily at unburned sites. In any given season of sampling, we did not observe any qualitative differences in the average stature of several herbaceous plant species in burned areas versus those outside of the burn.

We analysed trends in pika abundance, density and vegetation characteristics (biomass and species richness) with repeated-measures ANOVA. In each analysis, we used burn severity and sampling season as main effects and year as a repeated measure on each site. This analysis only included sites that were sampled in all five seasons ($n = 17$ sites).

Stress hormone analysis

To assess the health of individual pikas, we collected fresh faecal pellets at 11 occupied sites during the autumn sampling of 2013 ($n = 19$ samples, from five severely burned sites and six unburned or moderately burned sites). Each sample ($n = 19$) was collected from a separate home range; thus, samples likely came from distinct individuals. Samples were kept on ice in the field and were transferred to a -80°C freezer within 2 weeks of collection.

Faecal glucocorticoid metabolite (GCM) levels have been previously validated as a biologically relevant measure of chronic physiological stress in pikas (Wilkening *et al.* 2013; Wilkening 2014) and environmental samples collected within the same ecoregion in the same sampling season can be used reliably for comparisons (Wilkening *et al.* 2015). In our analysis, we followed previously validated protocols (Wilkening *et al.* 2013) to measure GCM in fresh faeces collected in August 2013 and in four faecal samples collected from trapped individuals in August 2011 before the fire. We used a commercially available corticosterone enzyme immunoassay kit (no. K014-H1; Arbor Assay Design, Ann Arbor, MI, USA) according to the manufacturer's instructions. Final concentrations of faecal GCM were expressed as ng GCM per g faeces.

One-way ANOVA was used to test for differences in GCM concentration between severely burned sites, unburned or moderately burned sites and samples collected before the fire. Prior to analysis, data were checked for outliers and a Fligner–Killeen test was conducted to check for homogeneity of variances.

Modelling pika density

At each site, we also collected biophysical and topographic information known to affect habitat suitability for pikas.

Table 2. Predictor variables used in modelling analysis

	Predictor variable	Description (units)
Vegetation availability	veg	Average biomass of vegetation in quadrats (g m^{-2})
	veg_rich	Average plant species richness in quadrats (n)
	moss ^A	Talus area covered in moss (%)
Topographic predictors	insol	Estimated potential solar insolation, $\text{sine}(\text{slope angle}) \times \text{cosine}(\text{aspect})$
	crevice	Deepest crevice in talus (cm)
	elevation	Site elevation (m above sea level)
Fire severity predictors	burncategory	Categorical classification of burn severity (levels = 'severe' or 'unburned or moderately burned')
	fireseverity	Average fire severity (quantified by rubric scores at the level of substrate, herbaceous cover, shrub cover and tree canopy)
	perim_burned	Linear talus patch perimeter burned (%)

^ATalus moss cover may also reflect microclimates (Varner and Dearing 2014b).

We estimated potential solar exposure at each site using a previously described insolation index (Jeffress *et al.* 2013). The aspect and slope angle of each site were measured using a compass and clinometer, and potential solar insolation was calculated as $\text{sine}(\text{slope}) \times \text{cosine}(\text{aspect})$. This index ranges from -1 to 1 , where 1 indicates steeper north-facing slopes with little solar exposure and -1 indicates steep south-facing slopes with high exposure (Jeffress *et al.* 2013). Talus depth is notoriously difficult to estimate (Rodhouse *et al.* 2010), but observers visually estimated the deepest crevice encountered at each site (i.e. the vertical distance between the lowest rock at the bottom of the crevice and the highest rock at the crevice opening). We also visually estimated percentage moss cover at each site because mosses are a food resource for pikas in this region (Varner and Dearing 2014a) and may also mediate microclimates (Varner and Dearing 2014b).

To evaluate the relative contributions of these traditional metrics of habitat suitability compared with the effect of the fire on pika density, we used an information theoretic framework to evaluate a suite of models including combinations of uncorrelated ($r < 0.6$) predictor variables (Table S1). Predictor variables were determined *a priori* and included metrics of vegetation availability, fire severity and topographic variables known to affect pikas (Table 2). All continuous predictors were centred and scaled by their standard deviation, which improves computation and simplifies the interpretation of model intercepts (Gelman and Hill 2007). We modelled pika density with linear regression in R (R Core Team 2014) using a *glm*. For each model, we calculated Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002). We considered models with $\Delta\text{AIC}_c < 2$ to have substantial support (Burnham and Anderson 2002).

Results

Effects of fire on microclimates

Serendipitously, of the three sites that we outfitted with dataloggers before the fire in 2011, one site was unburned, one was moderately burned and one was severely burned. Elevated temperatures were observed during the fire at the severely burned site only. The timing of the elevated talus temperatures (Fig. 1d) corresponded perfectly with infrared heat maps indicating that this site was a part of an intense heat zone from 11 to

13 September 2011, with the area cooling to isolated heat sources by 14 September 2011 (InciWeb Incident Management System 2011). During the fire, daily maxima at the talus surface were similar to temperatures observed before the fire; however, daily minima were elevated by 10 – 15°C during the fire relative to the daily minima before the fire. Similarly, sub-talus temperatures ranged from 18 – 19°C during the fire, compared with 7 – 14°C immediately before and after (Fig. 1d).

Following the fire, severely burned sites experienced fewer days of snowpack ($F_{4,36} = 69.0$, elevation $P = 0.003$, burn status $P = 0.001$, year $P < 0.001$, elevation \times year $P = 0.003$; Fig. 2a). However, even when accounting for elevation, we found no evidence that reduced snowpack translated into increased cold stress in the talus at severely burned sites. Burn status was not significant in explaining variation in winter minimum temperatures ($F_{2,38} = 29.5$, elevation $P < 0.001$, burn status $P = 0.24$, year $P < 0.001$; Fig. 2b) or the number of days where temperatures were less than -5°C ($F_{4,36} = 27.8$, elevation $P = 0.002$, burn status $P = 0.24$, year $P < 0.001$, elevation \times year $P = 0.002$; Fig. 2c).

Similarly, we found little evidence that severely burned sites experienced increased heat stress during the summer. Contrary to our predictions, there was no effect of elevation, year or burn status on August diel temperature range ($F_{7,38} = 0.5$, elevation $P = 0.36$, burn status $P = 0.32$, year $P = 0.66$; Fig. 2d). Burn status was a significant predictor of average August temperature; however, the presence of an interaction term with elevation makes this result difficult to interpret ($F_{4,41} = 15.9$, elevation $P < 0.001$, burn status $P = 0.03$, year $P < 0.001$, elevation \times burn status $P = 0.04$; Fig. 2e). Finally, burn status was not a significant predictor of the number of days where surface temperatures exceeded 28°C ($F_{1,43} = 9.1$, elevation $P = 0.004$, burn status $P = 0.81$, year $P = 0.95$; Fig. 2d).

Trends in pika occupancy and abundance

We never resighted any of the four tagged animals after the fire, either at the severely burned site where they were initially tagged (Fig. 1) or at any nearby talus patches. However, pikas were widely distributed after the burn, with overall occupancy rates $> 83\%$ (Table 1). In fact, overall occupancy rates did not significantly decrease from before the fire (89%) to approximately 10 months after the fire (83% ; $\chi^2 = 0$, d.f. = 1, $P = 1.0$; Table 1).

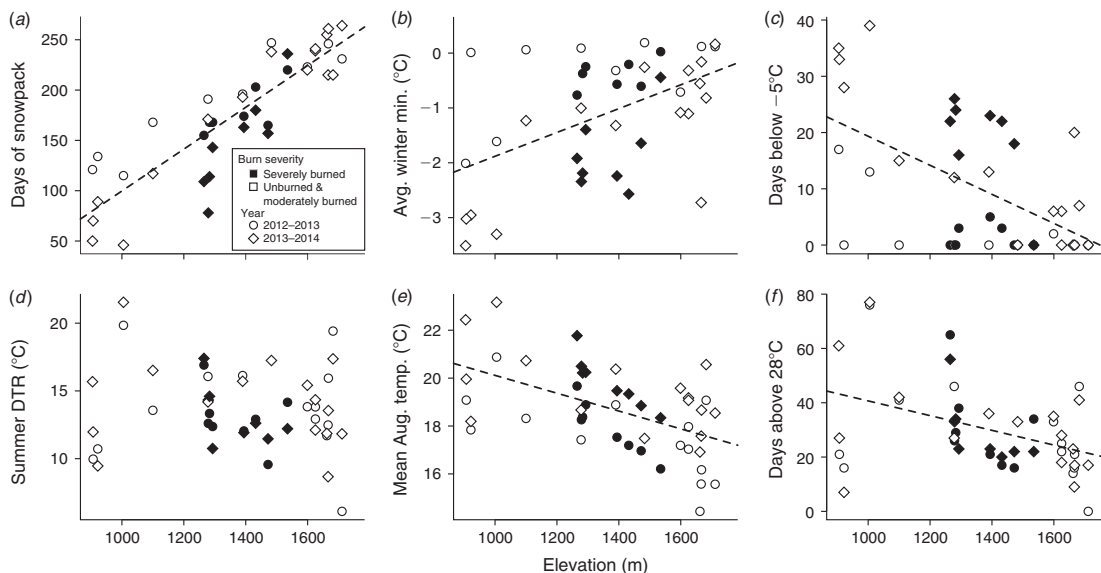


Fig. 2. Metrics of pika thermal stress determined by talus surface sensors following the fire. Thermal stress for pikas was estimated by six metrics (see Methods for details) in 2 years following the fire. Dashed lines indicate significant regressions against elevation using all data points. Chronic cold stress was estimated as (a) the number of days of snowpack and (b) average daily winter minimum temperature. (c) Acute cold stress was estimated as the number of days during which surface temperatures reached -5°C or lower. (d) Summer diel temperature range (DTR) is a metric of both chronic and acute heat stress and represents the average difference between each day's maximum and daily minimum temperatures. (e) Chronic heat stress was estimated as the mean surface temperature during August. (f) Acute heat stress was estimated as the number of days during which surface temperatures exceeded 28°C .

Furthermore, every moderately burned site was occupied in all seasons following the fire, and occupancy rates for severely burned sites recovered from 57.1% (summer 2012) to 87.5% (autumn 2013) in less than 14 months (Table 1). In autumn 2013, only one severely burned site was left unoccupied, and this site had been previously occupied in 2012. Thus, within 2 years of the fire, all sites were occupied by pikas in at least one season of sampling. By autumn 2014, all severely burned sites were occupied, and the only unoccupied site was a small, unburned site at high elevation.

In 2013 and 2014, both pika occupancy and average abundance increased from spring to autumn (Table 1); however, there was no significant effect of sampling period on pika abundance or density (i.e. number of individuals detected per 20-m diameter home range of suitable habitat; time $F_{1,14}=2.9$, $P=0.11$; Fig. 3a). Across all sampling periods, pika density was lowest at severely burned sites (burn status $F_{2,14}=9.8$, $P=0.002$; Fig. 3a). Vegetation availability was also lowest at severely burned sites in all sampling periods (burn status $F_{2,14}=7.0$, $P=0.008$; time $F_{1,14}=2.6$, $P=0.13$; Fig. 3b). Severely burned sites had fewer plant species in all sampling periods (burn status $F_{2,14}=15.2$, $P<0.001$; Fig. 3c): vegetation was typically limited to a few early colonisers (beargrass, *Xerophyllum tenax*; fireweed, *Chamerion angustifolium*; pearly everlasting, *Anaphalis margaritacea*; and white avalanche lily, *Erythronium montanum*). However, species richness increased significantly at these sites over the study (time $F_{1,14}=32.1$, $P<0.001$; Fig. 3c).

We hypothesised that vegetation availability would predict pika abundance. Indeed, a vegetation threshold of approximately 55 g m^{-2} dry weight vegetation appeared necessary to support a population of pikas with two or more individuals, which represents the minimum size of a reproducing population (Fig. 4; Fig. S2). Above this threshold, there were very few unoccupied sites and vegetation biomass appears to have little impact on pika abundance. In contrast, below this threshold, few sites have two individuals and no sites have more than two individuals (Fig. 4).

Stress hormone analysis

We found no difference in stress hormone concentrations between samples collected before the fire in 2011, at severely burned sites in 2013 and those collected at unburned or moderately burned sites in 2013 (mean (\pm s.e.) 11.55 ± 1.84 , 10.99 ± 0.82 and $12.49 \pm 1.49\text{ ng g}^{-1}$ respectively; $F_{2,20}=0.412$, $P=0.67$). These values are well within those reported previously across the range of the species (Wilkening *et al.* 2013, 2015; Wilkening 2014).

Modelling pika density

Pika density was best predicted by a single model that included terms for vegetation species richness and percentage moss cover on the talus (Table 3). The next-best models also included terms for vegetation species richness, but these models did not receive substantial support (Table 3). Burn severity predictors did not appear in any of the top models.

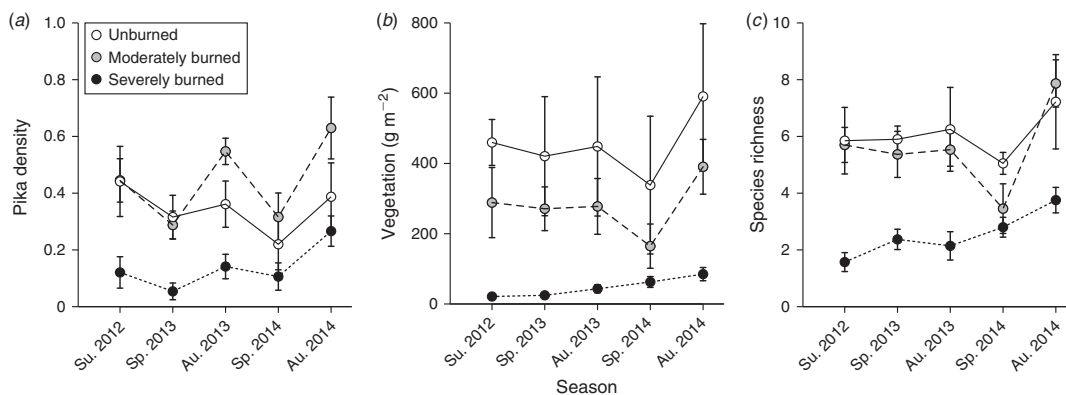


Fig. 3. Trends in pika density and vegetation across sampling periods. Trends in (a) pika density (i.e. pikas detected per 20-m diameter home range of talus), (b) vegetation biomass per m^2 and (c) plant diversity as measured by species richness per m^2 . Only sites that were sampled in all five seasons ($n = 17$) are shown. Sampling dates are given in the Methods. Su.: summer; Sp.: spring; Au.: autumn.

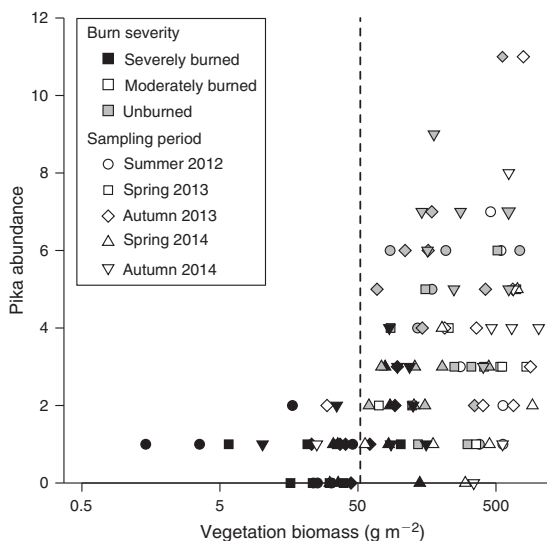


Fig. 4. Vegetation threshold for pika abundance. Shading indicates burn status, shape indicates sampling period. The horizontal axis represents the average vegetation biomass (across five quadrats) at each site in each sampling period. The threshold appears to be approximately 55 g m^{-2} dry weight vegetation.

Discussion

Although wildfires are predicted to increase in frequency and severity in many environments as a result of contemporary climate change (e.g. Westerling *et al.* 2006; Dennison *et al.* 2014), relatively little is known about how wildlife will respond to altered fire regimes (Driscoll *et al.* 2010). A better understanding of short- and long-term consequences of fire on habitat quality is needed on a species-by-species basis. In the present study, we investigated the effects of wildfire disturbance on

Table 3. Linear regression results from analysis of pika density at 17 study sites, including the top six models, plus the null model

Only the first model had substantial support. Variables are defined in Table 2.

AIC_c, Akaike's Information Criterion corrected for small sample size

Model	AIC _c	ΔAIC_c	K	Model weight
veg_rich + moss	22.1	0	4	0.9823
veg_rich	30.8	8.7	3	0.0129
veg + veg_rich	32.9	10.8	4	0.0045
insol + crevice + moss	40.5	18.4	5	<0.001
burncategory + insol	40.6	18.5	4	<0.001
burncategory	41.3	19.2	3	<0.001
null	60	37.9	2	<0.001

habitat quality for a sensitive, montane habitat specialist, namely the American pika. Consistent with their high-elevation distribution and specialisation to talus habitat, pikas exhibited an overall negative response to a severe burn (Fig. 3a). However, pikas exhibited high occupancy rates in all seasons of sampling, and the severe burn did not leave a lasting effect on pika-relevant microclimates. Together with the results of our modelling analyses, these results suggest that pikas may be relatively resilient to altered disturbance regimes in the future, at least in the Pacific Northwest ecoregion.

To our knowledge, these are also the first data to document the thermal effects of fire in talus, both during the fire and for 3 years following the fire. During the fire, temperatures in the talus were very different from typical patterns in soil, which have been well documented (Agee 1973; Swezy and Agee 1991). Although temperatures in the burrows of small mammals may exceed 50°C for many hours (Lawrence 1966), talus interstitial temperatures approximately 5 m from the burned perimeter remained between 18 and 19°C during the fire (Fig. 1d) and even temperatures at the talus surface at this location rarely reached 27°C . Measurements in the talus were

always well below our best estimate of a threshold for acute heat stress in pikas (2 h at 25.5°C; MacArthur and Wang 1974; Smith 1974b), suggesting that pikas and other animals may be able to survive fires *in situ* by retreating into the talus. Pikas could have been subject to oxygen depletion and smoke inhalation during this time. However, in this regard, talus microhabitats are likely similar to burrows, which appear to be relatively safe shelters from toxic gases (O'Brien *et al.* 2006).

In the longer term, soil surface temperatures tend to be warmer during the day and cooler at night due to loss of the insulating forest canopy after a severe burn (Fowler and Helvey 1978; Fontaine *et al.* 2010). Furthermore, charred surfaces absorb more sunlight and re-radiate more heat at night (Agee 1996). Because canopy cover and surface reflectivity are slow to recover after a severe fire, these microclimate effects can last for years (Vioreck 1973; Fowler and Helvey 1978; Engstrom 2010). Even microclimates measured 1.5 m into burrows can be altered for years by severe fire (Fellers *et al.* 2004). In contrast, we found little evidence that the fire affected talus microclimates at severely burned sites in the 3 years following fire (Fig. 2). Burn severity was only a significant predictor in two of our six metrics of thermal stress: average August temperature and duration of snowpack. However, the presence of an interaction term between burn severity and elevation makes the average August temperature result difficult to interpret: it may be a statistical artefact of the non-random distribution of burn severity with regard to elevation and not biologically significant. Furthermore, reduced snowpack duration at severely burned sites did not result in colder winter temperatures, at either acute or chronic time scales.

The fact that we did not observe substantial differences in microclimates between severely burned sites and unburned or moderately burned sites, despite marked changes in canopy cover and surface reflectivity, suggests that microclimates in these talus slopes are likely driven by sub-talus features rather than surface heat-transfer processes, such as incident radiation or convection. The relatively cool temperatures that we measured in the talus during the fire further reinforce the low thermal diffusivity of talus in this region, which buffers subsurface microclimates from surface processes. Together, these results highlight the capacity of talus to buffer against ambient temperatures and reinforce its conservation value as both a natural fire break (Baker 2009) and a thermal refuge for animals (e.g. Henry *et al.* 2012a; Shi *et al.* 2014; Varner and Dearing 2014b).

Several lines of evidence suggest that pikas may have survived the fire *in situ* and that these sites provide suitable habitat for pikas after fire. Because we did not re-sight any tagged animals after the fire, we cannot say for certain that animals survived the fire *in situ*. In addition, severely burned sites consistently had lower pika density compared with other sites (Fig. 3a). However, within 2 years of the fire, all 24 of our study sites were occupied by pikas in at least one season of sampling (Table 1). Furthermore, increased density in autumn (relative to spring, in both 2013 and 2014) suggests that juveniles are being recruited into the population at these sites (Fig. 3). Finally, stress hormone levels from pikas in severely disturbed habitat did not differ from pikas in other habitats, which further highlights the suitability of severely burned habitats. Stable talus microclimates may be an important

driver of the widespread distribution of pikas within severely disturbed habitat.

In many ways, wildfire disturbance can be viewed as a natural experiment in resource manipulation that permits critical habitat thresholds for persistence to be determined. Here, we found that pika abundance appeared closely related to a threshold in vegetation biomass (55 g m⁻²; Fig. 4). Below the threshold, few sites supported more than a single individual. Above the threshold, pika abundance was highly variable, suggesting that abundance depends on other factors when enough vegetation is present. These data provide a first quantitative estimate of resources necessary for a minimum reproducing population of pikas. Such thresholds could potentially be used both to inform predictions of species distributions under continued environmental changes and as evidence-based targets for conservation and management applications (Mawdsley *et al.* 2009; Touihri *et al.* 2014).

Although burned sites had less vegetation overall, the new plants at these sites may be more nutritious as a result of the burn. The fact that moderately burned sites had the highest pika densities of all sites in the autumn of both 2013 and 2014 (Fig. 3a) suggests that an intermediate level of disturbance may benefit pikas, perhaps through plant nutrition or diversity. Indeed, several studies have demonstrated increased nutritional quality after a burn (i.e. higher nitrogen content, fewer plant secondary compounds and greater digestibility; Leigh *et al.* 1991; Jakubas *et al.* 1994; Moe and Wegge 1997). However, reduced snowpack at severely burned sites (Fig. 2a) may also affect soil moisture and the pace of vegetation recovery.

Vegetation species richness was the most significant predictor of pika density (Table 3). As generalist herbivores, pikas feed on a diverse range of plant species (Huntly *et al.* 1986; Dearing 1996), which may explain the importance of diversity. The only significant model to predict pika density also included moss cover (Table 3). In our study region, pikas consume moss (Varner and Dearing 2014a); thus, the appearance of moss cover in our top model may indicate that pikas are supplementing their diets with moss. Alternatively, moss may also affect talus microclimates (Varner and Dearing 2014b) or may indicate microclimatic conditions (e.g. high humidity, cool temperatures) that are favourable for pikas. No other topographic predictors or metrics of burn severity were present in any of the top models, suggesting that the effects of the fire on habitat quality (as indexed by animal density) were most saliently mediated through food quality and diversity. Similarly, in arid Australia, mammalian communities and distributions were better predicted by food resources and geographic location (Letnic *et al.* 2004) or the timing and spatial distribution of rainfall events (Letnic and Dickman 2005) rather than habitat structure or burn severity, suggesting that post-fire succession did not directly influence mammalian species assemblages *per se*.

Even within a species, it may be difficult to generalise responses to fire because of existing variation in habitat quality. To this end, more research will be necessary to determine the response of pikas to fire in ecoregions where their distribution has already been affected by climate change (Beever *et al.* 2011; Jeffress *et al.* 2013). For example, in Yellowstone National Park in north-western Wyoming, a site burned during that park's

famous 1988 fires now has the highest pika density of any patch surveyed in the park (among 66 talus patches; E. Beever, unpubl. data). Similarly, in the western Great Basin, fire appears to have stimulated vegetation growth, favouring higher pika haypile densities at a recently burned site compared with nearby unburned areas (Millar *et al.* 2013). In contrast, only a single pika was detected on two mountains in semi-arid north-eastern California within the perimeter of fires from 1990, 2001 or 2012 (among 10 talus patches that collectively span hundreds of home ranges; E. Beever and T. Rickman, unpubl. data).

Several ecological factors could have influenced these differential responses to fire. In warmer and drier regions, post-fire food availability may be critical, particularly if native vegetation is replaced by unpalatable exotic species (D'Antonio and Vitousek 1992). Furthermore, warmer ecoregions may lack habitat features that functionally decouple talus microclimates from ambient conditions (e.g. sub-talus ice or water features, forest canopy or vegetation cover; Varner and Dearing 2014b), which are present in our study area. As a result, these ecoregions may experience longer-term post-fire alterations in microclimates that could affect the status and distribution of pika populations. This climatic harshness (i.e. high ambient temperatures and low annual precipitation) may also reduce the dispersal capabilities of pikas and thus their ability to recolonise burned areas (Henry *et al.* 2012b; Castillo *et al.* 2014). Finally, like temperature and precipitation (Henry and Russello 2013), fire regimes may act as a selective force driving pika evolution such that some populations of pikas are better adapted to recolonising disturbed habitat than others. Together, these factors may result in lags in recolonisation of burned patches in certain ecoregions, leading to protracted periods of reduced occupancy after a fire in parts of the species' range.

Increases in frequency and intensity of wildfires pose a complicated challenge for land managers. Our results highlight the importance of maintaining thermal refugia for sensitive species during wildfires and make an important first contribution towards understanding how pikas, climate-sensitive habitat specialists, may cope with changing disturbance regimes. Our results also reinforce the need for investigations to comprehensively portray the taxonomic, topographic, climatic and ecological contexts that mediate responses to wildfires. Such data will allow later meta-analyses to synthesise patterns that advance from species-by-species bases to a more holistic understanding (Driscoll *et al.* 2010).

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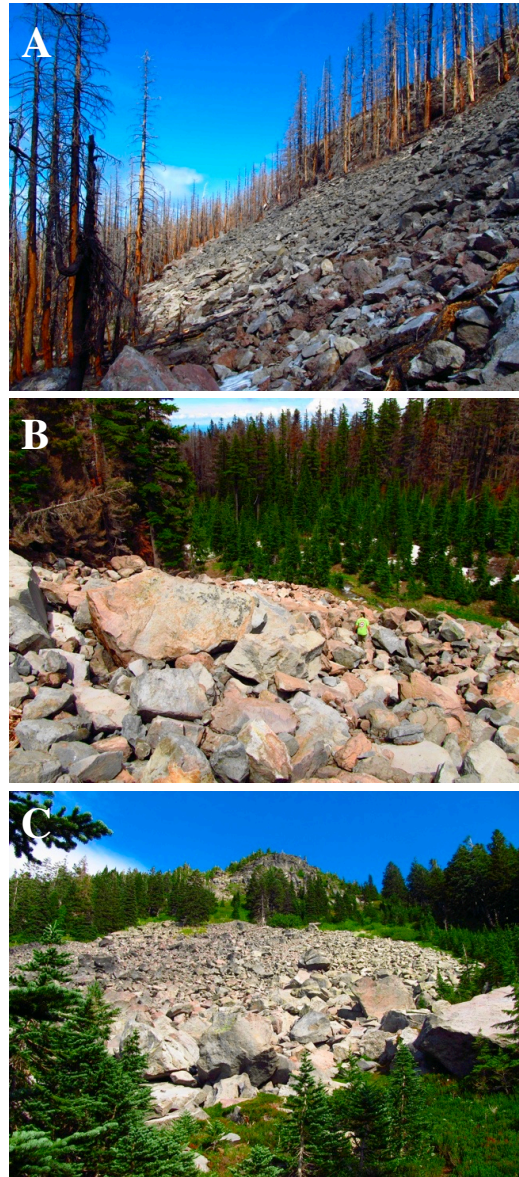
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References

- Agee JK (1973) 'Prescribed fire effects on physical and hydrologic properties of mixed-conifer forest floor and soil.' Water Resources Center, University of California, Contribution Report 143. (Berkeley, CA.)
- Agee JK (1996) 'Fire ecology of Pacific Northwest forests.' (Island Press: Washington, DC.)
- Albanesi S, Dardanelli S, Bellis L (2014) Effects of fire disturbance on bird communities and species of mountain *serrano* forest in central Argentina. *Journal of Forest Research* **19**, 105–114. doi:10.1007/S10310-012-0388-4
- Azeria ET, Ibarzabal J, Hébert C, Boucher J, Imbeau L, Savard J-PL (2011) Differential response of bird functional traits to post-fire salvage logging in a boreal forest ecosystem. *Acta Oecologica* **37**, 220–229. doi:10.1016/j.actao.2011.02.005
- Baker W (2009) 'Fire ecology in rocky mountain landscapes.' (Island Press: Washington, DC.)
- Beever EA, Wilkening JL, McIvor DE, Weber SS, Brussard PE (2008) American pikas (*Ochotona princeps*) in northwestern Nevada: a newly discovered population at a low-elevation site. *Western North American Naturalist* **68**, 8–14. doi:10.3398/1527-0904(2008)68[8:APOPINJ].2.CO;2
- Beever EA, Ray C, Mote PW, Wilkening JL (2010) Testing alternative models of climate-mediated extirpations. *Ecological Applications* **20**, 164–178. doi:10.1890/08-1011.1
- Beever EA, Ray C, Wilkening JL, Brussard PF, Mote PW (2011) Contemporary climate change alters the pace and drivers of extinction. *Global Change Biology* **17**, 2054–2070. doi:10.1111/J.1365-2486.2010.02389.X
- Beever EA, Dobrowski SZ, Long J, Mynsberge AR, Piekielek NB (2013) Understanding relationships among abundance, extirpation, and climate at ecoregional scales. *Ecology* **94**, 1563–1571. doi:10.1890/12-2174.1
- Braganza K, Karoly DJ, Arblaster J (2004) Diurnal temperature range as an index of global climate change during the twentieth century. *Geophysical Research Letters* **31**, L13217. doi:10.1029/2004GL019998
- Burnham KP, Anderson DR (2002) 'Model selection and multimodel inference: a practical information-theoretic approach.' (Springer: New York, NY.)
- Cahill AE, Aiello-Lammens ME, Fisher-Reid CM, Hua X, Karanewsky CJ, Ryu HY, Sbeglia GC, Spagnolo F, Waldron JB, Warsi O, Wiens JJ (2012) How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences* **280**, 20121890. doi:10.1098/RSPB.2012.1890
- Cansler CA, McKenzie D (2014) Climate, fire size, and biophysical setting control fire severity and spatial pattern in the northern Cascade Range, USA. *Ecological Applications* **24**, 1037–1056. doi:10.1890/13-1077.1
- Castillo JA, Epps CW, Davis AR, Cushman SA (2014) Landscape effects on gene flow for a climate-sensitive montane species, the American pika. *Molecular Ecology* **23**, 843–856. doi:10.1111/MEC.12650
- Crisafulli CM, MacMahon JA, Parmenter RR (2005) Small-mammal survival and colonization on the Mount St. Helens volcano: 1980–2002. In 'Ecological responses to the 1980 eruption of Mount St. Helens'. (Eds VH Dale, FJ Swanson, CM Crisafulli.) pp. 199–218. (Springer: New York, NY.)
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**, 63–87. doi:10.1146/ANNUREV.EC.23.110192.000431
- Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Hanson PJ, Irland LC, Lugo AE, Peterson CJ, Simberloff D, Swanson FJ, Stocks BJ, Wotton BM (2001) Climate change and forest

- disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *Bioscience* **51**, 723–734. doi:10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2
- Dearing MD (1996) Disparate determinants of summer and winter diet selection of a generalist herbivore, *Ochotona princeps*. *Oecologia* **108**, 467–478. doi:10.1007/BF00333723
- Dearing MD (1997) The function of haypiles of pikas (*Ochotona princeps*). *Journal of Mammalogy* **78**, 1156–1163. doi:10.2307/1383058
- Dennison PE, Brewer SC, Arnold JD, Moritz MA (2014) Large wildfire trends in the western United States, 1984–2011. *Geophysical Research Letters* **41**, 2928–2933. doi:10.1002/2014GL059576
- Driscoll DA, Lindenmayer DB, Bennett AF, Bode M, Bradstock RA, Cary GJ, Clarke MF, Dexter N, Fensham R, Friend G, Gill M, James S, Kay G, Keith DA, MacGregor C, Russell-Smith J, Salt D, Watson JEM, Williams RJ, York A (2010) Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* **143**, 1928–1939. doi:10.1016/j.biocon.2010.05.026
- Engstrom RT (2010) First-order fire effects on animals: review and recommendations. *Fire Ecology* **6**, 115–130. doi:10.4996/FIREECOL.0601115
- Erb LP, Ray C, Guralnick R (2011) On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*). *Ecology* **92**, 1730–1735. doi:10.1890/11-0175.1
- Fellers GM, Pratt D, Griffin JL (2004) Fire effects on the Point Reyes mountain beaver at Point Reyes National Seashore, California. *The Journal of Wildlife Management* **68**, 503–508. doi:10.2193/0022-541X(2004)068[0503:FEOTPR]2.0.CO;2
- Flannigan M, Stocks B, Turetsky M, Wotton M (2009) Impacts of climate change on fire activity and fire management in the circumboreal forest. *Global Change Biology* **15**, 549–560. doi:10.1111/j.1365-2486.2008.01660.x
- Fontaine JB, Kennedy PL (2012) Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in US fire-prone forests. *Ecological Applications* **22**, 1547–1561. doi:10.1890/12-0009.1
- Fontaine JB, Donato DC, Campbell JL, Martin JG, Law BE (2010) Effects of post-fire logging on forest surface air temperatures in the Siskiyou Mountains, Oregon, USA. *Forestry* **83**, 477–482. doi:10.1093/FORESTRY/CPQ030
- Fowler W, Helvey J (1978) 'Changes in the thermal regime after prescribed burning and select tree removal (Grass Camp, 1975).' U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Research Paper PNW-234. (Portland, OR.)
- Gelman A, Hill J (2007) 'Data analysis using regression and multilevel/hierarchical models.' (Cambridge University Press: New York, NY.)
- Henry P, Russello M (2013) Adaptive divergence along environmental gradients in a climate-change-sensitive mammal. *Ecology and Evolution* **3**, 3906–3917. doi:10.1002/ECE3.776
- Henry P, Henry A, Russello MA (2012a) Variation in habitat characteristics of American pikas along an elevation gradient at their northern range margin. *Northwest Science* **86**, 346–350. doi:10.3955/046.086.0410
- Henry P, Sim Z, Russello MA (2012b) Genetic evidence for restricted dispersal along continuous altitudinal gradients in a climate change-sensitive mammal: the American pika. *PLoS One* **7**, e39077. doi:10.1371/JOURNAL.PONE.0039077
- Huntly NJ, Smith AT, Ivins BL (1986) Foraging behavior of the pika (*Ochotona princeps*), with comparisons of grazing versus haying. *Journal of Mammalogy* **67**, 139–148. doi:10.2307/1381010
- InciWeb Incident Management System (2011) 'The Dollar Lake fire.' Available at: <http://inciweb.nwgc.gov/incident/2563> [Verified 1 October 2013].
- Jakubas WJ, Garrott RA, White PJ, Mertens DR (1994) Fire-induced changes in the nutritional quality of lodgepole pine bark. *The Journal of Wildlife Management* **58**, 35–46. doi:10.2307/3809546
- Jeffress MR, Rodhouse TJ, Ray C, Wolff S, Epps C (2013) The idiosyncrasies of place: geographic variation in the climate-distribution relationships of the American pika. *Ecological Applications* **23**, 864–878. doi:10.1890/12-0979.1
- Keane R (2007) 'Firemon: Plot description sampling methods.' Available at: http://www.frames.gov/documents/projects/firemon/PD_Text_062007.pdf [Verified 20 March 2015].
- Keeley JE (2009) Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* **18**, 116–126. doi:10.1071/WF07049
- Lawrence GE (1966) Ecology of vertebrate animals in relation to chaparral fire in the Sierra Nevada foothills. *Ecology* **47**, 278–291. doi:10.2307/1933775
- Leigh J, Wood D, Slee A, Holgate M (1991) The effects of burning and simulated grazing on productivity, forage quality, mortality and flowering of eight subalpine herbs in Kosciusko National Park. *Australian Journal of Botany* **39**, 97–118. doi:10.1071/BT9910097
- Leticic M, Dickman C (2005) The responses of small mammals to patches regenerating after fire and rainfall in the Simpson Desert, central Australia. *Austral Ecology* **30**, 24–39. doi:10.1111/j.1442-9993.2004.01410.x
- Leticic M, Dickman CR, Tischler MK, Tamayo B, Beh CL (2004) The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments* **59**, 85–114. doi:10.1016/j.jaridenv.2004.01.014
- Lundquist JD, Lott F (2008) Using inexpensive temperature sensors to monitor the duration and heterogeneity of snow-covered areas. *Water Resources Research* **44**, W00D16. doi:10.1029/2008WR007035
- MacArthur RA, Wang LCH (1974) Behavioral thermoregulation in the pika, *Ochotona princeps*: a field study using radiotelemetry. *Canadian Journal of Zoology* **52**, 353–358. doi:10.1139/Z74-042
- MacMahon JA, Parmenter RR, Johnson KA, Crisafulli CM (1989) Small mammal recolonization on the Mount St. Helens volcano: 1980–1987. *American Midland Naturalist* **122**, 365–387. doi:10.2307/2425924
- Mason TH, Stephens PA, Apollonio M, Willis SG (2014) Predicting potential responses to future climate in an alpine ungulate: interspecific interactions exceed climate effects. *Global Change Biology* **20**, 3872–3882. doi:10.1111/GCB.12641
- Mawdsley JR, O'Malley R, Ojima DS (2009) A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. *Conservation Biology* **23**, 1080–1089. doi:10.1111/j.1523-1739.2009.01264.x
- Millar CI, Westfall RD (2010) Distribution and climatic relationships of the American pika (*Ochotona princeps*) in the Sierra Nevada and western Great Basin, USA; periglacial landforms as refugia in warming climates. *Arctic, Antarctic, and Alpine Research* **42**, 76–88. doi:10.1657/1938-4246-42.1.76
- Millar CI, Westfall RD, Delany DL (2013) New records of marginal locations for American pika (*Ochotona princeps*) in the western Great Basin. *Western North American Naturalist* **73**, 457–476. doi:10.3398/064.073.0412
- Millspaugh J, Washburn B (2004) Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation. *General and Comparative Endocrinology* **138**, 189–199. doi:10.1016/j.ygcen.2004.07.002
- Moe SR, Wegge P (1997) The effects of cutting and burning on grass quality and axis deer (*Axis axis*) use of grassland in lowland Nepal. *Journal of Tropical Ecology* **13**, 279–292. doi:10.1017/S0266467400010452
- Mooney HA, Hobbs RJ (2000) 'Invasive species in a changing world.' (Island Press: Washington, DC.)

- Nappi A, Drapeau P, Saint-Germain M, Angers VA (2010) Effect of fire severity on long-term occupancy of burned boreal conifer forests by saproxylic insects and wood-foraging birds. *International Journal of Wildland Fire* **19**, 500–511. doi:10.1071/WF08109
- O'Brien JJ, Stahala C, Mori GP, Callahan MA, Jr, Bergh CM (2006) Effects of prescribed fire on conditions inside a Cuban parrot (*Amazona leucocephala*) surrogate nesting cavity on Great Abaco, Bahamas. *The Wilson Journal of Ornithology* **118**, 508–512. doi:10.1676/05-118.1
- Oakwood M (2000) Reproduction and demography of the northern quoll, *Dasyurus hallucatus*, in the lowland savanna of northern Australia. *Australian Journal of Zoology* **48**, 519–539. doi:10.1071/ZO00028
- Panzer R (2002) Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. *Conservation Biology* **16**, 1296–1307. doi:10.1046/J.1523-1739.2002.01077.X
- Parnesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology and Systematics* **37**, 637–669. doi:10.1146/ANNUREV.ECOLSYS.37.091305.110100
- Perry RW (2011) A review of fire effects on bats and bat habitat in the Eastern Oaks region. In 'Proceedings of the 4th Fire in Eastern Oak Forests Conference', 17–19 May 2011, Springfield, MO. (Eds DC Dey, MC Stambaugh, SL Clark, CJ Schweitzer.) USDA Forest Service, Northern Research Station, pp. 170–191. (Springfield, MO)
- R Core Team (2014) R: a language and environment for statistical computing. R foundation for statistical computing. Available at: <http://www.R-project.org/> [Verified 20 March 2015].
- Radford IJ (2012) Threatened mammals become more predatory after small-scale prescribed fires in a high-rainfall rocky savanna. *Austral Ecology* **37**, 926–935. doi:10.1111/J.1442-9993.2011.02352.X
- Ray C, Wilkening JL, Sweazea K (2009) Signs of demographic change and physiological stress in Rocky Mountain pikas. In 'Proceedings of the North American Pika Conference', 25–27 March 2009. (Jackson, WY). Available at: http://www.tetonscience.org/data/contentfiles/File/downloads/pdf/CRC/CRC/PikaPresentations/crc_pika_ppt_RayChris.pdf [Verified 14 May 2015]
- Roberts SL, van Wagtenonk JW, Miles AK, Kelt DA, Lutz JA (2008) Modeling the effects of fire severity and spatial complexity on small mammals in Yosemite National Park, California. *Fire Ecology* **4**, 83–104.
- Rodhouse TJ, Beaver EA, Garrett LK, Irvine KM, Jeffress MR, Munts M, Ray C (2010) Distribution of American pikas in a low-elevation lava landscape: conservation implications from the range periphery. *Journal of Mammalogy* **91**, 1287–1299. doi:10.1644/09-MAMM-A-334.1
- Rowe RJ, Terry RC, Rickart EA (2011) Environmental change and declining resource availability for small-mammal communities in the Great Basin. *Ecology* **92**, 1366–1375. doi:10.1890/10-1634.1
- Shi H, Paull D, Wen Z, Broome L (2014) Thermal buffering effect of alpine boulder field microhabitats in Australia: implications for habitat management and conservation. *Biological Conservation* **180**, 278–287. doi:10.1016/J.BIOCON.2014.10.019
- Smith AT (1974a) The distribution and dispersal of pikas: consequences of insular population structure. *Ecology* **55**, 1112–1119. doi:10.2307/1940361
- Smith AT (1974b) The distribution and dispersal of pikas: influences of behavior and climate. *Ecology* **55**, 1368–1376. doi:10.2307/1935464
- Smith AT (1978) Comparative demography of pikas (*Ochotona*): effect of spatial and temporal age-specific mortality. *Ecology* **59**, 133–139. doi:10.2307/1936639
- Smith AT, Ivins BL (1983) Colonization in a pika population: dispersal vs. philopatry. *Behavioral Ecology and Sociobiology* **13**, 37–47. doi:10.1007/BF00295074
- Smith A, Weidong L, Hik D (2004) Pikas as harbingers of global warming. *Species* **41**, 4–5.
- Smucker KM, Hutto RL, Steele BM (2005) Changes in bird abundance after wildfire: importance of fire severity and time since fire. *Ecological Applications* **15**, 1535–1549. doi:10.1890/04-1353
- Stavros EN, Abatzoglou J, McKenzie D, Larkin N (2014) Regional projections of the likelihood of very large wildland fires under a changing climate in the contiguous western United States. *Climatic Change* **126**, 455–468. doi:10.1007/S10584-014-1229-6
- Stewart JAE, Wright DH (2012) Assessing persistence of the American pika at historic localities in California's northern Sierra Nevada. *Wildlife Society Bulletin* **36**, 759–764. doi:10.1002/WSB.220
- Stewart JAE, Perrine JD, Nichols LB, Thorne JH, Millar CI, Goehring KE, Massing CP, Wright DH (2015) Revisiting the past to foretell the future: summer temperature and habitat area predict pika extirpations in California. *Journal of Biogeography*. doi:10.1111/JBI.12466
- Swezy DM, Agee JK (1991) Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. *Canadian Journal of Forest Research* **21**, 626–634. doi:10.1139/X91-086
- Tapper SC (1973) The spatial organisation of pikas, *Ochotona*, and its effect on population recruitment. PhD Thesis, University of Alberta, Edmonton.
- Touihri M, Villard M-A, Charfi F (2014) Cavity-nesting birds show threshold responses to stand structure in native oak forests of northwestern Tunisia. *Forest Ecology and Management* **325**, 1–7. doi:10.1016/J.FORECO.2014.03.050
- Tyser RW (1980) Use of substrate for surveillance behaviors in a community of talus slope mammals. *American Midland Naturalist* **104**, 32–38. doi:10.2307/2424955
- Varner J, Dearing MD (2014a) Dietary plasticity in pikas as a strategy for atypical resource landscapes. *Journal of Mammalogy* **95**, 72–81. doi:10.1644/13-MAMM-A-099.1
- Varner J, Dearing MD (2014b) The importance of biologically relevant microclimates in habitat suitability assessments. *PLoS One* **9**, e104648. doi:10.1371/JOURNAL.PONE.0104648
- Viereck LA (1973) Wildfire in the taiga of Alaska. *Quaternary Research* **3**, 465–495. doi:10.1016/0033-5894(73)90009-4
- Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* **416**, 389–395. doi:10.1038/416389A
- Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western U.S. forest wildfire activity. *Science* **313**, 940–943. doi:10.1126/SCIENCE.1128834
- Wiebe KL (2014) Responses of cavity-nesting birds to fire: testing a general model with data from the northern flicker. *Ecology* **95**, 2537–2547. doi:10.1890/13-1711.1
- Wilkening JL (2014) Characterizing metrics and outcomes of stress in a climate-sensitive species, the American pika. PhD Thesis, University of Colorado, Boulder.
- Wilkening JL, Ray C, Beaver EA, Brussard PF (2011) Modeling contemporary range retraction in Great Basin pikas (*Ochotona princeps*) using data on microclimate and microhabitat. *Quaternary International* **235**, 77–88. doi:10.1016/J.QUAINT.2010.05.004
- Wilkening JL, Ray C, Sweazea KL (2013) Stress hormone concentration in Rocky Mountain populations of the American pika (*Ochotona princeps*). *Conservation Physiology* **1**, cot027. doi:10.1093/CONPHYS/COT027
- Wilkening JL, Ray C, Varner J (2015) Relating sub-surface ice features to physiological stress in a climate sensitive mammal, the American pika (*Ochotona princeps*). *PLoS One* **10**, e0119327. doi:10.1371/JOURNAL.PONE.0119327
- Williams AA, Karoly DJ, Tapper N (2001) The sensitivity of Australian fire danger to climate change. *Climatic Change* **49**, 171–191. doi:10.1023/A:1010706116176



Supplementary Figure 1. Classification of study sites. (A) Severely burned sites had over 65% of the linear patch perimeter burned, and within this burned perimeter, there was nearly 100% canopy mortality. These sites also had white ashes present ubiquitously along the burned perimeter. (B) Moderately burned sites had less than 50% of the patch perimeter burned, less than 75% canopy loss within the burned perimeter, and white ashes present only sporadically along the perimeter. (C) Unburned sites had no evidence of burned vegetation within 5 m of the patch perimeter.



Supplementary Figure 2. Vegetation threshold for pika abundance/density. Example quadrats with (A) less than 10 g/m^2 , (B) 55 g/m^2 , and (C) over 200 g/m^2 .

Supplementary Table 1. Full model suite for density analysis. Variables are as defined in Table 2.

Model	Predictors
1	veg
2	veg_rich
3	veg + veg_rich
4	burncategory
5	fireseverity
6	perim_burned
7	insol
8	crevice
9	elevation
10	moss
11	insol + crevice
12	insol + crevice + moss
13	burncategory + insol
14	fireseverity + insol
15	burncategory + elevation
16	fireseverity + elevation
17	perim_burned + moss
18	veg + moss
19	veg_rich + moss
20	Null

APPENDIX A

A PCR-BASED PROTOCOL FOR DETECTING PIKA DIET FROM FECES

Introduction

American pikas (*Ochotona princeps*) are typically limited to high elevations in western North America; however, they persist near sea level in the Columbia River Gorge (CRG), well outside of their previously assumed climatic niche. In this unusual habitat, mosses comprised the majority of pika diet at 2 sites, more than observed for any mammalian herbivore in the wild (Varner and Dearing 2014). In this study, we sought to develop and validate a molecular technique to reconstruct pika diet from fecal samples. Specifically, we sought to compare molecular data with visual observations of marked CRG individuals and then use this technique to track seasonal changes in diet composition.

Methods

In 2011, individual pikas were trapped and marked with colored ear tags. Foraging behavior was then observed and fresh fecal samples were collected. Feces were stored on ice in a cooler in the field until they could be transferred to a -80C freezer. DNA from feces was extracted with a kit (DNA Stool Mini Kit, Qiagen Inc., Valencia, CA), following the manufacturer's protocols. We chose to amplify and sequence the plastid *psbA-trnH* spacer, following a validated protocol to identify bryophytes in the diet

of barnacle geese (*Branta leucopsis*; Stech et al. 2011). PCR products were then gel-purified for sequencing (Figure A.1), and sequences were identified to species using a BLAST search.

Results

Overall, we extracted 27 PCR bands from pika scat, 13 of which yielded sequences with clear chromatograms. Of these 13 samples, 12 sequences yielded BLAST results with > 75% sequence identity (Table A.1). These data contained few sequences from “typical” food resources for pikas (i.e., grasses and forbs; Dearing 1996). We also confirmed several unusual food resources for pikas, including liverworts, Douglas fir, and ferns. Surprisingly, we did not observe moss in the PCR sequences.

Discussion

In this study, we successfully identified 12 species of plants in the scat of pikas, using a molecular PCR technique. Each of these species was present in the environment at the site where the scat was collected; however, there were significant disparities between the frequency of sequences recovered in scat and field observations of pika diet. These disparities could be due to several reasons. First, although the DNA extraction kit that we used is designed to remove PCR inhibitors from fecal samples, these kits are typically designed and validated for model organisms and not wild animals; thus PCR inhibitors may still exist in our samples. Second, samples could have been improperly collected or stored, resulting in degraded DNA. In addition, the primers or PCR conditions from previous studies may underestimate the specific moss species found in the CRG and in pika diet (*Racomitrium lanuginosum* and *Pleurozium schreberi*; Varner

and Dearing 2014). Finally, plant DNA in pika feces could be inherently degraded because pikas are coprophagous and reingest their feces.

Notably, the technique does not currently allow for quantitative reconstruction of pika diet. This technique will need to be validated with pika feeding observations or a controlled feeding trial before it can be widely applied to analysis of diet across seasons or habitat types, or used in a quantitative fashion.

Acknowledgments

This was an independent project conducted by Mallory Lambert, an undergraduate at the U of U. Joshua Horns, Liz Westberg, Katelyn Wolfenberger, Rich Connors, and Jake Bevis assisted with feeding observations and sample collection in the field. Patrice Kurnath and Jael Malenke provided advice and assistance with molecular techniques.

References

- Dearing, M. D. 1996.** Disparate determinants of summer and winter diet selection of a generalist herbivore, *Ochotona princeps*. *Oecologia* 108: 467–478.
- Stech, M., E. Kolvoort, M. Loonen, K. Vrieling, and J. Kruijer. 2011.** Bryophyte DNA sequences from faeces of an arctic herbivore, barnacle goose (*Branta leucopsis*). *Molecular Ecology Resources* 11: 404–408.
- Varner, J. and M. D. Dearing. 2014.** Dietary plasticity in pikas as a strategy for atypical resource landscapes. *Journal of Mammalogy* 94: 72–81.

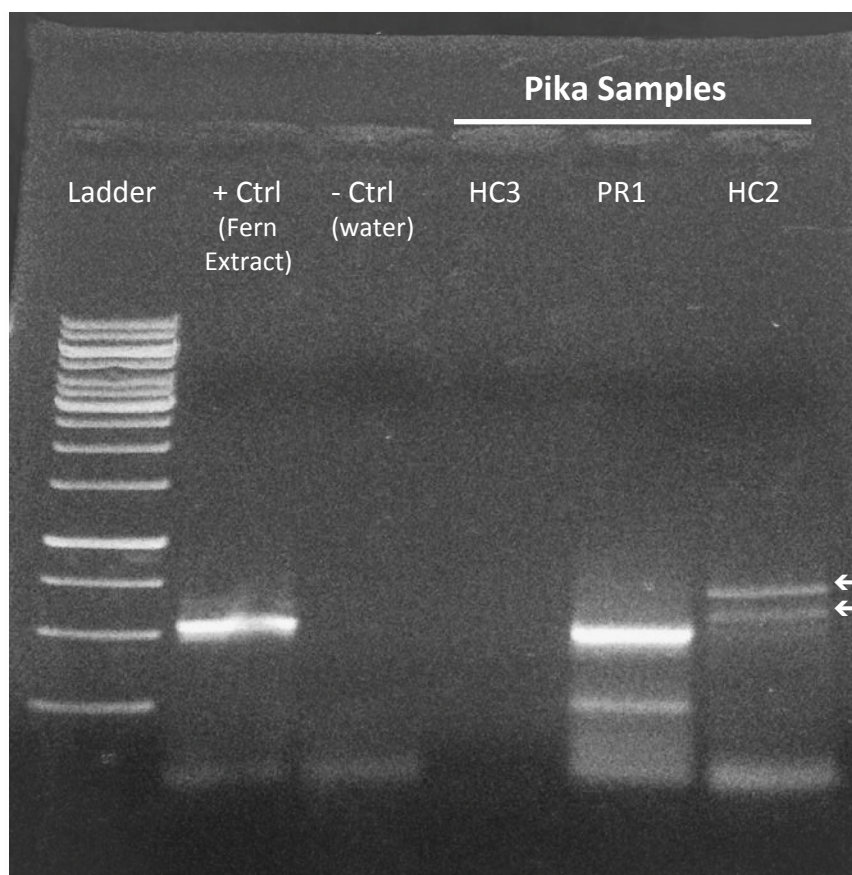


Figure A.1. Sample gel showing results of Polymerase Chain Reaction (PCR) with pika fecal DNA extracts, using primers to amplify the *trnH-psbA* intergenic spacer. Arrows indicate PCR products recovered from pika scat.

Table A.1. Sequencing and BLAST results from PCR products recovered in pika scat. # BPs: Number of base pairs of high quality sequence.

Pika ID	Plant Species	Common Name	Growth Form	# BPs	% Sequence Identity	GenBank Accession #
PR1	<i>Ptilidium pulcherrimum</i>	Naugehyde Liverwort	Liverwort	175	95%	HM222519.1
LR	<i>Polypodium montense</i>	Pacific Polypody	Fern	196	100%	NA - our sequence
OG	<i>Polypodium montense</i>	Pacific Polypody	Fern	289	100%	NA - our sequence
RG	<i>Arabis hirsuta</i>	Hairy Rockcress	Forb	35	92%	FR865086.1
LR	<i>Brassica rapa</i>	Field Mustard	Forb	37	100%	GQ184351.1
HC2	<i>Poa spp</i>	Poa Grass	Grass	113	100%	NA - our sequence
BG	<i>Vaccinium angustifolium</i>	Lowbush Blueberry	Shrub	260	99%	GU361910.1
PR1	<i>Vaccinium angustifolium</i>	Lowbush Blueberry	Shrub	422	99%	GU361910.1
HC2	<i>Vaccinium angustifolium</i>	Lowbush Blueberry	Shrub	85	99%	GU361910.1
RG	<i>Pseudotsuga menziesii</i>	Douglas Fir	Tree	353	100%	FR832553.2
HC2	<i>Bacteroides spp.</i>	Bacterial species	Other	476	74%	CP000139.1
OG	<i>Spinacia oleracea</i>	Spinach	Trap bait	187	99%	AJ400848.1
HC1	<i>Opuntia fragilis</i>	Prickly Pear Cactus	Contamination	73	100%	GQ248356.1

APPENDIX B

CHANGES IN NUTRITIONAL QUALITY IN PIKA DIET OVER 20 YEARS

AT NIWOT RIDGE, COLORADO

Introduction

Climate change could affect plant physiology in three key ways: changes in temperature (Newman et al. 2005), changes in precipitation (Rothman et al. 2014), and changes in atmospheric carbon dioxide concentrations (Couture et al. 2014). Increased atmospheric carbon availability may allow plants to easily invest in carbon-based toxic defense compounds, such as phenolics or tannins (Robinson et al. 2012). These changes could affect forage quality for herbivores (Owensby et al. 1996, Lindroth et al. 1997), which may already be nutritionally stressed due to the effects of climate change (Rowe et al. 2011, Kurnath and Dearing 2013).

American pikas (*Ochotona princeps*) have been previously shown to select two diets at Niwot Ridge, a long-term ecological research station in Colorado's Front Range. During summer, pikas tend to consume plants that are low in phenolics and high in nitrogen (Dearing 1996). They also collect and store plants in food caches called haypiles, which they will consume during the winter months; these plants tend to be high in phenolics (Dearing 1996). Although these phenolics can be acutely toxic to pikas (Dearing 1997a), they break down with time in storage and have antimicrobial properties, thereby preserving haypile material through the winter (Dearing 1997b, c).

The primary component of pika haypiles on Niwot Ridge is alpine avens (*Geum rossii*, previously known as *Acomastylis rossii*). We hypothesized that as carbon available to avens plants has increased due to anthropogenic activities, avens leaves have increased in phenolics and decreased in nutritional quality (i.e., lower nitrogen and higher fiber). These nutritional changes may result in a decrease in forage quality for pikas.

Methods

Alpine avens samples from previous studies (Dearing 1996, 1997c, a) were collected on the West Knoll of Niwot Ridge in 1992. These samples were stored in a -80°C freezer until 2014. Recent avens samples were collected (i.e., cut just above ground and kept on dry ice in the field) in 2013 and 2014. These samples were also stored in a -80°C freezer until analysis.

To assess forage quality of avens at each time point, we measured nitrogen, fiber, and phenolic activity. Total phenolic activity was measured using the Folin–Ciocalteu method (Waterman and Mole 1994). Although this method is unreliable in measuring absolute phenol content, it provides a consistent estimate of biological activity in ecological studies when activity depends on phenolic oxidation, as in plant–herbivore interactions (Appel et al. 2001). Furthermore, we wanted to compare our results with those of previous studies that used the same assay (Dearing 1996, 1997c, a). Phenolic contents of ~0.2 g of fresh plant material were extracted into a solution of 95% methanol by grinding with a Polytron PT3100 Mixer (Kinematica, Lucerne, Switzerland) at 12,000 rpm for 30 s. After 48 hours in the dark at room temperature, samples were centrifuged for 5 min at 3,300 rpm, and the supernatant was used in the Folin–Ciocalteu reaction following the protocol of Ainsworth and Gillespie (2007). As in previous studies, tannic

acid was used as the standard. Total phenolic activity is expressed as mg tannic acid equivalent (TAE) per g fresh weight of plant material. Total fiber content (neutral detergent fiber, NDF) and cellulose–lignin content (acid detergent fiber, ADF) were measured in a fiber analyzer (ANKOM 200 Fiber Analyzer; ANKOM Technology, Macedon, New York). Nitrogen content was measured by combusting 5 mg of plant material in an Elemental Combustion System (Costech Analytical Technologies, Valencia, California) coupled to a Delta Plus Advantage mass spectrometer (Thermo Finnigan, San Jose, California) operating in the continuous-flow mode.

Results were analyzed by ANOVA with three sample groups: those collected and analyzed in 1992, those collected in 1992 and reanalyzed in 2015, and those collected in 2014 and analyzed in 2015. Post-hoc Tukey tests were applied to determine differences between sample groups; however, samples collected and analyzed in 1992 are limited to 2-3 data points per analysis, thereby limiting statistical power for those comparisons.

Results

Across all nutritional analyses, we found no difference between plants collected and analyzed in 1992 to those plants collected in 1992 and reanalyzed in 2015 (Figure B.1). In contrast, avens phenolics have increased by 38% in recent samples, relative to the 1992 samples (ANOVA: $F_{(2,18)} = 3.88, p = 0.04$; Figure B.1A). We also found a trend towards reduced total fiber (NDF; $t = 2.47, df = 3.24, p = 0.08$; Figure B.1B) between 1992 samples and 2014 samples in our analyses. Data for NDF were unavailable for 1992 samples analyzed in 1992. Cellulose-lignin contents significantly differed between sample groups (ANOVA: $F_{(2,9)} = 5.12, p = 0.03$; Figure B.1C) compared to older samples; however, Tukey post-hoc tests did not indicate significant differences ($p = 0.06$ to 0.07

for comparisons with recent samples), likely because of small sample sizes. Finally, recent avens (2014) had 21% lower nitrogen content than the older samples in our 2015 analysis (ANOVA: $F_{(2,6)} = 12.23$, $p = 0.008$; Figure B.1D).

Discussion

In this study, we investigated changes in plant nutritional chemistry over a 20-year period. Across fiber, nitrogen, and phenolics measurements, we found no statistical differences between the nutritional chemistry of avens samples collected and analyzed in 1992 compared to the 1992 samples that were reanalyzed in 2015, suggesting that plant nutritional contents did not change substantially over 20 years of storage in a -80°C freezer. However, we did not measure water content, which may have affected phenolic activity if any water evaporated during storage.

In contrast, comparing samples collected in 1992 and 2014, we observed significant changes in plant nutritional characteristics. Our hypotheses regarding plant secondary compounds and protein content were supported: avens have increased phenolics by 38% and decreased nitrogen by 21% between 1992 and 2014. Previous studies that have experimentally elevated CO_2 concentrations (e.g., the Aspen Free Air Carbon Dioxide and Ozone Enrichment Experiment) have reported similar decreases in nitrogen (9-18%) and increases in phenolics (22-29%) as a result of elevated CO_2 concentrations (Lindroth et al. 1997, Couture et al. 2014). A recent meta-analysis also found that phenolics have increased and nitrogen has decreased in many plant genera that serve as hosts for arthropod herbivores (Robinson et al. 2012). Conventionally, decreased nitrogen content under elevated carbon concentrations is thought to be caused by nitrogen dilution (i.e., increased carbon biomass), reduction in the concentration of photosynthetic

enzymes (which can comprise up to 25% of total leaf nitrogen), or reduction in chlorophyll content (Owensby et al. 1996).

Contrary to our expectations, we also observed a 30% decrease in cellulose and lignin content of alpine avens leaves over the last 20 years. However, it should be noted that fiber measurements in 1992 were conducted in flasks, rather than in a fiber analyzer. In contrast, most previous studies have shown increases in either fiber content (10-15%; Rothman et al. 2014) or leaf toughness (a proxy for fiber content; Robinson et al. 2012). Importantly, because we observed similar declines in both nitrogen and fiber content, the protein-to-fiber ratio may not have changed significantly in alpine avens. This ratio is a strong driver of forage selection in many other species of mammals (Owensby et al. 1996, Rothman et al. 2014). In addition, our results could suggest that Avens is investing extra carbon resources in soluble carbohydrates, rather than fiber.

This study lays the foundation for several future directions. First, available nitrogen assays might be a promising future direction for these avens samples (Wallis et al. 2010). These in vitro assays integrate measurements of fiber, digestibility, tannins, and total nitrogen into a single measure of nitrogen that is “available” to herbivores (DeGabriel et al. 2008, Wallis et al. 2012). In addition, future studies will be necessary to determine how changes in the nutritional quality of alpine avens will affect pika diet selection, foraging behavior, and overwinter survival. These changes may also affect the preservation of winter diet in haypiles, which is mediated by an antimicrobial effect of phenolic contents in Avens plants (Dearing 1997b, c). However, preliminary behavioral data show no change in the relative abundance of avens at Niwot ridge or pika winter diet selection (C. Ray and L. Griswold, personal communication).

Acknowledgments

The nutritional analysis in this appendix was an independent project conducted by Loren Griswold. Recent avens samples were collected by C. Ray, L. Griswold, and undergraduate students at Niwot Ridge. Avens samples from 1992 were collected by M.D. Dearing.

Literature Cited

- Ainsworth, E. A. and K. M. Gillespie. 2007.** Estimation of total phenolic content and other oxidation substrates in plant tissues using Folin–Ciocalteu reagent. *Nature Protocols* 2:875-877.
- Appel, H. M., H. L. Govenor, M. D'Ascenzo, E. Siska, and J. C. Schultz. 2001.** Limitations of Folin assays of foliar phenolics in ecological studies. *Journal of Chemical Ecology* 27:761-778.
- Couture, J., L. Holeski, and R. Lindroth. 2014.** Long-term exposure to elevated CO₂ and O₃ alters aspen foliar chemistry across developmental stages. *Plant, Cell & Environment* 37:758-765.
- Dearing, M. D. 1996.** Disparate determinants of summer and winter diet selection of a generalist herbivore, *Ochotona princeps*. *Oecologia* 108:467-478.
- Dearing, M. D. 1997a.** Effects of *Acomastylis rossii* tannins on a mammalian herbivore, the North American pika, *Ochotona princeps*. *Oecologia* 109:122-131.
- Dearing, M. D. 1997b.** The function of haypiles of pikas (*Ochotona princeps*). *Journal of Mammalogy* 78:1156-1163.
- Dearing, M. D. 1997c.** The manipulation of plant toxins by a food-hoarding herbivore, *Ochotona princeps*. *Ecology* 78:774-781.
- DeGabriel, J. L., I. R. Wallis, B. D. Moore, and W. J. Foley. 2008.** A simple, integrative assay to quantify nutritional quality of browses for herbivores. *Oecologia* 156:107-116.
- Kurnath, P. and M. D. Dearing. 2013.** Warmer ambient temperatures depress liver function in a mammalian herbivore. *Biology Letters* 9:20130562.
- Lindroth, R., S. Roth, E. Kruger, J. Volin, and P. Koss. 1997.** CO₂-mediated changes in aspen chemistry: Effects on gypsy moth performance and susceptibility to

virus. *Global Change Biology* 3:279-289.

- Newman, Y. C., L. E. Sollenberger, K. J. Boote, L. H. Allen, J. C. V. Vu, and M. B. Hall. 2005.** Temperature and carbon dioxide effects on nutritive value of rhizoma peanut herbage. *Crop Science* 45:316-321.
- Owensby, C. E., R. C. Cochran, and L. M. Auen. 1996.** Effects of elevated carbon dioxide on forage quality for ruminants. Pages 363-371 *in* Carbon dioxide, populations, and communities. F. Bazzaz, ed., Academic Press, Waltham, MA.
- Robinson, E. A., G. D. Ryan, and J. A. Newman. 2012.** A meta-analytical review of the effects of elevated CO₂ on plant–arthropod interactions highlights the importance of interacting environmental and biological variables. *New Phytologist* 194:321-336.
- Rothman, J. M., C. A. Chapman, T. T. Struhsaker, D. Raubenheimer, D. Twinomugisha, and P. G. Waterman. 2014.** Long-term declines in nutritional quality of tropical leaves. *Ecology* 96:873-878.
- Rowe, R. J., R. C. Terry, and E. A. Rickart. 2011.** Environmental change and declining resource availability for small-mammal communities in the Great Basin. *Ecology* 92:1366-1375.
- Wallis, I., M. Edwards, H. Windley, A. Krockenberger, A. Felton, M. Quenzer, J. Ganzhorn, and W. Foley. 2012.** Food for folivores: Nutritional explanations linking diets to population density. *Oecologia* 169:281-291.
- Wallis, I. R., D. Nicolle, and W. J. Foley. 2010.** Available and not total nitrogen in leaves explains key chemical differences between the *Eucalypt* subgenera. *Forest Ecology and Management* 260:814-821.
- Waterman, P. G. and S. Mole. 1994.** Analysis of phenolic plant metabolites. Blackwell Scientific, Boston, MA.

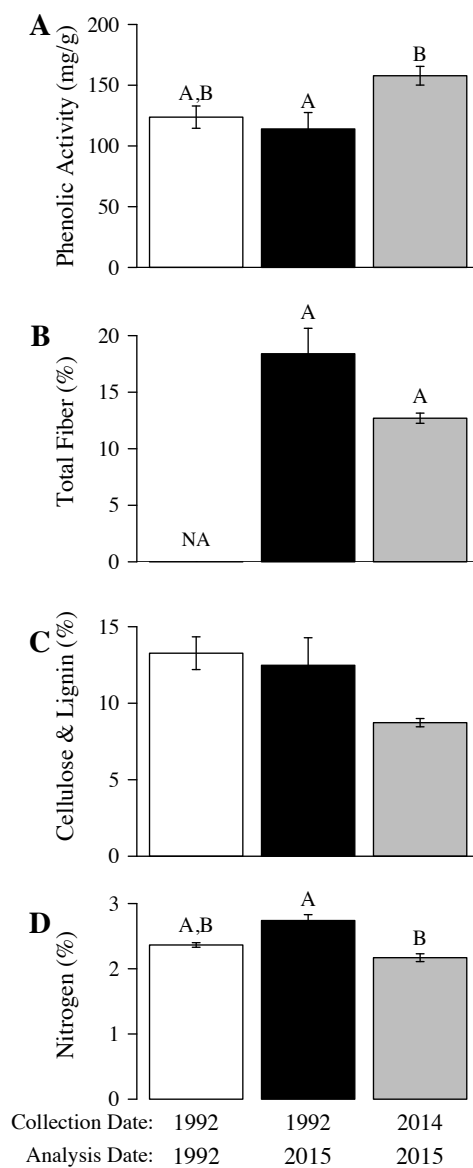


Figure B.1. Changes in nutritional chemistry of alpine avens (*Geum rossii*) collected at Niwot Ridge. Avens samples collected in 1992 and 2014 were tested for A) total phenolic activity (mg tannic acid equivalent/g fresh weight), B) total fiber content (NDF; % dry weight), C) cellulose and lignin content (ADF; % dry weight), and D) nitrogen content (% dry weight). Mean \pm SE for each year is shown. Letters indicate comparisons that are significantly different at $\alpha < 0.05$. Data for samples collected and analyzed in 1992 are from (Dearing 1996).

APPENDIX C

FECAL STRESS HORMONE ANALYSES FROM AMERICAN PIKAS (*OCHOTONA PRINCEPS*) IN TWO MOUNTAIN RANGES IN NORTHERN UTAH

Introduction

As a result of dramatic declines in parts of their range (Beever et al. 2011, Stewart et al. 2015), American pikas (*Ochotona princeps*) have been suggested as an early indicator of ecosystem health in response to global change (Smith et al. 2004, Wilkening et al. 2015). However, the species was denied protection under the federal Endangered Species Act in 2010, primarily because it remains unclear how climate change is immediately affecting them across their entire range (US Fish and Wildlife Service 2010). Since 2010, several studies have sought to resurvey pika habitat in other portions of the species' range, including Colorado (Erb et al. 2011) and California (Stewart and Wright 2012, Stewart et al. 2015). However, little systematic study has been devoted to pikas in Utah, despite the fact that the state hosts four of the five currently recognized subspecies of pikas in close proximity to each other (Hafner and Smith 2010).

Comprehensive historical records do not exist for pikas in Utah; thus, large-scale resurvey efforts like those conducted in other mountain ranges are not feasible. However, detailed studies of the distribution, status, and health of pikas have been recently validated as indicators of ecosystem health in alpine regions (Wilkening et al. 2015).

Specifically, fecal stress hormone concentrations (Gluco-Corticoid Metabolite; GCM) are being increasingly implemented as a noninvasive metric of population health (Romero 2004). Techniques for measuring fecal GCMs have been validated for pikas (Wilkening et al. 2013, Wilkening 2014, Wilkening et al. 2015) and can be used to test the mechanistic hypotheses by which the species may be affected by climatic change.

In this study, we tested stress hormone levels from pikas at several sites in the Uinta and Wasatch mountain ranges of northern Utah. We compare these stress hormone levels with values from other Rocky Mountain ecoregions in the literature collected in the same year. These data provide a baseline for future, more systematic efforts to disentangle the effects of climate change on pika status and distribution throughout the state.

Methods

In 2011, we conducted pika occupancy surveys at 3 sites in the Uinta mountains: Cobblerest (elev. 2591 m), Wall Lake (elev. 3092 m), and Bald Mountain Pass (elev. 3237 m). We also surveyed one site (Red Pine, elev. 2834 m) in the Wasatch Mountains near Salt Lake City. During these surveys, fecal samples were collected at each fresh latrine ($n > 10$ pellets per latrine, $n = 2 - 8$ latrines per site), stored on ice in a cooler in the field and then transferred to a -80°C freezer. Pikas typically defecate in central latrines within their territories (Smith and Weston 1990); thus each sample likely came from separate individuals. Finally, at each site in the Uintas, temperature dataloggers (HOBO UA-001-08 Pendant, Onset Computer Corp., Bourne, MA) were deployed to measure pika-relevant microclimates. One datalogger was placed near the surface and protected from direct solar radiation by multiple rocks. A second datalogger was threaded into the

talus interstices approximately 1 m below the surface logger (following Varner and Dearing 2014). Each datalogger recorded temperatures every two hours, beginning in August 2011. These sensors can also be used to estimate snowpack duration at each site (i.e., by counting the number of days in which diel surface temperature fluctuations were less than 2C°; Lundquist and Lott 2008).

Fecal glucocorticoid metabolite (GCM) levels have been previously validated as a biologically relevant measure of chronic physiological stress in pikas (Wilkening et al. 2013, Wilkening 2014), and environmental samples collected within the same ecoregion (i.e., the Rocky Mountains) in the same sampling season can be used reliably for comparisons (Wilkening et al. 2015). In our analysis, we followed previously validated protocols (Wilkening et al. 2013) to measure GCM in fresh feces collected in September 2011 from the Wasatch and Uinta sites. We used a commercially available corticosterone enzyme immunoassay kit (Arbor Assay Design, Inc., Ann Arbor, MI, no. K014-H1) and followed the manufacturer's protocols. Each biological replicate was run with three technical replicates on the plate, and standard curves were constructed using corticosterone provided in the kit. Final concentrations of fecal GCM were expressed as ng GCM/g feces.

For comparison, additional GCM data from other Rocky Mountain ecoregions collected in the same season (i.e., between July – September, 2011) were obtained from the literature (Wilkening et al. 2015, *in revision*). These ecoregions included Rocky Mountain National Park and Green Lakes Valley Watershed in Colorado (COLO), and samples collected from Yellowstone National Park (YELL).

Results

In an ecoregional comparison, we found no significant differences between stress hormones in Utah's pika populations, relative to sites in Colorado or Yellowstone NP during the summer and fall of 2011 ($F_{(3,44)} = 2.265, p = 0.09$; Figure C.1). Within the three sites in the Uinta Mountains, however, Wall Lake had significantly lower stress hormone concentrations than Cobblerest or Bald Mountain Pass ($F_{(2,8)} = 5.785, p = 0.03$; Figure C.2). Although temperature data were not collected prior to scat samples, two years of temperature data collected in the talus at each site suggest that Wall Lake consistently has more mild winter temperatures (Figure C.3). Specifically, a longer snowpack duration at Wall Lake kept winter temperatures near 0°C until late June, whereas winter minimum temperatures were typically below -5°C and frequently reached as low as -10°C at the other two sites. Wall Lake also had slightly cooler summer surface temperatures (i.e., fewer days that exceed 25.5°C, our best estimate of a threshold for acute heat stress in pikas; Figure C.3).

Discussion

Stress hormone concentrations in pika scat have recently validated as an indicator of population status and health, as well as potentially indicative of rock-ice features and water availability (i.e., rock-glaciers or sub-talus ice features; Wilkening et al. 2015). Here, we provide the first baseline survey of pika stress hormone levels in northern Utah, which are well within the values of pika stress reported in a multiregional analysis (Wilkening et al. *in revision*). Below, we propose several testable hypotheses as to how stress hormone concentrations (and by extension, pika population status and health) could be affected by habitat quality.

Habitat suitability for pikas and other talus-dwelling animals may be affected by both heat stress and cold stress, and these stresses can each act acutely or chronically (Beever et al. 2010, Beever et al. 2011). In future studies, samples should be collected in conjunction with temperature sensor data, such that effects of several previously validated metrics of thermal stress for pikas can be assessed. First, chronic cold stress can be assessed by estimating snowpack duration and average winter minimum temperatures at each site. Reduced snowpack (extent and duration) can result in lower winter minimum temperatures in the talus (Smith 1978, Beever et al. 2011). Acute cold stress can be assessed by counting the number of days during winter in which minimum temperatures were less than -5°C (Beever et al. 2010). In contrast, chronic summer heat stress may be indexed as the average August temperature, which is biologically relevant for pikas because it is: a) snow-free at all sites, b) the hottest month of the year, and c) the time at which pikas are most active constructing their winter food caches (Smith 1974, Dearing 1997). Acute heat stress can be indexed by the number of days each year that surface temperatures exceeded 28°C . Finally, we also suggest incorporating measures of diel temperature range (i.e., daily maximum – daily minimum), which is an indicator of both acute and chronic heat stress. This variable has only recently been considered in analyses related to pikas and climate change (Wilkening et al. 2015); however, climate change is known to affect diel temperature range, and other species appear to be responding to this increased temperature variability (Walther et al. 2002, Braganza et al. 2004).

Pika stress could be influenced by a number of other habitat factors besides microclimate, all of which could also be quantified in future studies. These habitat factors include pika population density, which could influence stress through social interactions,

increased aggression, or resource competition. Although we have no evidence that predator density (predominantly weasels; Smith and Weston 1990) varies between our sites, this variable could also affect chronic stress levels in pika populations. Finally, variation in persistent snowpack, such as that seen between our Uinta sites, could also affect vegetation availability and nutritional quality. Future work will involve more systematic sampling along elevational gradients in both the Uinta and Wasatch mountains to address these hypotheses.

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References

- Beever, E. A., C. Ray, P. W. Mote, and J. L. Wilkening. 2010.** Testing alternative models of climate-mediated extirpations. *Ecological Applications* 20:164-178.
- Beever, E. A., C. Ray, J. L., P. F. Brussard, and P. W. Mote. 2011.** Contemporary climate change alters the pace and drivers of extinction. *Global Change Biology* 17:2054-2070.
- Braganza, K., D. J. Karoly, and J. Arblaster. 2004.** Diurnal temperature range as an index of global climate change during the twentieth century. *Geophysical Research Letters* 31.
- Dearing, M. D. 1997.** The function of haypiles of pikas (*Ochotona princeps*). *Journal of Mammalogy* 78:1156-1163.

- Erb, L. P., C. Ray, and R. Guralnick. 2011.** On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*). *Ecology* 92:1730-1735.
- Hafner, D. J. and A. T. Smith. 2010.** Revision of the subspecies of the American pika, *Ochotona princeps* (Lagomorpha: Ochotonidae). *Journal of Mammalogy* 91:401-417.
- Lundquist, J. D. and F. Lott. 2008.** Using inexpensive temperature sensors to monitor the duration and heterogeneity of snow-covered areas. *Water Resources Research* 44:W00D16.
- Romero, L. M. 2004.** Physiological stress in ecology: Lessons from biomedical research. *Trends in Ecology & Evolution* 19:249-255.
- Smith, A., L. Weidong, and D. Hik. 2004.** Pikas as harbingers of global warming. *Species* 41:4-5.
- Smith, A. T. 1974.** The distribution and dispersal of pikas: Influences of behavior and climate. *Ecology* 55:1368-1376.
- Smith, A. T. 1978.** Comparative demography of pikas (*Ochotona*): Effect of spatial and temporal age-specific mortality. *Ecology* 59:133-139.
- Smith, A. T. and M. L. Weston. 1990.** *Ochotona princeps*. *Mammal Species* 352:1-8.
- Stewart, J. A. E., J. D. Perrine, L. B. Nichols, J. H. Thorne, C. I. Millar, K. E. Goehring, C. P. Massing, and D. H. Wright. 2015.** Revisiting the past to foretell the future: Summer temperature and habitat area predict pika extirpations in California. *Journal of Biogeography*: doi: 10.1111/jbi.12466.
- Stewart, J. A. E. and D. H. Wright. 2012.** Assessing persistence of the American pika at historic localities in California's northern Sierra Nevada. *Wild Soc Bull* 36:759-764.
- US Fish and Wildlife Service. 2010.** Endangered species act protection for the American pika is not warranted. News Release 2/5/2010.
- Varner, J. and M. D. Dearing. 2014.** The importance of biologically relevant microclimates in habitat suitability assessments. *PloS ONE* 9:e104648.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002.** Ecological responses to recent climate change. *Nature* 416:389-395.
- Wilkening, J. L. 2014.** Characterizing metrics and outcomes of stress in a climate

sensitive species, the American pika. Ph.D. Dissertation. University of Colorado, Boulder, CO.

Wilkening, J. L., C. Ray, and K. L. Sweazea. 2013. Stress hormone concentration in Rocky Mountain populations of the American pika (*Ochotona princeps*). *Conservation Physiology* 1:1-13.

Wilkening, J. L., C. Ray, and J. Varner. 2015. Relating sub-surface ice features to physiological stress in a climate sensitive mammal, the American pika (*Ochotona princeps*) *PloS ONE* 10: e0119327.

Wilkening, J. L., C. Ray, and J. Varner. *In revision.* When can we measure stress non-invasively? Post-deposition effects on a fecal stress metric confound a multi-regional assessment. *Methods in Ecology & Evolution*.

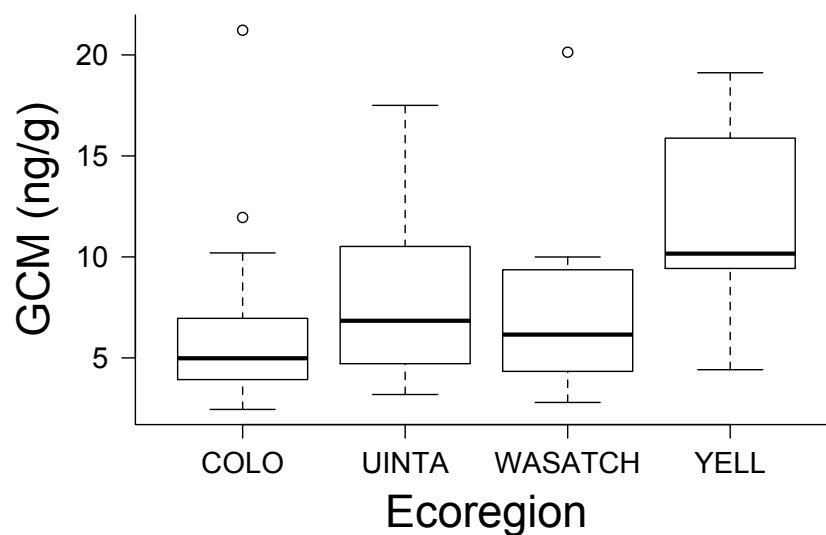


Figure C.1. Regional comparison of pika fecal stress hormone levels. Regions include the Front Range of Colorado (COLO; Rocky Mountain National Park and Green Lakes Valley Watershed), our three sites in the Uinta mountains (UINTA), Red Pine Lake in the Wasatch Mountains (WASATCH), and several sites in Yellowstone National Park (YELL).

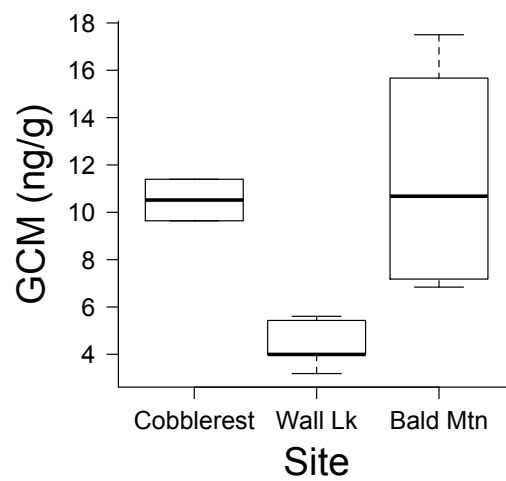


Figure C.2. Comparison of pika stress hormone concentrations from three sites in the Uinta Mountains of Northern Utah.

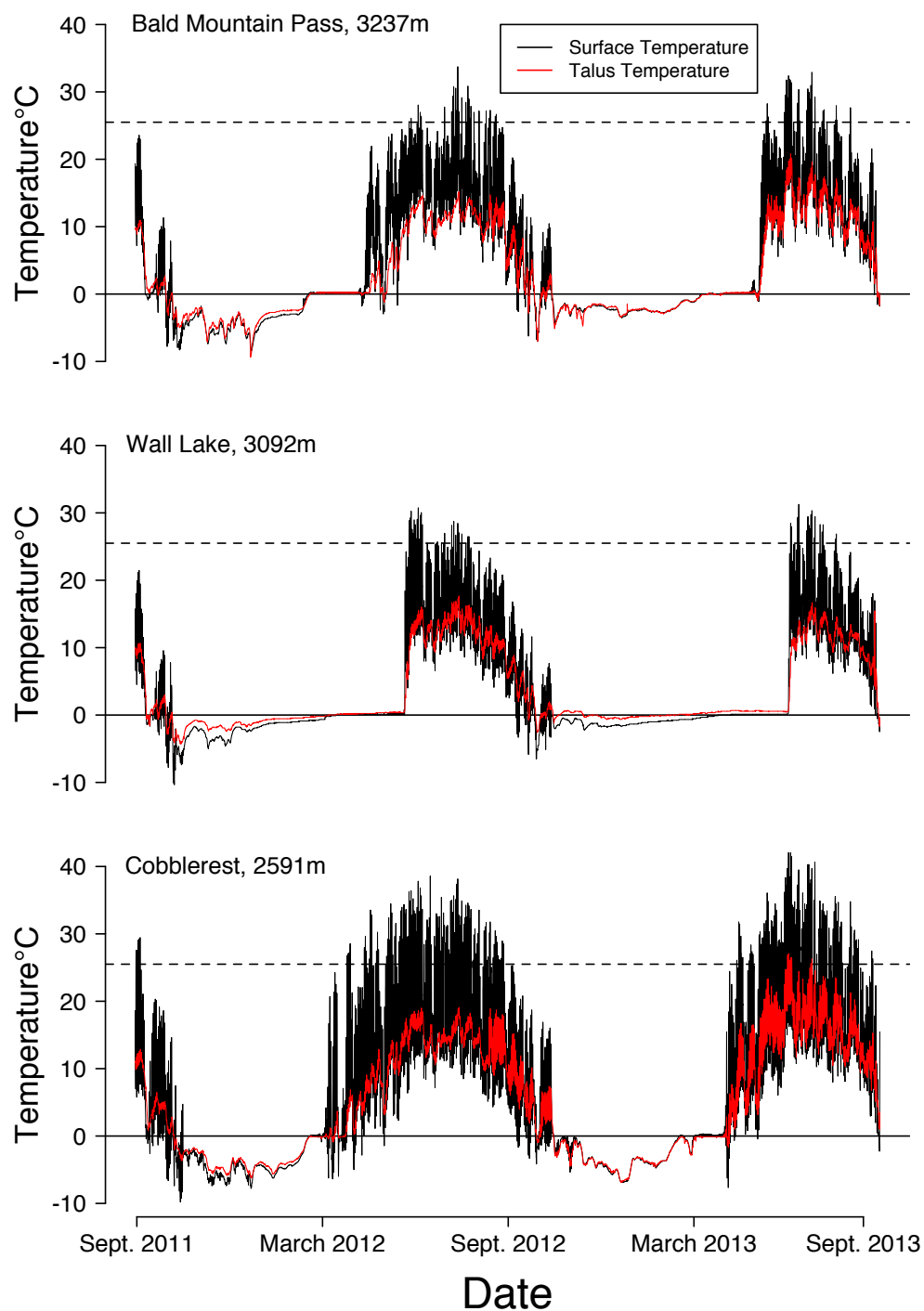


Figure C.3. Comparison of temperature data from three sites in the Uinta Mountains of Northern Utah. Dotted horizontal line represents the best estimate of a threshold for acute heat stress in pikas (25.5°C).