Dietary plasticity in pikas as a strategy for atypical resource landscapes

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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 their previously assumed climatic niche. We hypothesized that utilizing unusual food resources contributes to pika persistence in this unusual climate. Moss comprised more than 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.

Key words: behavioral plasticity, dietary specialization, foraging behavior, herbivore, moss, *Ochotona*, pika

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 species 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 above 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 1997a). 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 more than 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 p. 128), 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 1997a). 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

1996a, 1997b). However, heat sensitivity limits the time for pikas to forage and construct haypiles. Captive pikas overheat and die after 2 h 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 CRG near Wyeth at 2 large (approximately 15,000 m^2) 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 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: 10.1644/13-MAMM-A-099.S1]). 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 Wilkening 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, although 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, although 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 1996a). Observers ($n = 3$ in 2011, $n = 5$ in 2012, 2 observers present in both years) used 10×40 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 ear tags or identified by unique scar patterns on the eyes or ears. As in previous work (Dearing 1996a), 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 guidelines of the American Society of Mammalogists (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 1996a), and previous herbivory by insects (Barrio et al. 2013). Fiber content also is 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 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.

Phenolics are an important determinant of pika caching selection (Dearing 1996a); thus plants also were 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 (MAN-OVA), with fiber content (ADF and NDF), nitrogen content, and phenolic activity as dependent variables and plant growth form (i.e., moss, forb, fern, or 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 (1996a). 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: dry weight = fresh weight $\times$ (100 − % 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 also are north-facing talus patches on the Oregon side of the CRG that are similar in size to sites 1 and 2 (approximately 18,000 m^2). 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

TABLE 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	February	July	February
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
Total veg.	61.9	59.5	71.3	71.4

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 character-ization 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 Com-puter 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 1; Supporting Information 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 1). Moss cover changed little with season at both sites (Table 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.
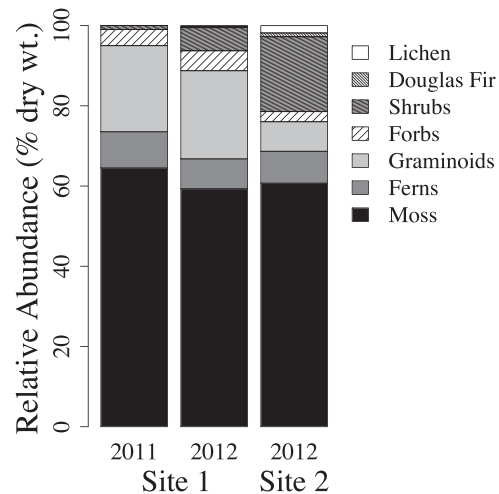

FIG. 1.—American pika (*Ochotona princeps*) diet at 2 sites in the Columbia River Gorge. Relative frequency of different plant items in pika diet in 2011 ($n = 4$ animals at site 1) and 2012 ($n = 7$ animals at site 1, $n = 11$ animals at site 2). Two animals were observed at site 1 in both years. Moss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

In total, we observed pikas consuming 31 different plant species, ranging from foliose lichens to Douglas fir needles. Moss represented more than half of the feeding observations and comprised roughly 60% of the diet by dry weight (Fig. 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 more than 80% of moss consumed and thus nearly 50% of each diet by dry weight. We also observed pikas consuming shrubs, primarily vine maple (*Acer circina-tum*), 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 1996a). 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. 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; Supporting Information S2, DOI: 10.1644/13-MAMM-A-099.S2). On average, mosses contained twice as much fiber as forbs, ferns, or shrubs (Fig. 2A). Mosses also had roughly twice the cellulose–lignin content of forbs, ferns, or shrubs (Fig. 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 because of low sample sizes.

All mosses contained less than 1% nitrogen (Fig. 2C). In contrast, forbs, ferns, and shrubs all had significantly higher nitrogen content (Fig. 2C). Interestingly, pika caecal pellets
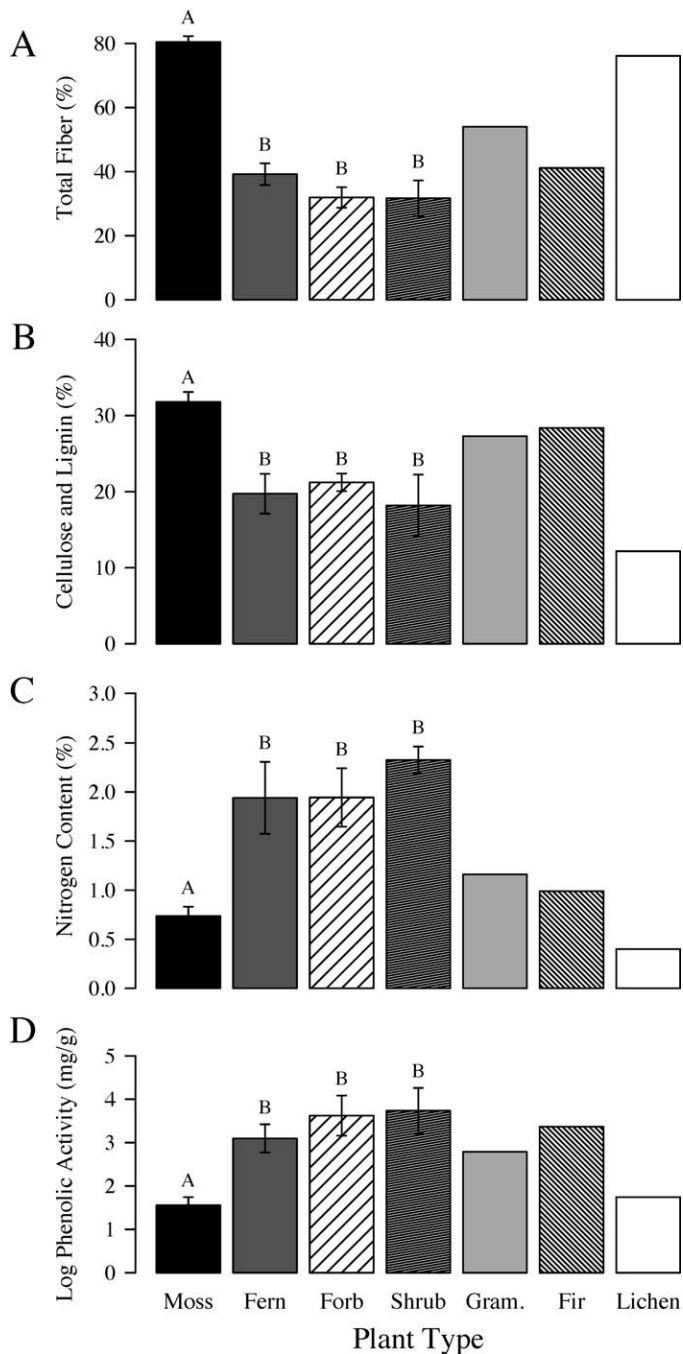
FIG. 2.—Nutritional content of plants in pika diet. The dominant species in the diet were tested for A) total fiber content (% dry weight), B) cellulose and lignin content (% dry weight), C) nitrogen content (% dry weight), and D) phenolic activity (mg gallic acid equivalent/g dry weight). "Gram." indicates 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, although the value represents the average of multiple biological replicates. Statistical analyses only include mosses, ferns, forbs, and shrubs because multiple species were tested.

(highly fermented digesta that are reingested) were nearly 6% nitrogen, far higher than any plant species that we tested (Supporting Information S2).

Similar to other studies (Dearing 1996a, 1997b), shrub, fern, and forb leaves had the highest phenolic activity, on average 1–3 orders of magnitude higher than that of mosses (Fig. 2D). Forbs had the greatest range in phenolic activity, ranging from 12.2 to 132.8 mg gallic acid equivalents/g (Supporting Information S2). Douglas fir needles also had high levels of phenolic activity (Fig. 2D) and also are known to contain terpenes (Kepner and Maarse 1970), although 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], and $\sim 30\%$ cellulose and lignin [ADF] [Table 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 $> 1,500$ 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 haytrips). 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 3]).

Across both years, we sampled 5 haypiles at sites 1 and 2 and an additional 6 haypiles at sites 3 and 4 (Table 3). Overall, haypiles ranged from 0.5 to 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 3; Supporting Information S2). In contrast, moss made up a small portion of haypiles, although 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 1997a; 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 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 4). At high elevations, a pika must collect roughly 22 g dry weight of vegetation per day of winter to sustain itself (Dearing 1997a). 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 1997a).

TABLE 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. NDF = neutral detergent fiber; ADF = acid detergent fiber.

	Site 1		Site 2
	2011	2012	2012
No. 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)

DISCUSSION

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

cialists 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 (Bjrkvoll et al. 2009; Heggberget et al. 2010). Brown lemmings (*Lemmus sibiricus*) also can 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 the 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 to 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 midsummer 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 also can 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), lower than that estimated for nonruminant herbivores to maintain nitrogen balance (~1.3%—Karasov 1982). As a result of these

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

TABLE 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] and Walker et al. [1994]). Haypile data from Niwot Ridge and Copper Creek, Colorado, are reprinted from Dearing (1997a). Haypile data and length of winter from Yukon, Canada, 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. NA = not available.

Site	n	Average fresh weight (kg)	Average dry weight (kg)	Length of winter (days)	Fresh weight/day (g)	Dry weight/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, Colorado	10	25.2	6.86	295	85	23
Copper Creek, Colorado	NA	20.9	5.69	180	116	32
Yukon, Canada	NA	NA	7.40	210	NA	35

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 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 1996a).

Because lichens and mosses absorb nutrients through air and water, they may become enhanced in nitrogen when they are downwind 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. 2C; Supporting Information 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 more than 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 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 and 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/m^2—J. Varner, pers. obs.), and an estimate of pika home-range size in the CRG (727 m^2—J. Varner and E. Westberg, 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 g/day between 10°C and 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 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, haypile sizes in our study may underestimate stored plant material.

Moss and some evergreen plants (e.g., Douglas fir and 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 1997a). However, pikas in the CRG collected a remarkably consistent 80–90 g of fresh weight for each day of persistent snowpack (Table 4), which is nearly identical to relative haypile sizes at Niwot Ridge, Colorado, where haypiles must sustain pikas for the long alpine winter (Dearing 1997a).

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 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 does 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 1997b), 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. 2D; Supporting Information 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 1997b; Torregrossa and Dearing 2009). In addition, long-term storage in haypiles can enhance the nitrogen content of pika winter diet (Dearing 1997b), which may be especially important for an herbivore consuming such a low-nitrogen diet (Table 2).

Finally, we speculate that the moss covering CRG talus slopes also may 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 m^2 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 also may 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 CRG, 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 1997b; 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.

SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—Study sites in the Columbia River Gorge.
Found at DOI: 10.1644/13-MAMM-A-099.S1
SUPPORTING INFORMATION S2.—Nutritional content of common plants in the diet or environment at study sites.
Found at DOI: 10.1644/13-MAMM-A-099.S2

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