

## Plastic pikas: Behavioural flexibility in low-elevation pikas (*Ochotona princeps*)



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### ABSTRACT

Behaviour is an important mechanism for accommodating rapid environmental changes. Understanding a species' capacity for behavioural plasticity is therefore a key, but understudied, aspect of developing tractable conservation and management plans under climate-change scenarios. Here, we quantified behavioural differences between American pikas (*Ochotona princeps*) living in an atypical, low-elevation habitat versus those living in a 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 at midday. Finally, pikas living in the atypical habitat had smaller home range sizes compared to those in typical habitat or any previously published home ranges for this species. Our findings indicate that behavioural plasticity likely allows pikas to accommodate atypical conditions in this low-elevation habitat, and that they may rely on critical habitat factors such as suitable microclimate refugia to behaviourally thermoregulate. Together, these results suggest that behavioural adjustments are one important mechanism by which pikas can persist outside of their previously appreciated dietary and thermal niches.

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### 1. Introduction

Globally, climate change is occurring at an ever-accelerating rate and has already caused changes in population dynamics (Boggs and Inouye, 2012; Kausrud et al., 2008; Townsend et al., in press), distribution and range shifts (Chen et al., 2011; Hannah et al., 2005; Lawler et al., 2009; Moritz et al., 2008), and localized extinctions of many species (Cahill et al., 2013; Prost et al., 2013; Urban et al., 2012; Williams et al., 2007). One rapid mechanism by which individuals of a species can respond to changes in climate is through behavioural plasticity (Muñoz et al., 2015; Sih et al., 2012; Snell-Rood, 2013). Indeed, an organism's capacity for plasticity is a key component of adaptive capacity, or the ability of a species or population to cope with climatic changes (Beever et al., in press; Nicotra et al., 2015). Behavioural changes operate on a much faster time

scale than distributional or range shifts, particularly for species with low vagility (Huey et al., 2012). Many behavioural responses have already been documented in response to changing environmental conditions (Tuomainen and Candolin, 2011), including shifts in phenology (Visser and Both, 2005; Walther et al., 2002), reproduction (Blaustein et al., 2012; Lane et al., 2011), and use of food resources (Dawson et al., 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 favourable time periods (e.g. Murray and Smith, 2012; Sinervo et al., 2010).

The American pika (*Ochotona princeps*) is a small mammalian herbivore that is largely a habitat specialist in high-elevation talus (rock slides and boulder fields) across western North America. Pikas are an ideal species for investigating behavioural 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 behaviours that vary among habitats (Smith, 1974). Since they do not hibernate, pikas spend the short alpine growing season collecting and storing vegetation in

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food caches called haypiles, which sustain them over the winter (Dearing, 1997). In this study, we use the term “plasticity” in the sense of “developmental behavioural plasticity”, defined by Snell-Rood (2013) as the ability of a population to adopt different behaviours in different environments (as opposed to “activational plasticity,” or the ability of an individual to express different behavioural syndromes throughout its lifetime; Snell-Rood, 2013).

Although pika distribution has waxed and waned in concert with glacial-interglacial cycles (Grayson, 2005), more-rapid distributional declines associated with contemporary climate change have occurred in many parts of the species’ range (Beever et al., 2013, 2011; Stewart et al., 2015). This species tends to be found in alpine habitats with short, cool summers and long winters with extended snowpack (Hafner, 1993), and it is thought that warmer summer temperatures may preclude foraging, resulting in low-quality food caches for winter (Ray et al., 2009). Furthermore, reduced snowpack observed across western North America (Mote et al., 2005) may expose the animals to more extreme winter temperatures (Beever et al., 2010; Smith, 1978). However, the relationship between climate and pika distributions appears complex. For example, certain aspects of climate (e.g. temperature, precipitation, humidity, etc.) may not constrain the species in the same way across its entire geographic range (Jeffress et al., 2013). Furthermore, the persistence of many low-elevation populations in anthropogenic or seemingly marginal habitats (e.g. Beever et al., 2008; Manning and Hagar, 2011; Millar et al., 2013; Rodhouse et al., 2010; Shinderman, 2015; Simpson, 2009) suggests that pikas may possess more plastic behaviours than is commonly thought. These populations may also be behaviourally capitalizing on favourable microclimates found in otherwise unfavourable thermal landscapes.

Although pikas are known to exhibit a range of behaviours that vary across habitat types (e.g. Smith, 1974), their capacity for behavioural plasticity in the context of warmer climates is still not well understood. For example, pikas may be able to mitigate the effects of warmer summer temperatures by restricting their surface activity to times of day when ambient temperatures are tolerable and by spending the hottest parts of the day in the cooler talus microclimates (Bhattacharyya et al., 2014; MacArthur and Wang, 1973, 1974; Smith, 1974). However, this restriction could also constrain essential activities, such as reproduction (Sinervo et al., 2010) or foraging (Ray et al., 2009), and therefore be of limited advantage. Furthermore, some aspects of climate change could simply become so extreme that they cannot be accommodated by behavioural shifts alone, particularly if the thermal buffering capacity of the talus refuge is reduced (Nicotra et al., 2015).

In many cases, studying behavioural plasticity in a marginal habitat can provide information about habitat features that are crucial for persistence under unfavourable 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), which may become more frequent in the future under continued climate change. The Columbia River Gorge (CRG) in Oregon, USA, provides an excellent opportunity for investigating the behavioural plasticity of this species in response to both atypical resource availability and climate. The ca. 50-km stretch of the CRG in which pikas are distributed is generally characterized by dense Douglas fir (*Pseudotsuga menziesii*) forest, and talus patches in this region are often covered in a thick carpet of moss. Furthermore, the CRG exhibits steep gradients in ambient temperature, relative humidity, precipitation and insolation; thus, a range of environmental conditions can be sampled within a relatively small area, especially compared with the species’ geographic range.

The CRG also represents the lowest elevations at which American pikas have been detected (Horsfall, 1925; E. Beever, unpubl. data.), and the species persists here in a climate that appears to

be unsuitable, based on the species’ previously described thermal niche (Simpson, 2009). However, the microclimates in this habitat are highly spatially heterogeneous, in part because the moss cover insulates the talus interstices from temperature fluctuations at the surface (Varner and Dearing, 2014b). Specifically, temperatures measured within a few meters of each other in talus interstices may differ by 3–5 °C, providing pikas with a unique opportunity to adjust their thermoregulation. This region also contains vegetation resources that are unusual for this species, and pikas in this habitat demonstrate plasticity in their diet by facultatively specializing on the abundantly available mosses (Varner and Dearing, 2014a).

In this study, we observed the foraging, thermoregulatory and territorial behaviours of pikas living in the atypical, low-elevation habitats of the CRG. We then compared these behaviours to those of pikas living 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 versus low elevations. First, we systematically investigated the use of off-talus forest microhabitats as a potential midday thermal refuge. We hypothesized that, due to higher ambient temperatures at low elevations, pikas in the CRG would use these refuges at a higher rate, particularly at sites of low moss cover. We also measured the sizes of home ranges in the CRG and Mt. Hood as indicators of space use. We hypothesized that, due to increased resource availability at low elevations, CRG pikas would have smaller home ranges and reduced territorial behaviour, compared to high-elevation pikas. Understanding whether behavioural modifications are present in a highly atypical habitat may provide critical information about a species’ capacity for behavioural plasticity in tolerating new environmental conditions and, by extension, its capacity to tolerate future changes (Beever et al., in press; Nicotra et al., 2015).

## 2. Methods

### 2.1. Study area and sites

Behavioural observations were conducted at six, north- to northwest-facing talus patches (i.e. “sites”). Each site was nested within a “region”: either the low-elevation CRG ( $N=4$  sites, 194–437 m elevation) or high-elevation Mt. Hood ( $N=2$  sites, 905 and 1682 m elevation).

Sites in the CRG were ca. 15 000 m<sup>2</sup> each, 32–35° in slope angle, and surrounded by a dense forest dominated by Douglas fir, 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 that covers the surface of each rockslide (Varner and Dearing, 2014a,b). Low-elevation sites varied in moss cover from over 65% (“high moss cover”: sites 1 & 2) to less than 30% (“low moss cover”: sites 3 & 4); however, forb and grass communities were similar among sites. The average pairwise distance between sites in the CRG was mean  $\pm$  SD = 17.7  $\pm$  16.6 km (range: 0.64–35.9 km), as measured by the Path Ruler tool in Google Earth. This tool takes into account the contours of the landscape, thereby providing a more biologically meaningful assessment of distance between sites. Importantly, each of these sites is approximately 1000 m lower in elevation than pikas are predicted to occur at this latitude and longitude (Hafner, 1993), based on their previously described bioclimatic envelope (Simpson, 2009).

For comparison with more typical, high-elevation habitat, we also conducted behavioural surveys at two sites (sites 5 and 6) on

the north face of Mt. Hood in montane habitats typical for pikas. These sites are separated from those in the CRG by  $31.9 \pm 5.0$  km (mean  $\pm$  SD; range 27.1–39.3 km), but they differ in elevation by a thousand meters and thus experience vastly different climate regimes and resource availability. Sites on Mt. Hood were 27–28° in slope angle, and neither site had considerable moss cover. Site 5 was located in dense forest dominated by Douglas fir, western redcedar, and western hemlock (*Tsuga heterophylla*). Site 6 was located in a similar forest, but near the timberline. Sites 5 and 6 were separated from each other by 5.9 km.

A recent study of population genetics in CRG pikas revealed that our sites 1–3 group together in a Bayesian clustering analysis, suggesting some genetic connectivity between these sites (Robson et al., in press). That study did not explicitly analyse samples from our other sites, but all of our sites clearly comprise the same lineage, *O. p. fenisex*, which appears to be the most basal lineage of this species (Galbreath et al., 2010; Hafner and Smith, 2010).

## 2.2. Foraging behaviour surveys

Foraging observations were primarily conducted in July of 2012 and 2013, although five foraging observations were collected in July 2011 at site 6 ( $N=2$  observers in 2011). There were five observers in 2012 and four observers in 2013; three of these observers (J.V., J.J.H., and M.S.L.) were present in both 2012 and 2013. In total, we observed 5250 pika detections in 417 observer-hours of behavioural data across our 6 sites.

Upon arrival at a site, observers selected a high vantage point near the edge of the talus and used binoculars to document foraging activity and microhabitat use. As in previous studies, pikas habituated rapidly to observers on the talus (Conner, 1983; Dearing, 1996; Smith and Ivins, 1984); however, activities were not recorded for the first five minutes. Each observer recorded activities in non-overlapping focal areas of the site for up to 3 h. Following Moyer-Horner (2011) and Henry et al. (2012), surveys started 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 (i.e. out of sight and not vocalizing; following Moyer-Horner, 2011). Each detection was then classified into one or more behaviour categories as defined by Smith and Weston (1990) (Fig. 1). Foraging behaviours included grazing (consuming vegetation) or haying (caching vegetation or carrying a plant clipping below a rock). Territorial behaviours included cheek rubbing (making territorial markings with apocrine glands on their cheeks) and aggression (active chases and fights). Other behaviours not specifically analysed in this study included surveying (perching on a prominent rock), running, grooming, coprophagy, and vocalizing. When possible, individuals were identified by coloured eartags placed for a previous study (Varner and Dearing, 2014a) or by distinctive scars on the ears or eyes.

For each detection, we also noted the microhabitat type in which the pika was detected. Talus slopes in both regions (i.e. CRG and Mt. Hood) were surrounded by a forest with herbaceous plants, shrub cover, and tree canopy cover, which may represent an important foraging arena or midday thermal refuge (Varner and Dearing, 2014b). Although rocks were occasionally present beyond the patch margin under the forest canopy, the degree to which the talus extended into the forest was not consistent. We therefore chose to classify detections as occurring either in the open talus or under forest canopy cover. In some cases, forest canopy detections included

calls that were clearly heard from the forest although the animals were not seen due to dense understory vegetation.

## 2.3. Foraging behaviour analysis

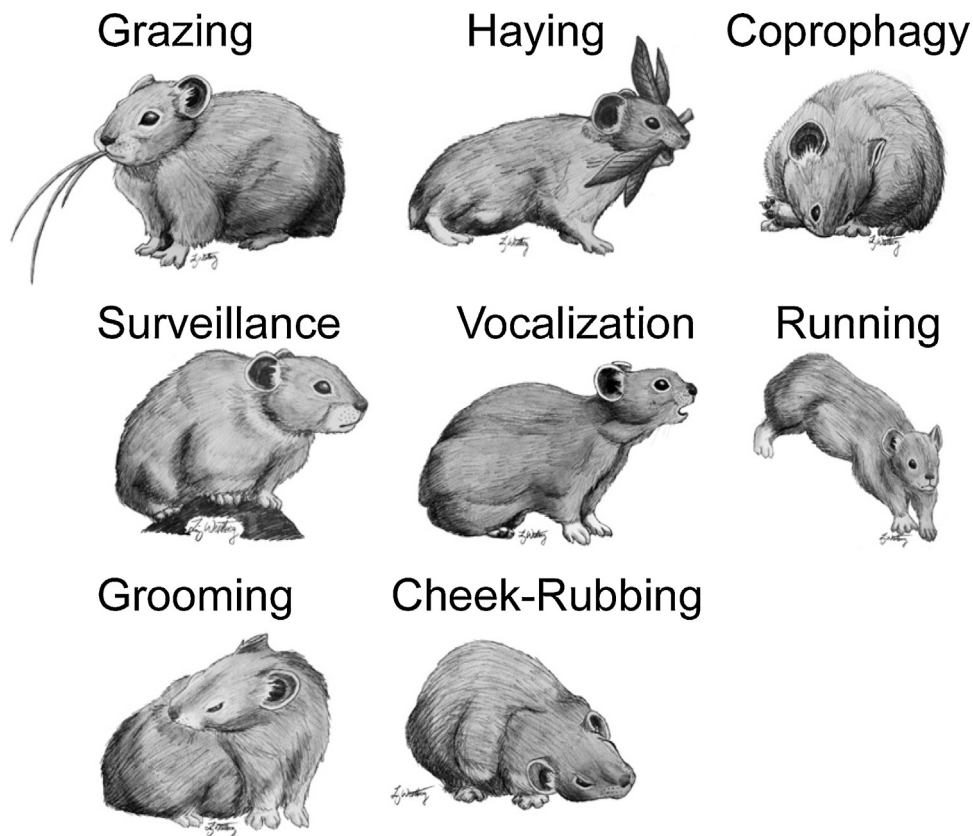
To assess the effect of region (i.e. CRG versus Mt. Hood) on foraging behaviour, we used a generalized linear mixed model (GLMM) to predict the probability of haying versus grazing behaviour for marked individuals only. For this analysis, an observation was defined as the total number of grazing versus haying detections for each individual within a year ( $N=38$  observations). 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 ( $N=30$ ) and sites ( $N=6$ ) were modelled as random effects to control for repeated measures and their intrinsic variation. For all GLMM results, asymmetrical SEs are reported in the text because these values are back-transformed from logit data. Symmetrical SEs are available in the statistical output tables in the Appendix.

## 2.4. Forest microhabitat analyses

We conducted three analyses to explore variation in the use of off-talus forest microhabitats by all pikas (i.e. including unmarked individuals). In the first analysis, we assessed the effect of region (i.e. CRG versus 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. All pika detections were classified as either occurring in forest or talus; therefore we used a binomial GLMM with a logit link. For this analysis, an observation was defined as a period when a single observer at one of the six sites monitored pika activity for up to 3 h ( $N=117$  observations). Although observations varied in total time and number of pika detections, these discrepancies are taken into account by pairing the number of forest detections directly to the number of talus detections in each observation. Region was treated as a fixed effect, and date ( $N=20$ ), observer ( $N=6$ ), and site ( $N=6$ ) were modelled as random effects to control for repeated measures and variation due to those factors.

In the second analysis, we assessed the effect of ambient temperature, moss cover, and time of day on forest microhabitat use in the CRG, where large spatial and diel variations in ambient temperature and moss cover are present. We used a GLMM to predict the probability of a detection occurring under forest canopy cover versus in open talus. An observation was defined as above ( $N=81$  observations). Ambient temperature, moss cover (high versus low), and time of day (morning, midday, evening) were modelled as fixed effects. Date ( $N=18$ ), observer ( $N=6$ ), and site ( $N=4$ ) were modelled 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 an ambient-temperature 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 (Richards, 2005).

Because we found that time of day influenced forest microhabitat use in the CRG, we conducted an additional analysis in which we assessed the effect of region on forest microhabitat use for midday observations only ( $N=23$  observations). We used a GLMM with the same structure as in the previous two microhabitat analyses (date  $N=8$ , observer  $N=6$ , and site  $N=5$ ).



**Fig. 1.** Ethogram of pika behaviour. Pika detections were classified as one or more of these behaviours. Aggression and social tolerance are not depicted. Sketches by E. Westberg.

### 2.5. Home range size and aggressive behaviour

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 individual pika location at the beginning of each detection on an aerial satellite image. These maps were then scanned and locations within a site were scaled and digitized using Image J (Schneider et al., 2012). Only adult resident animals that could be reliably identified were included in this analysis (site 1:  $N=3$ ; site 2:  $N=6$ ; site 5:  $N=3$ ). The number of points per animal ranged from 11–64 (mean  $\pm$  SD =  $36.6 \pm 17.5$ ), but did not significantly differ between regions ( $t_{2,68} = 0.48$ ,  $P=0.67$ ).

Sizes of pika home ranges 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 Koeppl et al. (1975). We also divided the talus into  $5\text{ m} \times 5\text{ m}$  quadrats and tallied the area of quadrats within which pikas were observed. This is a more conservative measure of home range because it does not include unoccupied 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 utilisation distribution using the reference bandwidth (Calenge et al., 2011; Worton, 1989). Sizes of pika home ranges in 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 analysis of variance (ANOVA) and Tukey's multiple comparisons tests. A separate ANOVA was employed for each home range estimator.

Finally, to determine whether aggressive behaviours 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 versus non-aggressive detections replaced the response variable. As above, an observation was defined as a single observer at a specific site, monitoring the activity of all pikas for up to three hours ( $N=112$  observations), and observations included activities from all pikas at a site (i.e. including those that were unmarked).

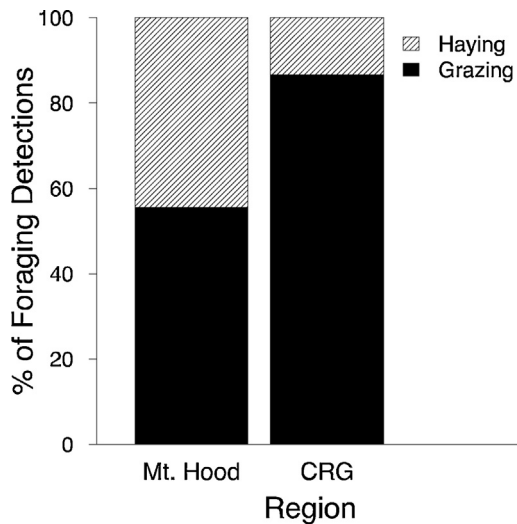
### 2.6. Ethical note

All research on live animals was approved by the University of Utah institutional animal care and use committee (IACUC protocol no. 11-02013). Appropriate permits were also obtained from the Oregon Department of Fish and Wildlife (permit nos. 098-13, 017-12 and 033-11).

## 3. Results

### 3.1. Foraging behaviour

Foraging behaviours constituted 15% of total detections across both regions and years. However, the proportion of grazing versus haying behaviours differed significantly between regions (GLMM:  $Z=3.38$ ,  $P<0.001$ ; Appendix Table A1, Fig. 2). Specifically, CRG pikas were observed haying in 11.7% (SE:  $+6.8-4.5$ ) of foraging detections and grazing the remainder, whereas Mt. Hood pikas were observed haying in 45.0% ( $+10.2-9.8$ ) of foraging detections and grazing the remainder.



**Fig. 2.** Haying and grazing behaviours as a proportion of all foraging detections in the CRG versus Mt. Hood. As a proportion of total detections, foraging detections did not vary between regions or across years.

3.2. Forest microhabitat use

Although pikas in both regions had access to conifer forest habitat off the open talus, CRG pikas were marginally more likely to be detected in the forest than those on Mt. Hood throughout the day (GLMM:  $Z = 1.72, P = 0.085$ ; Appendix Table A2, Fig. 3A). Specifically, CRG pikas were detected in forest microhabitats 19.0% (+30.6–13.7) of the time, whereas Mt. Hood pikas were only detected in the forest 1.9% (+4.2–1.3) of the time.

Within the low-elevation sites of the CRG, only time of day had a significant effect on the frequency of forest microhabitat use. Specifically, we observed the highest proportion of detections in the forest at midday (22.0% of all detections, SE +12.0–8.6; Fig. 3B). Forest use in the morning (8.8% of detections, SE: +3.5–2.7) was significantly lower than midday (GLMM:  $Z = -2.68, P = 0.007$ ; Appendix Table A3). Forest use in the evening (9.4% of detections, SE: +3.3–2.5) was also significantly lower than midday (GLMM:  $Z = -3.00, P = 0.002$ ; Appendix Table A3). Neither ambient temperature nor moss cover strongly influenced forest microhabitat use (Appendix Table A3).

When we restricted observations to midday, pikas in the CRG used the forest far more often than did those on Mt. Hood (GLMM:  $Z = 3.27, P = 0.001$ ; Appendix Table A4; Fig. 3C). During midday, CRG pikas were detected in forest microhabitats 38.6% (+25.3–20.4) of the time, whereas Mt. Hood pikas were only detected in the forest 2.1% (+3.5–1.3) of the time.

3.3. Home range size and territorial behaviour

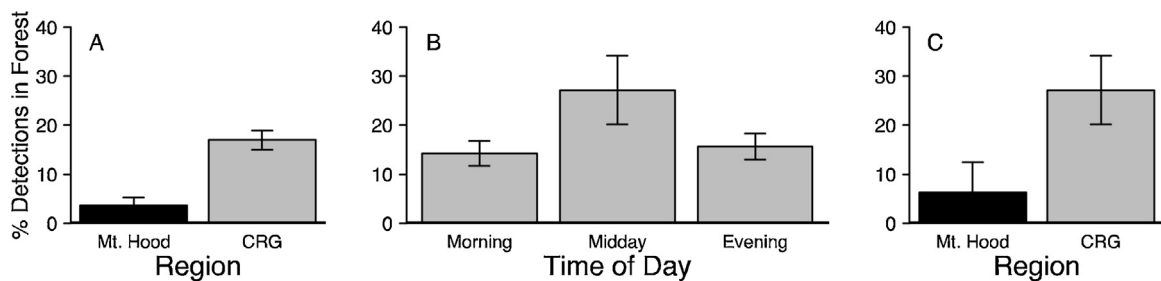
For each estimator of home range size, pika home ranges were significantly smaller in the CRG than any previously published estimates of pika home range size (Table 1). Home ranges in the CRG were significantly smaller than those on Mt. Hood according to the minimum convex polygon estimator (ANOVA:  $F_{2,27} = 10.92, P = 0.0003$ ; Tukey post-hoc test:  $P < 0.01$ ). Although sizes of pika home ranges did not differ significantly between the CRG and Mt. Hood by the quadrat, kernel density, or bivariate estimators, the largest home range for a CRG pika was still smaller than the smallest home range on Mt. Hood by any estimator.

Territorial behaviours (aggression or cheek rubbing) were rare in our study (less than 1 per 10h of observation, and <1% of total detections). Despite having small home ranges and living at high densities, pikas did not exhibit more frequent aggressive behaviours in the CRG than on Mt. Hood, as a proportion of total detections: both groups engaged in these activities at a frequency of 0.06% of total detections (GLMM:  $Z = 0.28, P = 0.783$ ; Appendix Table A5).

4. Discussion

Here, we document substantial differences in behaviour between pika populations living in atypical, low-elevation habitat in the Columbia River Gorge (CRG) and those in more typical montane habitat on nearby Mt. Hood. Specifically, we showed that low-elevation pikas do not invest as much time or energy in caching food for winter (Fig. 2). Pikas in low-elevation habitats were also more likely to use forested areas off the open talus at midday than those living at high elevations. The temporal pattern of off-talus detections (Fig. 3) suggests that the forest may serve as a refuge during times of the day that may be most thermally stressful for pikas. Although pikas in the CRG are living at high densities with smaller home ranges, they do not exhibit higher frequency of territorial behaviours than those on Mt. Hood, perhaps because food resources are abundant in the CRG and because these pikas are not defending large winter food caches against kleptoparasitism (Varner and Dearing, 2014a).

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 foraging pikas were observed haying 25–50% of the 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, foraging pikas in the CRG were observed haying less than 12% of the time. Because foraging represented approximately 15% of detections across sites and years, CRG pikas spent approximately 2% (i.e.,  $12\% \times 15\%$ ) of their daily activity budgets haying.



**Fig. 3.** Use of forested habitat in 2013. Mean frequency ( $\pm 1$  SE) at which pikas were detected in the forest (A) by region across all time points, (B) by time of day within the CRG only, and (C) by region at midday only. Note: Raw values here differ slightly from those in the text because the mean  $\pm$  SE values presented in the text are back-transformed from a GLMM leveled for pikas in high moss cover at 25.5 °C.

**Table 1**  
 Sizes of pika home ranges in the CRG, Mt. Hood and two other regions from the existing literature. Mean  $\pm$  SD home range size in m<sup>2</sup> for four different home range estimators.

Region	Pikas	Quadrat	Bivariate	Min. convex polygon	Kernel density
CRG	9	327 $\pm$ 112.8 (a) <sup>a</sup>	111.2 $\pm$ 70.7 (a)	289.9 $\pm$ 188.3 (a)	675.5 $\pm$ 426.3 (a)
Mt. Hood	3	550 $\pm$ 263.4 (a,b)	647.1 $\pm$ 224.4 (a)	1712.3 $\pm$ 187.4 (b)	11 721.9 $\pm$ 13 653.2 (a)
Gothic, CO <sup>b</sup>	25	1106 $\pm$ 112 (b)	3918.5 $\pm$ 676.5 (b)	NA	NA
Loveland pass, CO <sup>c</sup>	18	1840 $\pm$ 768 (c)	NA	1367.4 $\pm$ 763.7 (b)	NA

<sup>a</sup> Letters indicate means within a home range estimator that significantly differ.

<sup>b</sup> Data from Rocky Mountain Biological Lab (Smith and Ivins, 1984).

<sup>c</sup> Data from Kawamichi (1982).

Seasonal progression can be an important cue for pikas to collect and store food (Smith, 1974). Although we minimized the impact of season by collecting foraging observations in July, sites may be seasonally more advanced in different geographic locations, thus triggering earlier and more-frequent haying behaviour. However, the pattern of haying versus grazing detections that we observed corroborate the results of a previous study in which pika haypile size corresponded closely to the duration of winter across several habitat types (Varner and Dearing, 2014a). Unlike other populations, pikas in the lowest elevations of the CRG do not need to expend as much time or energy investing in winter food caches because winters are comparatively short and food resources such as evergreen trees and shrubs or mosses are available year-round (Varner and Dearing, 2014a). Together, these results suggest that pikas have a large degree of behavioural flexibility with respect to foraging, such that they can modify their grazing and haying to suit climatic conditions, at least at the population level.

Pikas also appear to modulate their use of off-talus forest microhabitats across different regions and times of day. Specifically, we observed pikas in the coniferous forest most frequently at midday in the CRG, when and where ambient temperatures are highest. Although ambient temperature measured at the location of the observer was not predictive of forest use in our model, temperatures in CRG microhabitats are highly heterogeneous and sometimes uncorrelated with ambient temperatures (Varner and Dearing, 2014b). This result suggests that ambient temperature recorded at one location may not predict pika behaviour in this habitat. Furthermore, temperatures measured in the forested areas adjacent to open talus at sites 1–4 in the CRG suggest that this forest may constitute an important midday thermal refuge, particularly at sites with lower moss cover (Varner and Dearing, 2014b).

In contrast, pikas on Mt. Hood were rarely detected in the forest. These animals might be forced to remain active in the talus at midday to construct the large haypiles necessary for winter survival, or the forest microhabitat in this region might not provide the same magnitude of midday thermal refuge as occurs in the CRG. Importantly, pikas may still be able to forage in the forest in the CRG, which has ample food resources, as opposed to simply restricting their activity below the talus surface. If such microhabitats are available, other pika populations might be able to utilize non-talus thermal refuges to mitigate the continued effects of climate change. Indeed, in north-eastern Wyoming, pikas have recently been observed constructing haypiles in downed logs and slash piles up to 100 m from the nearest talus, and paired temperature measurements suggest that these non-talus habitats may buffer pikas against extreme winter temperatures (E. Hall and A. Loosen, personal communication, 16 October 2012; Beaver et al., in press). Collectively, these results may also highlight the need to conserve non-talus thermal refuges for this species, such as dense forest that surrounds sub-alpine pika habitat.

The high degree of year-round resource availability in the lowest elevations of the CRG may also affect space use in this habitat. Indeed, CRG pikas also utilized significantly smaller home ranges than previously reported in the literature. Pika home ranges in the CRG were also smaller than those on Mt. Hood, although the

number of marked animals on Mt. Hood ( $N = 3$ ) limited our ability to detect statistical differences between these regions. However, despite 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 h observation) was lower than values reported in the literature (2.8 acts per 10 h observation; calculated from data in Smith and Ivins, 1983). Notably, Smith and Ivins (1983) only collected data during the morning and evening, when pikas were most likely to be active; however, when we removed midday observations from our dataset, we still observed less than 1 aggressive act per 10 h of observation in the CRG.

In selecting our sites, we tried to control for biogeographic factors that could drive behavioural differences. For example, rocks at all sites had roughly the same clast size (means = 40–50 cm; Varner and Dearing, 2014b), and all sites had similar aspects. We specifically selected for sites that varied in moss cover, and this factor was included as a fixed effect in the relevant analyses. One factor that differed between regions was slope steepness: CRG sites were a few degrees steeper than those on Mt. Hood, which could potentially affect the vegetation present at each site through water drainage and soil properties. However, we believe that the macroclimatic differences (i.e. patterns of temperature and precipitation) between our regions are likely stronger drivers of pika foraging and thermoregulatory behaviour than slope steepness, as has been reported in previous studies (e.g. Bhattacharyya et al., 2014; Smith, 1974).

It is important to note that genetic differentiation may exist between the high- and low-elevation pikas in this study. A recent study found evidence of fine-scale genetic structure between pika populations across the CRG (Robson et al., in press), suggesting that significant genetic differentiation may exist between our CRG and Mt. Hood sites. It is therefore possible that some of the behavioural differences that we observed between regions could actually represent local adaptation (i.e. the product of geographic variation due to genetic isolation). In this case, the behavioural differences in our study could be developmentally canalized within a population, rather than the result of plasticity. However, it remains unclear to what degree genetic differentiation between our study populations may be adaptive versus neutral, or whether it has any direct bearing on the behavioural patterns that we observed in this study. Furthermore, genetic differences could act synergistically with cues from different environments or habitats to produce behaviours.

To unequivocally determine the heritability of the behavioural patterns we observed, a transplant or common-garden experiment would be necessary. However, determining the mode of heritability (i.e. fixed genetic differences between populations versus more plastic mechanisms such as maternal effects or learned “cultural” behaviours, etc.) would require extensive work in a laboratory setting. Such experiments are not feasible or ethical to conduct with pikas because they have low survival rates in captivity (C. Ray & P. Somers, personal communication, 17 April 2015; Dearing, unpubl. data) and are extremely difficult to trap in this environment (Varner, unpubl. data). Considering the genetic component of behavioural differences between populations is a fruitful area

for future research, particularly where it relates to the adaptive capacity of a population or species (Beever et al., in press).

In spite of potential underlying genetic differences, behavioural plasticity may have been adaptive during the biogeographic history of pikas as a family, enabling them to move into different habitats. 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 species *Ochotona collaris*), which are thought to have dispersed across the Bering land bridge during the Pleistocene Epoch (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 likely the ancestral form of the genus (Reese et al., 2013). Thus, substantial behavioural 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 are also found in non-talus habitats, including woodpiles (Northern pika, *Ochotona hyperborea*) or old rock walls (Glover’s pika, *Ochotona gloveri*; Smith, 2008), suggesting a higher degree of plasticity within the genus than may be commonly assumed.

We suggest that future research is needed to understand the degree to which pikas can modify their behaviour to accommodate changes in climate, across a variety of biogeographic and climatic contexts. Pikas can clearly alter their foraging behaviour based on 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 behaviourally plastic in other ecoregions, where habitat quality has been degraded as a result of grazing or lack of suitable microclimates. In other habitats, pikas may simply not have access to spatially variable microhabitats that provide behavioural opportunities (e.g. pikas inhabiting alpine areas above tree line may not be able to access dense forests immediately adjacent to the talus, as observed in our study region). In addition, although pikas appear able to reduce investment in haying for winter in habitats where winters are short and food resources are widely available throughout the year, restricting haying behaviour may not be beneficial in other habitats where large food caches are necessary to survive harsh winters.

This work contributes to a growing body of literature describing the behaviour of different populations of pikas, and is an important step towards a better understanding of pika foraging behaviour and microhabitat use in atypical habitats. Our results indicate that behavioural adjustments are one important mechanism by which pikas can persist outside of their previously described dietary and macroclimatic niches. They also suggest that, given appropriate food resources and midday thermal refugia, some populations of pikas may be able to adjust their behaviours to accommodate certain aspects of future climate change. A more-mechanistic understanding of whether and how behavioural plasticity can be used to accommodate climate is suggested to best inform conservation and management to mitigate the ecological effects of climate change (Muñoz et al., 2015; Nicotra et al., 2015).

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### Appendix A.

**Table A1**

Results of a binomial GLMM comparing foraging behaviour (hay versus grazing) by region (CRG versus Mt. Hood).

Fixed effect <sup>a</sup>	Estimate	SE	Z	P
Intercept	−0.200	0.409	−0.488	0.6253
Region (CRG)	−1.818	0.537	−3.384	0.0007*

<sup>a</sup> Individual pikas (N = 36) were nested within sites (N = 6) as random effects.

\* Indicates P < 0.05.

**Table A2**

Results of a binomial GLMM comparing forest microhabitat use (forest versus talus) by region (CRG versus Mt. Hood).

Fixed effect <sup>a</sup>	Estimate	SE	Z	P
Intercept	−3.922	1.190	−3.295	0.0099*
Region (CRG)	2.470	1.434	1.722	0.0851

<sup>a</sup> Date (N = 20), observer (N = 6), and site (N = 8) were included as random effects.

\* Indicates P < 0.05.

**Table A3**

Results of a binomial GLMM comparing forest microhabitat use in the CRG by ambient temperature, moss cover and time of day.

Fixed effect <sup>a</sup>	Estimate	SE	Z	P
Intercept (high moss at midday)	−1.264	0.600	−2.109	0.0350*
Ambient temperature	−0.024	0.029	−0.842	0.3996
Site type (low moss)	1.287	0.819	1.573	0.1158
Time (morning)	−1.071	0.399	−2.687	0.0072*
Time (evening)	−1.007	0.336	−2.998	0.0027*

<sup>a</sup> Date (N = 18), observer (N = 6), and site (N = 4) were included as random effects.

\* Indicates P < 0.05.

**Table A4**

Results of a binomial GLMM comparing forest microhabitat use (forest versus talus) at midday by region.

Fixed effect <sup>a</sup>	Estimate	SE	Z	P
Intercept	−3.850	1.015	−3.795	0.0001*
Region (CRG)	3.387	1.037	3.267	0.0011*

<sup>a</sup> Date (N = 8), observer (N = 6), and site (N = 5) were included as random effects.

\* Indicates P < 0.05.

**Table A5**

Results of a binomial GLMM comparing territorial behaviour by region.

Fixed effect <sup>a</sup>	Estimate	SE	Z	P
Intercept	−5.086	0.679	−7.488	<0.0001*
Region (CRG)	0.199	0.725	0.275	0.783

<sup>a</sup> Date (N = 18), observer (N = 4), and site (N = 5) were included as random effects.

\* Indicates P < 0.05.

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