

Distribution of a climate-sensitive species at an interior range margin

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Abstract. Advances in understanding the factors that limit a species' range, particularly in the context of climate change, have come disproportionately through investigations at range edges or margins. The margins of a species' range might often correspond with anomalous microclimates that confer habitat suitability where the species would otherwise fail to persist. We addressed this hypothesis using data from an interior, climatic range margin of the American pika (*Ochotona princeps*), an indicator of relatively cool, mesic climates in rocky habitats of western North America. Pikas in Lava Beds National Monument, northeastern California, USA, occur at elevations much lower than predicted by latitude and longitude. We hypothesized that pika occurrence within Lava Beds would be associated primarily with features such as "ice caves" in which sub-surface ice persists outside the winter months. We used data loggers to monitor sub-surface temperatures at cave entrances and at non-cave sites, confirming that temperatures were cooler and more stable at cave entrances. We surveyed habitat characteristics and evidence of pika occupancy across a random sample of cave and non-cave sites over a 2-yr period. Pika detection probability was high (~0.97), and the combined occupancy of cave and non-cave sites varied across the 2 yr from 27% to 69%. Contrary to our hypothesis, occupancy was not higher at cave sites. Vegetation metrics were the best predictors of site use by pikas, followed by an edge effect and elevation. The importance of vegetation as a predictor of pika distribution at this interior range margin is congruent with recent studies from other portions of the species' range. However, we caution that vegetation composition depends on microclimate, which might be the proximal driver of pika distribution. The microclimates available in non-cave crevices accessible to small animals have not been characterized adequately for lava landscapes. We advocate innovation in the acquisition and use of microclimatic data for understanding the distributions of many taxa. Appropriately scaled microclimatic data are increasingly available but rarely used in studies of range dynamics.

Key words: distributional limits; Lava Beds National Monument; microclimate; microhabitat; *Ochotona princeps*; plant–animal association; plant–herbivore interaction; range dynamics; refugia.

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INTRODUCTION

Latitude, longitude, and elevation index not only a geographic location but also the many

processes interacting to determine which species will persist at that location. Among these processes, climatic controls on a species' distribution are most often associated with latitude and

elevation. For example, ecologists have long observed (Merriam 1892) that cold-adapted species are increasingly absent from lower elevations at lower latitudes. Climate can also vary strongly with longitude, such as when longitude is the main factor describing distance from a coastline. Therefore, the geographic range of a species—described in dimensions of latitude, longitude, and elevation—serves as a first approximation of its climatic envelope. A useful refinement to this approximation involves accounting for variation in the density of occurrence records within the species' range, allowing for the identification of outliers. An occurrence identified as an outlier in latitude, longitude, and/or elevation suggests a local anomaly in range determinants, such as an anomaly in the relationship between climate and geographic position.

Microclimates, defined here as persistent, local anomalies in climate, can result from the interactive effects of geographic, topographic, climatic, and even biological processes. Microhabitat use will appear to extend a species' climatic envelope if the microclimates responsible for habitat suitability are not recognized or appropriately characterized (Potter et al. 2013, Varner and Dearing 2014a). Colonizing a suitable microhabitat can also extend a species' geographic range. In fact, range margins might often correspond with anomalous microclimates that confer habitat suitability where a species would otherwise fail to persist, a pattern that would help explain why many species persist primarily at a margin during range contraction (Lomolino and Channell 1995, Channell and Lomolino 2000). Thus, research at a range margin can be especially valuable for ascertaining range determinants and suggesting strategies for management and conservation in an era of accelerated climate change (Potter et al. 2013, Razgour et al. 2013).

Identifying a range margin suitable for study of climatic controls on a species' distribution requires consideration of the species' natural distribution. If occurrence rates rise toward the geographic center of a species' range, then climatic controls should be most evident at a geographic range margin defined by latitude and longitude. But, if occurrence is naturally patchy within the geographic range, then even interior populations may be located at a margin—an "interior range margin." In this case, we would expect climatic

controls to be most evident where they are most extreme; for example, at extreme elevations.

We evaluated predictors of occurrence in a model taxon at an interior range margin to test hypotheses about the process of observed range retraction. The American pika (*Ochotona princeps*; hereafter, "pika") has been studied extensively as a model of small mammal range dynamics within the intermountain region of the western United States (Brown 1971, McDonald and Brown 1992, Hafner 1993, 1994, Hafner and Sullivan 1995, Beever et al. 2003, 2010, 2011, 2013, Galbreath et al. 2009, 2010, Millar and Westfall 2010, Rodhouse et al. 2010, Erb et al. 2011, 2014, Wilkening et al. 2011, Calkins et al. 2012, Jeffress et al. 2013, Stewart et al. 2015), and each of these studies has emphasized the importance of climatic controls on the species' range. The pika is a non-hibernating, cold-adapted species (Grinnell 1917, Hall 1951) that requires access to cool microclimates during the warm season in order to shed heat generated during surface activities (MacArthur and Wang 1974, Smith 1974b). Hafner (1993) focused specifically on the microclimatic conditions necessary for pika persistence, modeling the lower elevational margin of the species' range as a decreasing function of latitude and longitude. Beever et al. (2011) employed a similar model to predict recent extirpations within the Great Basin, where pikas have disappeared from a majority of locations that occur significantly below an elevational margin predicted by latitude. Using this model, we have identified Lava Beds National Monument (LBE) as an extreme outlier in the species' distribution (Fig. 1), where pikas occur at elevations more than 1000 m lower than predicted. The anomalous persistence of pikas in this landscape provides a natural opportunity for elucidating factors governing species occurrence at interior range margins.

Lava Beds National Monument is located more than 150 km inside the western edge of the pika's range, at the northwestern edge of the American Basin and Range Province. The LBE landscape is dominated by several lava flows and a network of "lava tubes" or subterranean channels that open to the surface as "caves" wherever the roof of a tube has collapsed. Persistent ice deposits have been discovered in many of these tubes or "ice caves" (Fuhrmann 2007). Given the pika's status as a biogeographic indicator of permafrost and rock-ice features (Hafner 1994, Millar and

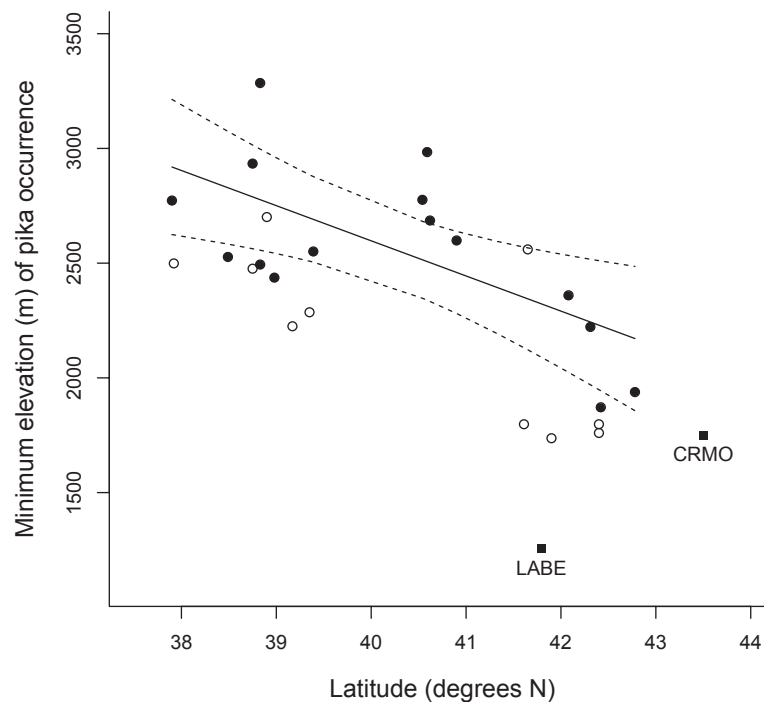


Fig. 1. Minimum elevation of pika occurrence vs. latitude for 27 sites within the interior of the American pika's range, including 25 locations within the hydrographic Great Basin (circles) and two National monuments adjacent to the Basin (squares): Lava Beds (LBE) and Craters of the Moon (CRMO). The linear model and 95% confidence intervals were based on 15 Great Basin locations where pikas were extant in 2008 (filled circles), using data from appendix V of Beever et al. (2011). Open circles represent historically occupied locations where pikas were extirpated as of 2008.

Westfall 2010), we hypothesized that pikas would be associated with ice caves in this landscape. Hafner (1994) observed that extant pika populations in the southern Rocky Mountains were located within 5 km of 20th-century permafrost, and we expected an even tighter association between pikas and ice in the warm LBE climate. With summer temperatures averaging 18.4°C (Western Regional Climate Center, www.wrcc.dri.edu), LBE is warmer than most pika habitats (cf. Millar et al. 2013a, Smith and Nagy 2015, Stewart et al. 2015). An association between pikas and ice caves within LBE would suggest that pikas elsewhere will become more closely tied to sub-surface ice as climate change continues.

The process of climate-mediated range retraction may include direct effects such as physiological stress in response to altered temperatures, as well as indirect effects such as those related to competitive or predator-prey relationships, changes in resource availability, and

increased exposure or susceptibility to pathogens (Glennon et al. 2002, Thomas 2010). We used site occupancy estimation and modeling to evaluate the relative support for different effects on the probability of species occurrence (MacKenzie et al. 2003). Our objectives were to characterize spatial and temporal variation in microhabitat use within an extralimital population of a climate-sensitive species. Using data from repeated surveys, we estimated pika detection probabilities and modeled pika occurrence probabilities along environmental gradients representing different mechanisms governing site use, including availability of thermal refuge, variation in forage quality, and competition with other species. We hypothesized that pikas would be closely associated with ice caves and, more generally, with sites that were cooler in summer than unoccupied locations. We also tested for variation in occupancy rates with distance from anthropogenic corridors, and across years.

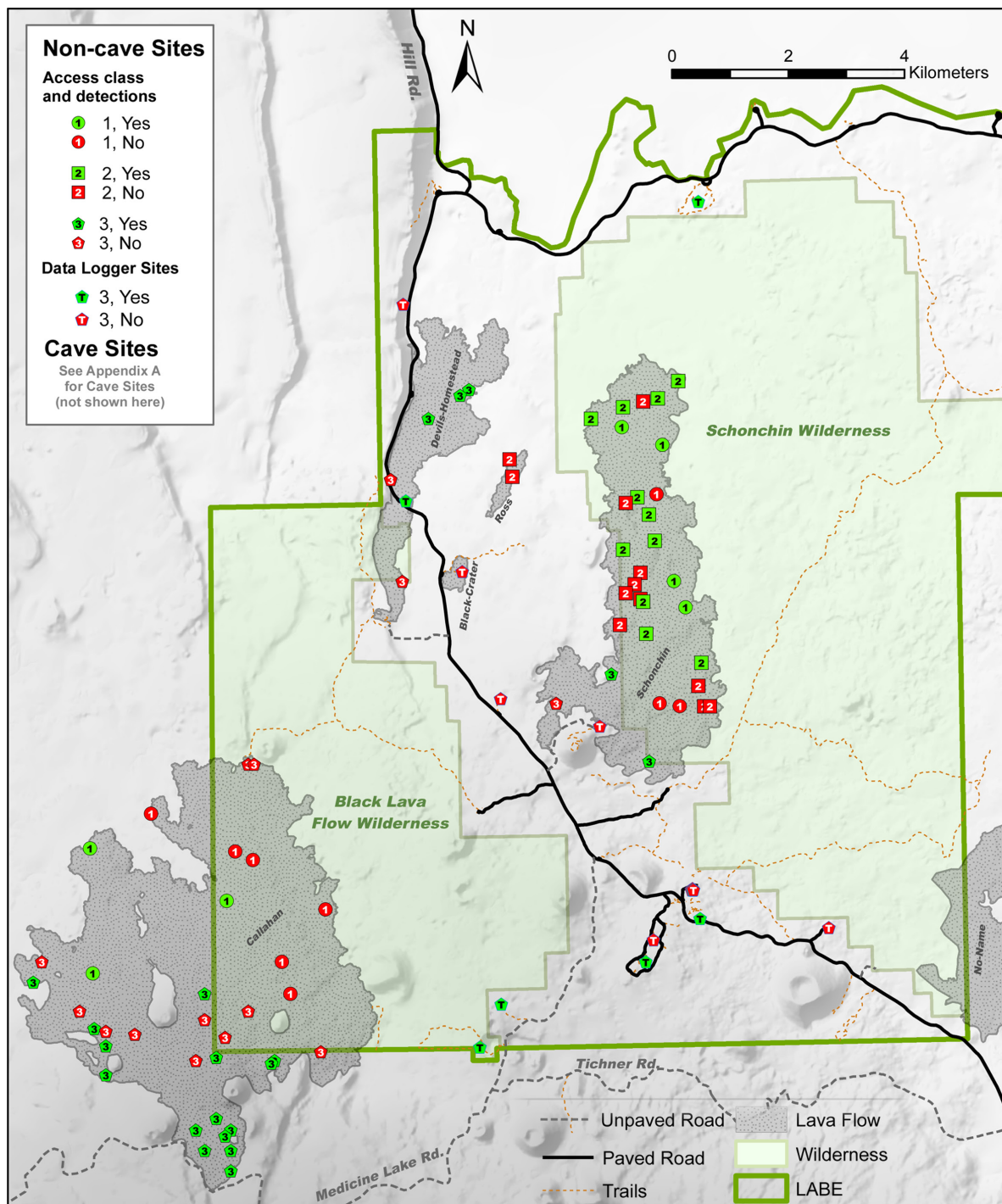


Fig. 2. Map of survey area and selected 2005–2006 pika survey sites at Lava Beds National Monument. All non-cave sites and microclimatic monitoring sites are shown. Site icons indicate accessibility class (3 = most accessible) and occupancy (Yes = occupied). Ecologically sensitive cave sites (data not shown) all occur within the park boundary (see also Appendix S10).

Table 1. Predictor variables used in modeling detection probability, site occupancy, and site-use intensity of the American pika in Lava Beds National Monument (LBE).

Process	Predictor	Definition
Detection probability	<i>effort</i>	Time spent searching for signs of pika site use
	<i>date</i>	Ordinal date on which the site survey was conducted
	<i>temperature</i>	Ambient temperature during the site survey
	<i>wind</i>	Maximum gust speed during the site survey
	<i>skies</i>	Cloud cover during the site survey (classes 0–3)
	<i>moonrise and phase</i>	Rise time and lunar phase on the night preceding the site survey
Biogeography of site occupancy and site-use intensity	<i>site type</i>	Cave or non-cave
	<i>access class</i>	Accessibility of site to humans (classes 1–3, where 1 is least accessible)
	<i>aspect</i>	Average slope aspect within the site (cosine-transformed)
	<i>gradient</i>	Average slope gradient within the site
	<i>elevation</i>	Elevation of the site center
	<i>visHRs</i>	Number of potential pika home ranges visible from the survey site
	<i>contigHRs</i>	Number of potential, contiguous home ranges within 0.25 km of the site
	<i>goodroad</i>	Distance from site center to nearest non-four-wheel-drive road
	<i>anyroad</i>	Distance from site center to nearest road
	<i>woodrat</i>	Type of woodrat sign within the site (classes 0–3)
	<i>insulation</i>	Maximum depth of creviced lava within the site (classes 0–4)
	<i>dist2edge</i>	Distance from the site center to the nearest edge of the flow containing the site
Land-cover relationships with site occupancy and site-use intensity	<i>forb</i>	Summed cover of all forb species within the site
	<i>rock</i>	Cover of creviced rock (lava or talus) within the site
	<i>gram:chem</i>	Ratio of graminoid cover to cover of other plant species higher in secondary compounds (forbs, shrubs, and trees) within the site, indexing forage quality
	<i>litter:soil</i>	Ratio of litter cover to cover of bare ground within the site
	<i>sage</i>	Cover of sagebrush (<i>Artemisia tridentata</i>) within the site
	<i>fernbush</i>	Number of fernbush plants within the site
	<i>veg_complex</i>	Ratio of graminoid and shrub cover to cover of forbs and trees, reflecting the vegetation complex within the site

METHODS

Study domain and context

Lava Beds National Monument (LBE) covers ~19,000 ha in northern California, USA, on the flank of a shield volcano that erupted 17 times between 800 and 12,800 yr ago (Donnelly-Nolan et al. 1990). Lava flows and cave entrances composed of creviced rock potentially suitable for pikas (Rodhouse et al. 2010, Jeffress et al. 2013) occur throughout LBE at elevations of 1,230–1,650 m. LBE supports no surface water resources, and there is some evidence that sub-surface ice deposits historically fed by runoff captured in lava tubes are in decline (Fuhrmann 2007, Adamus et al. 2013). Vegetation reflects Great Basin affinities and is especially sparse within the lava beds.

Annual precipitation, as summarized from continuous weather observations during 1959–2010 at LBE headquarters (41°44' N, 121°31' W;

1454 m elevation), averaged 36.8 cm, most of which fell as snow in winter. During 1971–2000, minimum temperatures in January averaged 5.3°C and maximum temperatures in July averaged 29.3°C (Western Regional Climate Center). During the same period, July maxima averaged at least 4°C cooler at several other “comparatively warm” sites occupied or formerly occupied by pikas (Millar et al. 2013a, Smith and Nagy 2015), and July maxima ranged 16.8–21.6°C across a multitude of non-lava sites in national parks sampled by Jeffress et al. (2013).

Research design and survey sites

Survey sites ($n = 143$) were selected at random from cave ($n = 70$) and non-cave ($n = 73$) sites within LBE and adjacent lands (Fig. 2). Sites were further stratified by accessibility class: 1 = remote sites more than 1 km from any road or trail, 2 = sites within 1 km of a trail but more than 1.5 km from the nearest road, and

3 = highly accessible sites less than 1 km from a road. Non-cave sites were selected from a GIS layer that identified lava flows composed of relatively exposed, creviced rock typical of pika habitats. This layer was rasterized, using a 50-m grid, and grid cells were selected at random ($n = 16$ cells from class 1, 23 from class 2, and 34 from class 3). The centroid of each selected cell became the center of a survey site 24 m in diameter (452 m²). This diameter reflects territory size indexed as the midpoint of nearest-neighbor distances reported for *O. princeps* (14–34 m, Smith and Weston 1990), and has been widely used for pika site occupancy surveys across much of the western United States (Rodhouse et al. 2010, Jeffress et al. 2013). Cave sites, also 24 m in diameter and each centered at a cave entrance, were randomly selected from the complete list of known LABE caves using the same classified GIS layer as described for non-cave sites ($n = 11$ from accessibility class 1, 26 from class 2, and 33 from class 3). Finally, 13 highly accessible sites were chosen for studies of microclimate. These 13 sites represented the variety of geologic features (cave and non-cave), slopes, aspects, and elevations of pika habitats available in this landscape, but were located near roads to facilitate frequent data retrieval.

Occupancy and site-use intensity

Site surveys were conducted during summer, ending prior to July 31 in both years of study: 2005 and 2006. To assess the effects of season on pika detection, additional surveys were conducted in September–November of 2006. Pika sign was classified as “direct” (detection of a live pika by sight or sound) or “indirect” (detection of a pika food cache or pika scat in the form of characteristic fecal pellets). Indirect sign was further classified as “fresh” or “old,” based on color and texture (Nichols 2010, Jeffress et al. 2013). Definitively fresh pika food caches or “haypiles” were never discovered during our surveys at LABE, but survey crews reported that apparently “old” hay (lacking chlorophyll) was common where pikas or fresh scat were observed. We defined current pika occupancy according to any one of three conditions: (1) direct detection within the site; (2) fresh scat within the site; or (3) any pair of signs including a) old scat within the site, b) hay

within the site, and c) direct detection within less than 100 m of the site center. Direct detections were recorded at any time during the site survey, and indirect signs were recorded during a search of 20–30 min (depending on terrain complexity). Site-use intensity was indexed as the combined number of direct detections and fresh scat piles.

Candidate predictors of pika detection and occupancy

Site occupancy was modeled as a function of site type (cave or non-cave) and accessibility class, while accounting for effects of search effort on detection. Site-use intensity, also corrected for search effort, was modeled as a function of site and survey variables hypothesized to affect pika ecology and detection (Table 1).

Weather and moonlight.—Detection probability is often influenced by effects of weather on animal surface activity. Pikas are less active on the surface during hot, windy, and rainy weather (Krear 1965, Smith 1974b, Hayes and Huntly 2005). Moonlight may also affect detection, if it alters nocturnal and, subsequently, diurnal activity levels. During site surveys we recorded ambient temperature (*temp*) and maximum *wind* speed via hand-held thermometer and anemometer, and we classified *skies* according to broad classes of cloud cover. Lunar *phase* on the night preceding each survey was coded as either 1 (gibbous) or 0 (crescent or new). The potential for moonlight during the night was coded as *moonrise* time, tent transformed to obtain a maximum at 18:00 h (moonrise in the evening) and a minimum at 6:00 h (moonrise in the morning). Actual moonlight, potentially reduced by cloud cover, was not estimated.

Other mammals and potential competition.—We recorded all mammal sign observed during surveys. Aside from pikas, however, only woodrats (*Neotoma* spp.) were detected with regularity. Because woodrats and pikas occupy very similar habitats (creviced rock), we hypothesized a priori that woodrats might compete with pikas through interference, exploitation, or disease-mediated processes. The type of *woodrat* sign within each site was coded as 0 (none), 1 (scat or urine stains), 2 (both scat

and urine), or 3 (nest/midden with scat and urine).

Geologic features and biogeography of survey sites.—During each survey, *site type* (cave or non-cave) was groundtruthed and recorded. To estimate local habitat size, we used our plot size (roughly the size of a pika's home range) as the unit of measure for a visual estimate of the potential number of pika home ranges visible from the site (*visHRs*). We calculated the potential number of contiguous home ranges (*contigHRs*) using GIS to determine how many of our plots could fit on lava within 0.25 km of the site. Assuming the depth of creviced rock (lava) determines its potential to insulate small mammals from surface conditions, we indexed *insulation* by recording a visual estimate of maximum crevice depth within the site as 0 (no lava present), 1 (< 0.5 m), 2 (0.5–1.0 m), 3 (1.0–1.5 m), or 4 (> 1.5 m). As a metric of proximity to forage or edge effects, we estimated distance from the center of the survey site to the nearest edge of the flow containing the site. This *dist2edge* was determined via a GIS analysis complemented by groundtruthing for sites near flow edges, and was coded as 1 m for cave sites not located within lava flows. In 2006, we also measured *clast_size*, the longest axis of the largest rock within 1 m of each pika sign detected, as an index of preferred clast size.

Land cover.—Within each site, total cover of each plant species was estimated using either visual estimates (in 2005) or point-intercept sampling along radial transects (in 2006). In 2005, the survey crew stood at the site center and visually estimated the percent cover of each species within the site, excepting only species with trace cover, similar to Daubenmire (1959). For each species, cover estimates were averaged among crew members ($n = 2$). In 2006, cover was sampled along each of six 12-m transects arrayed in a radially symmetric design converging at the site center. A point-intercept sample was completed at each meter along each transect (without repetition at the center) by standing a meter-long pin vertically on the substrate (rock or soil). Height and identity of each species touched by the pin was recorded, along with the presence/absence of litter and type of substrate. To address generalized hypotheses regarding pika habitat affinities and foraging behavior, we aggregated

our species data to estimate total cover for each of the following classes: graminoids, forbs, shrubs, trees, litter, bare soil, and rock. This classification scheme allowed us to test for the effects of pika access to larger, more nutritious plants (Huntly et al. 1986), and plants higher in secondary compounds that could preserve well in haypiles (Dearing 1997b). Seeking vegetative indices potentially informative for habitat management, we also considered the abundance (Table 1) of two shrub species, fernbush (*Chamaebatiaria millefolium*) and big sagebrush (*Artemisia tridentata*), hypothesized as covariates of pika occurrence based on preliminary observations. After further refining variables to reduce covariance, our candidate set of predictors relating to land cover were: *forb* cover, *rock* cover, the ratio of graminoid cover to cover of other plant species higher in secondary compounds (*gram:chem*), the ratio of litter to soil cover (*litter:soil*), cover of *sage*, and the number of *fern* plants within each survey site. Finally, as an alternative to *gram:chem*, we also considered a predictor indexing each site's vegetation complex (*veg_complex*) as the ratio of graminoid and shrub cover to cover of forbs and trees.

Microclimatic conditions.—Automated data loggers were placed at 13 survey sites to record microclimatic conditions at hourly intervals from approximately 9/14/2004 through 9/8/2006. Five cave and eight non-cave sites were monitored, each by one to four HOBO data loggers (www.onsetcorp.com) of model H02 ($n = 12$) or H08 ($n = 5$) recording temperature and relative humidity. Model H02 loggers were placed within waterproof containers (Otter Box model 1000, www.otterbox.com). Loggers were placed in protected crevices continuously shaded from direct sunlight, in locations with fresh pika sign or, barring fresh sign, in locations with old sign or apparently suitable microhabitat (as determined by E. Beever). Data were downloaded every four months.

Analyses

We used data from all 67 sites surveyed in 2006, including 24 sites surveyed in both summer and fall, and the occupancy modeling software PRESENCE (v. 2.0, www.mbr-pwrc.usgs.gov/software) to estimate the probability of site occupancy, ψ , while accounting for the

probability that survey crews were able to detect pikas when present, p . We included search effort as a covariate of p , and effects of site type and accessibility class on ψ .

Because estimated detection probability was very high in our occupancy models (see *Results*), we did not estimate p in subsequent analyses. We used generalized linear models (implemented in SAS v. 9.1) to explore effects of search effort and survey conditions on the detection of different types of sign, and to model the intensity of site use as a function of candidate predictors (Table 1). We indexed site-use intensity as $U = U_D + U_I$, where U_D = the number of direct detections of pikas within 100 m of the site and U_I is the number of indirect detections within the site including both fresh and old sign. The variance in each of these counts was modeled according to a Poisson distribution, using a scale parameter to account for any overdispersion in residuals. Overdispersion was assessed by examining the ratio of unexplained variance (uv , estimated as the scaled Pearson χ^2) to degrees of freedom (df) in a full (parameter-rich) model. If the ratio uv/df was greater than two, we fit a similar model assuming negative-binomial variance in the residuals, using scale parameter $\theta = (uv/df)^{0.5}$ from the full model. Support for the negative-binomial model was determined by likelihood ratio test.

The relative support for different models of the same response variable was determined using an information criterion corrected for small sample sizes, Akaike's information criterion AIC_c , or by $QAIC_c$ (quasi- AIC_c adjusted by scale parameter θ) in cases with evidence for overdispersion in model residuals (Burnham and Anderson 2002). The difference in relative support between models (e.g., ΔAIC_c) was used to differentiate models with good support ($\Delta AIC_c < 2$) from those with relatively weak support ($\Delta AIC_c > 4$) and to calculate the relative support (Akaike weight) for each model as well as the relative support for each predictor X_i as the sum of Akaike weights across models based on X_i .

Collinearity among the candidate predictor variables prompted us to model site-use intensity in three stages. We modeled U first as a function of site biogeography, next as a function of land-cover variables related to forage, and finally as a function of the best predictors identified from analyses of biogeography and forage. For

each analysis, we began with a parameter-rich model based on predictors with little covariance (pairwise $|r| < 0.5$), and used a manual, semibackward selection process to cull predictors.

Microclimatic data were prepared for analysis by removing outliers caused by incident sunlight and issues related to waterproofing. High diurnal temperature records caused by incident sunlight during logger displacements prompted us to omit data recorded by (1) each logger for two hours following data retrieval, and (2) the logger at "Captain Jack's" (Appendix S1) after it was unexpectedly moved to an unshaded position on 8/20/2006. Waterproofing affected records of relative humidity (RH) in two ways: waterproofed H02 loggers recorded few RH values below 23%, and non-waterproofed H08 loggers recorded 100% RH at least once during most days in situ. Therefore, we omitted data from waterproofed loggers when testing for differences among sites Days < 30% RH, and we omitted data from non-waterproofed loggers when testing for differences in Day > 70% RH. We also omitted data from "Valentine Cave" for all statistics influenced by high temperature or low RH, because that site generally was not monitored during summers. Finally, we avoided pseudoreplication by omitting data from a secondary logger at "Blue Grotto" and by averaging data from four loggers at "Rd2CG."

Microclimatic statistics summarized from the remaining data included the number of days with maximum temperature (T) > 28°C, minimum T < -5°C, maximum RH > 70%, and minimum RH < 30%. To test for the effects of waterproofing on these statistics, and for differences in temperature or RH associated with occupancy, we used either the Student's t test or, if parametric assumptions were not met, the Wilcoxon two-sample test. Welch's correction to the Student's t test was applied when an F -test suggested inequality of variances.

RESULTS

We surveyed 156 different sites during 2005–2006, including 143 randomly selected sites and 13 microclimatic monitoring sites. Combining randomly selected and microclimatic monitoring sites, 74 surveyed sites were caves and 82 were not. In summer 2005, 90 sites were surveyed, including 55 caves. In summer 2006, 67 sites were surveyed, including 19 caves. In fall 2006,

Table 2. Relative support for modeled estimates of pika detection probability (p) and site occupancy (ψ) based on data from all primary surveys ($n = 67$) and resurveys ($n = 24$) conducted in 2006.

Model	$k^\dagger$	ΔAIC_c	$w_i^\ddagger$	$p^* \S$ (SE)	ψ Covariate(s)	$\psi^* \S$ (SE)
ψ, p	2	0	1	0.97 (0.03)	...	0.7 (0.06)
ψ (Cave), p	3	0.62	0.73	0.97 (0.03)	Cave	0.59 (0.12)
					Non-cave	0.74 (0.07)
ψ (Class), p	3	1.94	0.38	0.97 (0.03)	Class 3	0.69 (0.08)
					Class 2	0.70 (0.06)
					Class 1	0.72 (0.11)
ψ (Cave, Class), p	4	2.49	0.29	0.97 (0.03)	Cave, Class 3	0.56 (0.15)
					Cave, Class 2	0.59 (0.09)
					Cave, Class 1	0.62 (0.18)
					Non-cave, Class 3	0.72 (0.33)
					Non-cave, Class 2	0.75 (0.43)
					Non-cave, Class 1	0.77 (0.70)
ψ, p (Effort)	3	34.45	0	1.00 (0.00)	...	0.67 (0.06)

Notes: The model with best support (in **bold**) included no covariates of occupancy or detection, while model “ ψ (Cave), p ” included an effect of site type on ψ^* . Class 3 sites were most accessible by road or trail.

† Number of fitted parameters.

‡ Akaike weight, a measure of model support.

$\S$ Estimated values of p and ψ are denoted with asterisks.

50 sites were surveyed, including 25 caves. Twenty-seven sites were surveyed in both years, and 24 sites were surveyed twice in 2006. Most surveys (72%) were conducted in the morning hours.

Site occupancy

Apparent occupancy of these randomly selected sites averaged 45% across years and more than doubled from summer 2005 (27%) to summer 2006 (69%). Pika sign was apparent in 25% of cave sites vs. 29% of non-cave sites in 2005, compared with 58% of cave sites vs. 73% of non-cave sites in 2006. We estimated an exceptionally high detection probability (0.97 ± 0.03 SE) and found no support for an effect of search effort on detection (Table 2).

Although there was good support ($\Delta AIC_c < 2$) for effects of site type and accessibility class on occupancy, the model with highest support included no effects of site type or accessibility (Table 2). Effects of accessibility class aligned with our hypothesis, but occupancy in the most remote sites was only slightly higher (72%) than in the most accessible sites (69%). Effects of site type were contrary to our prediction, with true occupancy estimated at 59% for cave sites vs. 74% for non-cave sites in 2006. At the plot level, cave sites often looked similar to non-cave sites (cf. photos in Appendix S2), but there were

significant differences in biogeography and land cover between site types. A comparison of means for each metric of habitat quality (Appendix S3) suggests that cave sites occurred within smaller patches of lava ($t = -26.18$, $df = 59.47$, $P < 0.001$ for *contigHRs*; $t = -6.70$, $df = 47.00$, $P < 0.001$ for *dist2edge*), and supported higher cover of most vegetation classes ($t = 8.09$, $df = 60.05$, $P < 0.001$ for total vegetative cover; $t = 4.05$, $df = 25.18$, $P < 0.001$ for graminoid cover; $t = 3.19$, $df = 18.75$, $P = 0.005$ for *forb*), excepting only our metrics of shrub cover, which were similar between site types ($t = 0.56$, $df = 64.00$, $P = 0.577$ for *sage*; $t = -1.71$, $df = 50.86$, $P = 0.093$ for *fernbush*). Cave sites occurred at slightly lower elevations (*elevation* mean $\pm$ SE = 1386 ± 12 m for caves vs. 1464 ± 20 m for non-caves; $t = -3.41$, $df = 125.09$, $P = 0.001$). Importantly, we found no difference between cave and non-cave sites in our metric of crevice depth ($t = -1.06$, $df = 65.00$, $P = 0.293$ for *insulation*), but the maximum size of rocks associated with pika sign was somewhat smaller at cave sites (*clast_size* mean $\pm$ SE = 1.06 ± 0.12 m at caves vs. 1.47 ± 0.15 m at non-cave sites; $t = -2.11$, $df = 37.4$, $P = 0.042$).

Patterns in the amount and types of sign detected

The vast majority of our determinations of site occupancy were based at least in part on the detection of a pika by sight or sound: 62%

of detections (20% of surveys) in summer 2005 and 81% of detections (54% of surveys) in summer 2006. A reassuring combination of both direct and indirect sign was observed in 46% of the 67 surveys conducted in 2006. Using the $n = 66$ summer 2006 surveys in which we recorded full counts of the number of different types of sign encountered, some form of direct or indirect sign was detected in 80% of surveys, and only two (3%) of these surveys reported old scat in the absence of other signs. Old scat was reported within 32% of these 66 sites, fresh scat within 65%, and old haypiles within 24%. Fresh haypiles were not reported within any site, in keeping with other pika studies at low elevation (Aho et al. 1998, Simpson 2009, Rodhouse et al. 2010, Jeffress et al. 2013, Varner and Dearing 2014b, but see Millar et al. 2013a).

Although we found no support for an effect of search effort on determinations of occupancy, we did find significant relationships between effort and the detection of indirect sign, and support for effects of search effort and other survey conditions on the amount and type of sign detected. These patterns are illustrated using data from summer surveys in 2006, when we consistently recorded the amount of each type of sign detected.

Occupancy: Longer searches were more likely to result in the discovery of indirect sign. Logistic regression of indirect detection on search effort fit the data well: by the Hosmer and Lemeshow goodness-of-fit test, $P = 0.680$ for summer data ($\text{logit}(p) = -3.77 + 0.19 \times \text{minutes}$, $P < 0.001$, $n = 66$) and $P = 0.684$ for fall data ($\text{logit}(p) = -15.33 + 0.73 \times \text{minutes}$, $P < 0.001$, $n = 50$). Seasonality alone did not explain these results: a logistic regression relating the discovery of indirect signs to survey date was not supported ($\Delta\text{AIC}_c > 15$) relative to the regression based on search effort. However, a model exhibiting positive effects of both search effort and date garnered support ($\Delta\text{AIC}_c = 1.91$). In contrast, the direct detection of pikas by sight or sound was not related to total time spent at a site ($P = 0.26$ by logistic regression; $\Delta\text{AIC}_c = 0.67$ relative to the null model).

Site-use intensity: There was mixed evidence for seasonality in site-use intensity, U . The number of both direct (U_D) and indirect (U_I) signs of site use peaked during early June of 2006. The best (Poisson) model of U_D included significant

linear and quadratic effects of ordinal date ($P < 0.01$ for each effect), and the null model was not supported by the data ($\Delta\text{AIC}_c > 10$). However, a similar (negative binomial) model of U_I included linear and quadratic effects of date that were only marginally significant ($0.07 < P < 0.11$), and the null model exhibited similar support ($\Delta\text{AIC}_c < 1$). Instead, the best model of U_I was based on a positive effect of search effort, similar to the best model of occupancy based on indirect sign. The model of U_I based on date garnered no support ($\Delta\text{AIC}_c > 13$) relative to the model of U_I based on search effort.

The number of direct detections at a site, U_D , was well predicted by the number of indirect signs observed, U_I (Poisson regression, $P < 0.001$). Support for the predictive ability of indirect signs was very strong ($\Delta\text{AIC}_c > 10$ for the null model).

Higher temperatures and higher wind speeds resulted in fewer direct detections, lower U_D . Temperature had the stronger effect (Akaike weight $w = 0.84$ for *temp* and 0.76 for *wind*), but wind speed was a significant ($P = 0.04$) explanatory variable in this multiple regression, despite maximum gusts of just 15 mph. Cloud cover was not a significant predictor of detection in any model tested (all $P > 0.52$), and *skies* ($w = 0.02$) was not supported relative to *temp* and *wind*. Using data from $n = 61$ sites with complete weather data, the top model of direct signs was still based on ordinal date, but the best weather-based model garnered similar support ($\Delta\text{AIC}_c = 1.78$). Date and weather variables were not highly correlated ($0.13 \leq |r| \leq 0.45$; Appendix S4).

Effects of moonlight on U_D were not apparent. There was no interaction effect of moon *phase* and time of *moonrise*, nor univariate effects of *phase* or *moonrise* (all $P > 0.34$ by Poisson regression).

Correcting for effects of survey effort and date on site-use intensity

Being the sum of direct and indirect signs observed at a site, U was affected separately by effects of date on U_D (the observed number of direct signs) and effects of search effort on U_I (the observed number of indirect signs). Therefore, we defined a corrected metric of site-use intensity, U' , as the sum of residuals from Poisson regressions of (1) direct sign on *date* and (2) indirect sign on *effort*, plus a constant to ensure $U' > 0$, for modeling by Poisson

Table 3. Support for various candidate models of pika site-use intensity.

Model set	Model (predictor variables)	<i>k</i>	AIC _c †	ΔAIC _c
Biogeography	<i>aspect, gradient, elevation, insulation, woodrat, visHRs, dist2edge</i>	14	– 490.84	17.04
	<i>elevation, insulation, dist2edge</i>	5	– 507.88	0.00
	<i>elevation, insulation</i>	4	– 506.98	0.90
	<i>elevation</i>	3	– 506.39	1.49
	<i>elevation, dist2edge</i>	4	– 506.36	1.52
	<i>elevation, woodrat, dist2edge</i>	7	– 506.03	1.85
Land cover	<i>forb, gram:chem, litt2soil, rock, fernbush, sage</i>	8	– 516.49	3.01
	<i>forb, gram:chem, fernbush</i>	5	– 519.50	0.00
	<i>forb, gram:chem, fernbush, sage</i>	6	– 518.54	0.96
	<i>forb, gram:chem, rock, fernbush, sage</i>	7	– 518.17	1.33
Biogeography and land cover	<i>elevation, insulation, dist2edge, forb, gram:chem, fernbush, sage</i>	12	– 508.03	7.90
	<i>elevation, insulation, dist2edge, gram:chem, sage</i>	7	– 515.93	0.00
	<i>elevation, insulation, dist2edge, forb, gram:chem, fernbush, sage</i>	9	– 515.67	0.26
	<i>dist2edge, gram:chem</i>	4	– 515.18	0.74
	<i>elevation, dist2edge, gram:chem</i>	5	– 514.54	1.39
	<i>elevation, dist2edge, gram:chem, sage</i>	6	– 514.54	1.39
	<i>elevation, insulation, dist2edge, forb, gram:chem, fernbush</i>	8	– 514.37	1.56
	<i>elevation, insulation, dist2edge, gram:chem</i>	6	– 514.34	1.59
Null	...	2	– 501.61	14.32

Notes: Within each analysis, the model with highest support (in **bold**) has the lowest AIC_c. AIC_c can be compared across model sets within Table 2: in each case, the response variable is site-use intensity (*U'*) based on sites surveyed appropriately in 2006 (*n* = 66).

† ΔAIC_c ≤ 2 for all supported models; aside from full and null (intercept-only) models, models with ΔAIC_c > 2 are not shown.

regression. Correcting for effects of survey *effort* and *date* eliminated significant overdispersion in the response variable, and the set of models with good support was very similar between response variables *U* and *U'*; therefore, we present results only for models of *U'*.

Effects of biogeography on site-use intensity

We first considered models of site-use intensity, *U'*, as a function of site biogeographic variables (Table 1). Strong covariance among biogeographic variables was sparse (Appendix S5), allowing a parameter-rich “full” model (Table 3) that reduced to reveal several biogeographic patterns. First, site use was not explained by either slope *aspect* or slope *gradient*, perhaps because topographic relief was often low at the scale of our sites. Second, although we found fresh sign at both the lowest (1248 m) and highest (1804 m) sites, site-use intensity was positively associated with *elevation*. Third, pikas were more likely to occur where visible crevices appeared to be deeper, suggesting better available *insulation* from the surface climate. Fourth, pika sign was negatively associated with *dist2edge*, suggesting pikas

were more likely to occur near the edges of lava flows.

The best model of *U'* included positive effects of *elevation* ($P < 0.01$) and *insulation* ($P = 0.05$), as well as negative effects of *dist2edge* ($P = 0.08$). Effect signs were as expected and consistent across models in this set. Across all biogeographic models, the best predictor of site use by pikas was *elevation* ($w_i = 0.96$), followed by *dist2edge* ($w_i = 0.64$), and *insulation* (0.59).

No evidence for interspecific competition

We found no evidence for the hypothesized inverse relationship between pika and *woodrat* sign. One well-supported model (ΔAIC_c = 1.85) actually included a positive effect of woodrat presence (class 1 of *woodrat*) on pika site-use intensity. However, we found no support for the predictive ability of additional types of woodrat sign (classes 2 or 3), and woodrat presence garnered relatively poor support ($w = 0.22$) among biogeographic predictors of *U'*. Woodrat sign was positively associated (Appendix S5) with caves, lower elevations, and lava-flow edges. Woodrat sign was also associated with steeper local gradients in the lava, good roads, and more

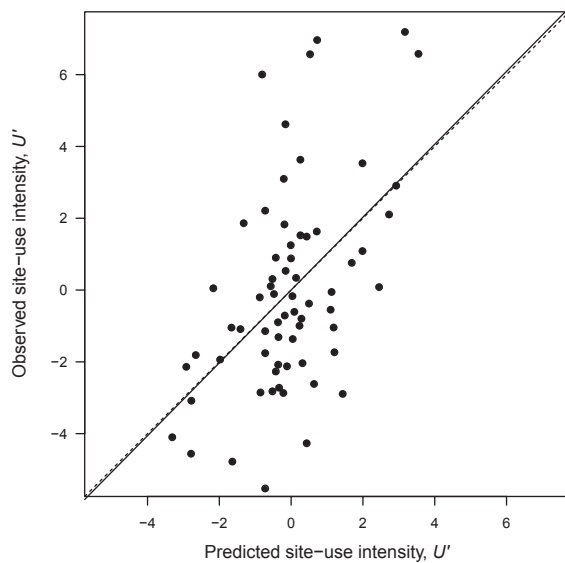


Fig. 3. Site use by the American pika as a function of land-cover variables in Lava Beds National Monument. U' is a metric of site-use intensity corrected for effects of date on the direct detection of pikas and effects of search effort on detection of indirect sign (fresh scat). The model with highest support in Table 3 resulted in a nearly 1:1 (dashed line) relationship between predicted and observed (solid line).

isolated patches of habitat; however, all of these features were also positively associated with caves. Woodrat sign showed no relationship with insulation, and was only slightly more prevalent on north-facing aspects.

Table 4. Effect sign and relative support for biogeographic and land-cover variables used to predict pika site-use intensity during May–July of 2006.

Predictor	$w^\dagger$	Effect sign
<i>gram:chem</i>	0.98	Negative
<i>forb</i>	0.82	Positive
<i>fernbush</i>	0.74	Positive
<i>sage</i>	0.49	Positive
<i>dist2edge</i>	0.16	Negative
<i>elevation</i>	0.12	Positive
<i>insulation</i>	0.08	Positive

† Akaike weight; for predictors not shown, $w \ll 0.01$.

Effects of land cover on site-use intensity

Strong covariance among land-cover variables (Appendix S6) prompted us to reduce the number of predictors a priori, and to construct composite predictors (*gram:chem* and *litter:soil*) to index hypothesized processes. The potential winter forage value of available vegetation (Dearing 1997a) was represented by *gram:chem*, and *litter:soil* separated sites along a continuum from low to relatively high productivity.

The best model of U' based on land cover (Fig. 3) included negative effects of *gram:chem* and positive effects of both *forb* and *fernbush*, and this model garnered far more support than the best model based on biogeography ($\Delta AIC_c = 11.62$ for the best biogeographic model). Across all models in this set, the negative effect of *gram:chem* garnered highest support ($w = 0.98$), followed by positive effects of *forb* ($w = 0.94$), *fernbush* (0.85), and *sage* (0.51); other predictors garnered much lower support ($w < 0.25$).

Table 5. Temperature ($^{\circ}\text{C}$) and relative humidity (RH) recorded within cave and non-cave sites.

Metric	Cave sites		Non-cave sites		$P^\dagger$	$N_{\text{Cave}}^\ddagger$	$N_{\text{Non-cave}}$
	Mean	SE	Mean	SE			
Mean temperature	8.0	0.9	9.4	0.6	0.097	4	8
Days > 28 $^{\circ}\text{C}$	33.0	19.0	97.0	25.8	0.025	4	8
Days < -5 $^{\circ}\text{C}$	14.0	3.6	37.0	7.8	0.020	5	8
Maximum temperature	27.8	4.9	36.8	1.7	0.058	4	8
Minimum temperature	-7.5	1.1	-12.1	0.9	0.003	5	8
Days > 70% RH	241.5	98.5	137.5	11.3	0.242	2	6
Days < 30% RH	204.0	22.3	362.0	63.0	0.032	3	2
Maximum RH	90.0	0.3	86.0	1.8	0.037	2	6
Minimum RH	9.7	1.1	4.5	1.4	0.029	3	2

† One-tailed probability that data loggers at cave and non-cave sites were sampling the same distribution, based on either a parametric t test (mean, maximum, and minimum temperature metrics, Days < 30% RH, and minimum RH) or a non-parametric t test (Days > 28 $^{\circ}\text{C}$, Days < -5 $^{\circ}\text{C}$, Days > 70% RH, and maximum RH; Wilcoxon two-sample test).

‡ Sample sizes varied by statistic due to missing or compromised data for certain sites and seasons (see *Methods: Analyses*).

To determine whether the predictive power of *gram:chem* could be attributed to factors other than forage value, we analyzed a similar full model after replacing *gram:chem* with *veg_complex* (Table 1). The pattern of covariance among forb, graminoid, shrub, and tree cover (Appendix S6) indicated that most sites were dominated either by a graminoid-shrub complex suggesting a more xeric site, or a forb-tree complex suggesting a more mesic site, so *veg_complex* could be interpreted as separating sites more by microclimate than by plant chemistry. The full model based on *veg_complex* achieved an AIC_c score 1.48 units lower than the full model based on *gram:chem*; that is, both full models shared similar support. Across all models in this new set, a negative effect of *veg_complex* garnered highest support ($w = 1.00$), followed by positive effects of *sage* ($w = 0.99$), *fernbush* ($w = 0.93$), and *forb* ($w = 0.63$), while remaining predictors garnered much lower support ($w < 0.10$).

Finally, we considered models of U' as a function of the best biogeographic and land-cover predictors, which exhibited low covariance (Appendix S7). However, these models failed to explain more variation than those based on land cover alone (compare AIC_c values in Table 3). The best predictors of site-use intensity across all models (Table 4) were metrics of vegetation appearing in our best land-cover models.

Microclimatic conditions

Cave sites were relatively cool and mesic, with fewer extremes of temperature than non-cave sites (Table 5). Poisson regression (rescaled due to significant overdispersion) confirmed the negative effect of caves on the number of days above 28°C ($P = 0.04$, $n = 12$) and below -5°C ($P = 0.01$, $n = 13$). These patterns were not affected by waterproofing; data from waterproofed vs. non-waterproofed loggers did not differ in average daily temperature, days above 28°C, days below -5°C, maximum temperature, or minimum temperature recorded (all $P > 0.16$).

There were no significant differences in microclimate between occupied ($n = 7$) and unoccupied ($n = 6$) sites monitored by data loggers (Appendix S8). Notably, however, all observed differences in temperature and humidity were counter to expectations based on other pika studies (e.g., Smith 1974b, Hafner 1993, Grayson 2005, Millar and Westfall 2010, Beever et al. 2011, Varner and Dearing

2014a, Stewart et al. 2015). Sites that were occupied during 2005–2006 tended to experience higher average daily temperatures, more daily highs over 28°C, higher maximum temperatures, more daily lows below -5°C, lower minimum temperatures, lower average RH, fewer daily highs over 70% RH, lower maximum RH, more daily lows under 30% RH, and lower minimum RH during 2004–2006 (Appendix S8). Temperature profiles (Appendix S9) suggested that occupied sites experienced many more days with high temperatures above 16°C, while unoccupied sites experienced many more days with high temperatures between zero and 4°C.

DISCUSSION

Biogeographic and conservation importance of range margins under climate change

The abundant-center hypothesis (Antonovics 1976, Hengeveld and Haack 1982, Brown 1984) suggests that range edges are often where changes in species distributions and abundance occur first or most conspicuously (Thomas 1993). Climate-induced declines often occur at trailing (e.g., southern or low elevation) edges, but may instead track microclimates or non-climate factors (Rapacciuolo et al. 2014). Range-edge populations have been considered for use in genetic engineering and managed relocations (Schwartz et al. 2012), given their putative potential to cope with environmental changes via phenotypic plasticity as a result of accommodating selection under marginal and varied climatic conditions (Bridle and Vines 2007, Sexton et al. 2009). For these reasons, studies of spatio-temporal variation in population distribution and abundance at range margins are important to both basic and applied ecology and conservation.

In contrast with the abundant-center hypothesis, we estimated very high rates of occupancy at an especially low-elevation margin of the American pika's range. Occupancy during the second year of our study was comparable to the highest rates estimated by Jeffress et al. (2013) in a study of eight National Park landscapes that included many sites at much higher elevations than LABE. However, occupancy was also more variable in LABE during our study than during the similar, 2-yr study by Jeffress et al. (2013); occupancy more than doubled during our study, but changed only 3–69% (relative difference)

in the larger study. Pikas have exhibited stable population size in a core portion of their range (Southwick et al. 1986), but can also suffer high mortality (Kreuzer and Huntly 2003) and high turnover in occupancy (Jeffress et al. 2013). Therefore, our study suggests that abundance might be especially variable at a range margin, consistent with the abundant-center hypothesis.

Our estimates of occupancy depended in part on visual estimation of scat age, a technique recently used by others (e.g., Jeffress et al. 2013, Erb et al. 2014). Although Millar et al. (2014a) and Nichols (2010) demonstrated that old scat can persist for decades, Nichols (2010) provided compelling evidence that fresh pika scat ages quickly in a dry climate, supporting the use of fresh scat as a metric of recent site use. To age scat, we used destructive sampling, opening pellets to observe color (fresh chlorophyll) and consistency (moisture level). Several lines of evidence increase our confidence in this approach. First, we observed good overlap in our metrics of direct and indirect sign at each site, as reported above. Second, we observed strong dynamics between years in the amount of fresh scat observed. If old scat could be mistaken for fresh, dynamics should be attenuated because a fluctuating population could leave enough scat in years of high occupancy to obscure years of low occupancy. Unfortunately, because we observed higher occupancy in the second year of our study, it can be argued that our study began at the end of a period of depressed occupancy. However, using similar survey methods in another lava park (Craters of the Moon National Monument), Jeffress et al. (2013) observed a decline in occupancy from 21% to 7% over 1 yr, suggesting that 1-yr-old scat can be distinguished from fresh scat in lava landscapes. Third, our destructive sampling in summer 2006 removed scat from sites resurveyed in fall 2006, and yet fresh scat was found in all previously occupied sites that were resurveyed. While inconclusive, these lines of evidence increase our confidence in aging scat. Moreover, our focus on the relationship between habitat quality and site-use intensity should be robust to some degree of error in scat age; it makes little difference whether the habitat affinities we demonstrate apply to 2005–2006 or to a somewhat broader range of years. Finally, while our estimates of site occupancy, ψ , depend critically on accurate

estimates of sign age, any error in ψ due to errors in age should apply to both cave and non-cave sites. Therefore, problems with aging scat were not likely to affect our conclusion that pikas did not prefer ice caves.

Occurrence in anomalous microhabitats

Caves were located in smaller patches of lava at slightly lower elevations than non-cave sites, which might have resulted in biogeographic effects on occupancy patterns. However, site-use intensity was not especially affected by metrics of patch size, isolation, or elevation. Cave sites also supported more soil and vegetation, being located within an older lava flow surrounding the relatively barren flows that contained most of our non-cave sampling sites (Appendix S10, Donnelly-Nolan 2010). Although cave and non-cave sites offered crevices similar in depth, providing presumably similar shelter from climate and predators, the vegetation surrounding cave sites may have had an isolating effect, reducing immigration to these sites. In that case, site-use intensity should have declined with soil and vegetation cover, another result not supported by our analysis. A final scenario congruent with high occupancy at both cave and non-cave sites might be a source-sink effect (Pulliam 1988) in which emigration from cave sites had filled non-cave sites. However, occupancy was always higher in non-cave sites, especially in the year of highest overall occupancy. This result seems particularly surprising because cave microclimates were relatively cool and mesic, while the macroclimate at LABE is consistently hotter and drier than in the adjacent Great Basin at sites where pikas have been completely extirpated (Beever 2002). The persistence of pikas at LABE and the prevalence of pikas in non-cave sites suggest additional hypotheses related to microrefugia and thermoregulation. We consider three hypotheses here.

First, the non-cave portions of these lava beds might provide small animals such as pikas with sufficient microrefugia from the macroclimate. As in taluses, creviced lava can support cold-air pooling, seasonal Balch effects (persistent pools of dense, cold air), and evaporative cooling (Millar et al. 2014b). Thus, it seems likely that the persistent ice found in lava tubes throughout LABE also occurs deep in many smaller crevices,

as in other lava landscapes (Loney 1968). The high sub-surface humidity so frequently recorded by our non-waterproofed loggers might reflect evaporation from sub-surface ice features, which would contribute to evaporative cooling of the lava matrix and could be one of the several processes that might maintain a cool microclimate for pikas (Millar et al. 2014b). The process driving the pika's association with sub-surface ice features (Hafner 1994, Millar and Westfall 2010) remains unclear, but one mechanism was suggested by a recent study comparing levels of physiological stress in pikas at two adjacent sites: stress was much lower where pika territories were underlain by ice (Wilkening et al. 2015). Just as the structure of talus landforms can provide critical habitats by buffering air temperatures and preserving sub-surface water resources (Millar et al. 2013b), lava beds might offer increasingly important microhabitats in a warming climate.

The microclimates available deep in pika-sized crevices are just now being characterized for lava landscapes (Millar et al., *in press*). At our sites, data loggers were positioned in near-surface locations. A logger in the mouth of a cave is likely bathed in the relatively cool and mesic air "exhaled" daily. At non-cave sites, it is much less likely that cool air from deep crevices would be channeled past a logger near the surface. Thus, we may have simply missed the presence of cooler microclimates in non-cave sites. Characterizing the microclimates available to climate-sensitive species is an important challenge for projecting species ranges (Ashcroft et al. 2012, Franklin et al. 2013, Potter et al. 2013, Varner and Dearing 2014a, Millar et al. 2015).

Second, pikas might manage their exposure through behavioral thermoregulation (MacArthur and Wang 1973, Smith 1974b), becoming more crepuscular or nocturnal in LABE than in other parts of their range (e.g., Varner et al. 2016). In this case, we might expect to observe effects of moonlight on pika detection. Moonlight affects the nocturnal activity of some mammals (e.g., Orrock et al. 2004, Upham and Hafner 2013), including lagomorphs (Griffin et al. 2005). Although *O. princeps* is considered diurnal, nocturnal vocalizations have been reported, especially in warmer habitats (e.g., Smith 1974b), and we hypothesized that moonlight-mediated activity

levels during the night could affect pika surface activity and detection on the following day. We found no evidence of an effect of moonlight on detection, but our methods did not account for nocturnal cloud cover, which could obscure a relationship between potential moonlight and pika activity.

Third, the thermal tolerance of pikas in LABE might differ from conspecifics elsewhere, through local adaptation to warmer summers. Recent results suggest adaptive genetic variation in the American pika along a gradient in temperature (Henry and Russello 2013), and temperature-related variation in physiological stress (Wilkening et al. 2015) suggests a mechanism for selection along these gradients. Although gene flow between populations in LABE and surrounding habitats has not been characterized, adaptation in marginal populations is expected even in the presence of significant gene flow from populations in less marginal environments (Holt and Gomulkiewicz 1997).

Occupancy and the potential for anthropogenic disturbance

Occupancy of the most remote sites was only slightly higher than occupancy of the most accessible ones. The magnitude of this effect might have been diminished by the fact that high-occupancy edge habitats are commonly near roads and trails, which tend to follow flow edges (Fig. 2). Aside from the potentially confounded occurrence of flow edges and roads/trails, LABE would be an especially suitable landscape for testing effects of anthropogenic disturbance on pika occurrence. The lava beds are extremely difficult to navigate off trail, so the isolation of pikas in the least accessible class is virtually assured. But it is unlikely that LABE pikas are sensitive to anthropogenic disturbance, given other observations. *O. princeps* are well known along hiking trails across western North America, and have been reported to inhabit road cuts, rock quarries, riprap along rivers, and stone walls (Aho et al. 1998, Millar and Westfall 2010, Manning and Hagar 2011). Livestock grazing is the only anthropogenic disturbance suggested to affect pika occurrence (Beever et al. 2003, 2013, Millar 2011), although direct competition between pikas and livestock is unlikely in most situations (Beever et al. 2010).

Biogeography of site-use intensity

Site variables related to biogeography were not well-supported after accounting for effects of local land cover. However, it is informative to compare the effects of our most predictive biogeographic variables with the effects of similar predictors from other studies.

Elevation, lava depth, and an edge effect were the most predictive variables in our biogeographic model set. The edge effect, indexed by *dist2edge*, suggested that site use was higher near the periphery than within the interior of a lava bed. The consistently negative coefficient of *dist2edge* supports the hypothesis that pikas use mainly the edges of their rocky habitats (Smith 1974a), presumably for ease of access to forage (Huntly et al. 1986).

Given the limited range of elevations surveyed (1248–1804 m), it is perhaps surprising that we found a significant effect of elevation on site use by pikas, especially since fresh sign was found even at the lowest elevation surveyed (1248 m). However, a similar effect of elevation was observed in low-elevation (1301–1985 m) lava beds at Craters of the Moon National Monument (CRMO) in southern Idaho (Rodhouse et al. 2010). In CRMO, occupancy rose strongly with elevation above ~1600 m, the lowest occupied elevation. The effect of elevation in CRMO was well supported even after accounting for the effects of vegetation cover, and was congruent with previous work on pika biogeography; the lowest occupied habitats were just inside Hafner's (1993) elevational envelope for pikas at the latitude and longitude of CRMO. In LABE, where we found pikas well below Hafner's envelope, the effect of elevation was not supported after accounting for effects of cover. This distinction between LABE and CRMO might be due to differential effects of elevation on a third factor, such as the distribution of sub-surface ice. For example, if the lava beds at LABE are especially effective at decoupling surface from sub-surface temperatures so as to preserve more sub-surface ice, then perhaps sub-surface temperatures or water resources are less dependent on elevation at LABE than in other lava landscapes.

Within CRMO, pikas were most likely to occur in sites that exhibited more structural complexity, including lava depth (Rodhouse et al. 2010).

Similarly, we found a direct effect of lava depth (*insulation*) on site-use intensity within LABE. This significant effect of lava depth might be even more important than suggested by our analyses, because depth is inherently difficult to measure. Our proxy, the minimum depth of the deepest crevice, is likely estimated with great error (as discussed by Jeffress et al. 2013) because these crevices tend to meander out of view. Montane talus, the more typical habitat of the American pika throughout its range, appears to be less complex than these lava beds, which may explain why low-elevation lava habitats act as interior edge (range margin) refugia (see also Shinderman 2015). Even within these lava-dominated landscapes, pikas appear to have been lost from taluses. Although old fecal pellets and old haypiles were observed in LABE taluses on Gillem's Bluff in 2005, subsequent surveys have never uncovered fresh sign. The loss of pikas from taluses adjacent to occupied lava beds suggests that only lava habitats continue to harbor refugial microclimates at these low elevations. Refugial microclimates may be an important determinant of species range that is not accounted for in typical species-distribution modeling (Potter et al. 2013, Varner and Dearing 2014a).

Evaluating the potential for interspecific competition

Woodrat sign was positively associated with caves, suggesting that competition might have reduced pika use of cave sites. However, contrary to our hypothesis of direct or apparent competition between these species, site use by pikas was positively associated with the "whitewash" resulting from woodrat urine. Importantly, this positive association between pika sign and whitewash was not improved by considering additional types of woodrat sign (scat or middens). Therefore, we suggest that pikas and woodrats prefer similar microhabitats (often conveniently marked by whitewash), but we do not suggest that pikas prefer to use sites currently occupied by woodrats. Further analyses are needed to determine whether pikas and woodrats are truly syntopic in low-elevation lava beds. Impacts of contemporary climate change on interspecific interactions remain an understudied research frontier (Stenseth et al. 2015).

Vegetation as a predictor of site-use intensity

Pika site use was best predicted by characteristics of the available vegetation, including forb and graminoid cover as well as indices involving specific shrubs and a metric of the dominant vegetation complex. The importance of vegetative characteristics might indicate the importance of forage quality for pika persistence (Erb et al. 2014). However, it is also possible that pikas influence the composition of the plant community (Huntly et al. 1986, Roach et al. 2001, McIntire and Hik 2005), or that site microclimate drives plants and pikas in parallel (Wilkening et al. 2011, Erb et al. 2014). Here, we consider the evidence for each of these potentially interacting processes.

The plant community at a site might reflect microclimatic conditions or sub-surface water resources that affect site use by pikas. Each of the supported models linking pikas and vegetation in LABE was in keeping with the hypothesis that pikas prefer relatively mesic sites within their rocky habitats (Hafner 1993). Although our predictor variables represent imperfect metrics of the qualities we would like to quantify, it is worth noting that support for our metric of vegetation complex was even higher than support for our metric of forage quality. After accounting for an effect of the vegetation complex, fern-bush and big sagebrush were important positive predictors of pika sign. In xeric sites, an association with shrubs can indicate a preference for mesic microhabitats, because shrubs increase soil moisture through shading and hydraulic lift (Caldwell et al. 1998). Additional support for parallel effects of microclimate on plants and pikas comes from other studies. Results from the Great Basin indicate that vegetative productivity alone, without reference to forage quality, can predict pika abundance and density (Beever et al. 2013). Pikas at very low elevations in the Columbia River Gorge, where winters are quite mild, forage primarily on low-nutrient mosses (Varner and Dearing 2014b), also suggesting the primacy of microclimate as a driver of broad-scale patterns in pika distribution.

Arguments for effects of forage quality on the American pika's distribution come from studies conducted at higher elevations where seasonality is extreme. In alpine environments, pikas are predicted to benefit from season-specific diets,

grazing on graminoids during the growing season while caching a winter diet of forbs and other plants higher in secondary compounds. Fresh graminoids are relatively digestible, whereas plants higher in secondary compounds become increasingly digestible during storage, and retain nutrients longer after harvest (Dearing 1997b). Graminoids are also smaller, so caching a given volume of graminoids would require more energy expenditure (and exposure to predation) than caching the same volume of forbs (Huntly et al. 1986). Dearing's (1997b) demonstration of pikas manipulating plant toxins to optimize forage quality involved a population living above 3500 m in the southern Rocky Mountains. More recent studies link selective foraging to pika density throughout the entire southern Rocky Mountain region. In this region, pikas selectively cache plants higher in nutrients, especially where higher summer temperatures should curtail caching activities (Smith and Erb 2013), and sites with a higher diversity and cover of forbs exhibit higher pika densities (Erb et al. 2014).

Pika occupancy has also correlated positively with forb cover and negatively with graminoid cover in other environments (Wilkening et al. 2011, Jeffress et al. 2013, Erb et al. 2014), including the lava beds at CRMO (Rodhouse et al. 2010). Although the positive association with forbs is likely a robust indicator of pika habitat preference (Rodhouse et al. 2010, Wilkening et al. 2011, Erb et al. 2014), interpreting the negative association with graminoids is complicated (Rodhouse et al. 2010) because selective summer grazing (Johnson 1967, Dearing 1997b, Smith and Erb 2013) might reduce graminoid cover (Huntly et al. 1986, Roach et al. 2001). Given the low level of caching activity observed in our study, LABE pikas might forage mainly on graminoids, resulting in a negative relationship between site-use intensity and graminoid cover. However, because graminoid cover also varies inversely with pika occurrence in alpine habitats, where cached forbs should be the primary forage, we hypothesize that pikas select rather than create habitats lower in graminoid cover.

Cahill et al. (2013) cited food-resource decline as the most common mechanism through which contemporary climate change has caused extirpations. For the pika and perhaps many species, it is important to consider whether climate-mediated,

indirect effects of food-resource decline are confounded with direct effects of climate, and whether a high-quality food resource can mitigate the effects of climate (Erb et al. 2014).

The conspicuous absence of fresh haypiles throughout LABE during our study also deserves consideration as an indication of declining site use or a shift in foraging behavior. The haypiles we observed appeared old in that they contained very dry hay lacking in color (chlorophyll), but some of these dry and colorless haypiles also appeared fresh in that they had not been broken down by precipitation, wind, animal, or microbial activity. Perhaps haypiles at LABE appear dry and colorless at or soon after harvest due to high surface temperatures. Surface temperature might also explain the apparent rarity of haypiles, if it causes LABE pikas to hide their hay in cooler spaces beneath the surface.

Temporal patterns

Our study was bracketed by LABE pika surveys conducted in 1995 (Beever 2002) and 2010–2011 (Jeffress et al. 2013). Surveys in 1995 targeted 15 sites with historical records of pika presence, including several caves. Each site (up to 100 m in radius) was searched for up to 2.5 h or until a pika was detected, resulting in 10 total pikas detected (by sight or sound) within eight sites (Beever 2002). Our random sample in 2005–2006 included only three of these sites (all caves). Within our plots (12 m in radius), we found continued occupancy at one of these sites, extirpation at the second, and colonization at the third, using 1995 occupancy as a baseline. The 1995 survey was based on sites historically occupied, so the occupancy determined from those sites (about 0.5) should be biased high relative to a random sample of suitable habitats.

Surveys in 2010–2011 (Jeffress et al. 2013) were completed on 101 sites each year, including 42 sites surveyed in both years, and employed a protocol similar to our 2006 surveys, except that cave sites were not sampled. Pikas occupied 24% of sites in 2010 and 29% in 2011, with turnover on 12 (28%) of 42 resurveyed sites (seven moving from presence to absence, and five conversely). The pattern of pika occupancy observed in 2010–2011 was similar to that in Fig. 2 except for higher occupancy in the southwest corner of the

park, which might have been related to higher sampling density. Accounting for resurveys, the number of unique sites sampled was similar in 2005–2006 ($n = 156$) and 2010–2011 ($n = 160$), but the sampled area was smaller and sampling density was higher in 2010–2011 because the sampling frame excluded sites > 1 km from roads. Given the slightly higher occupancy we observed at sites > 1 km from roads, occupancies estimated in 2010–2011 might be biased low relative to a random sample of suitable non-cave habitats, and (because caves were not sampled) these estimates of occupancy cannot be extrapolated to cave sites. Because of the random component to survey site selection in both studies, there was no significant overlap in sites surveyed.

However, given our model of occupancy as a function of site type and accessibility (Table 2), and given that our estimate of high detection probability should apply to the similar sampling protocol of 2010–2011 (Jeffress et al. 2013), we can compare occupancies across 2005–2011. For 2006, we estimated occupancy at $\sim 74\%$ across non-cave sites < 1 km from roads (classes 2 and 3 in Table 2). Comparing 74% in 2006 to 24–29% in 2010–2011 suggests a decline in occupancy of non-cave sites equivalent to the increase we observed from 2005 to 2006; in 2005, the observed occupancy of non-cave sites was 29%, which translates to 27–28% after accounting for the positive effect of including remote sites in our sample. Aside from these simplistic comparisons, any evaluation of trends in pika occupancy at LABE awaits data from comparable surveys or the development of a modeling framework that can harness the disparate data from 1995 to 2011 to infer the temporal process.

Broader implications

At a range margin where climate lies outside the norm for a species' range, that species might appear to occupy an anomalous extension in its bioclimatic envelope. However, upon characterization of microclimates, the conditions experienced by animals in these peripheral locations might be found to be comparable to conditions experienced near the center of the species' geographic range (Varner and Dearing 2014a). In our example, the American pika appears to occur (and persist: Jeffress et al. 2013) at much lower elevation in this lava landscape than is otherwise predicted by latitude and

longitude. Our study, consistent with others addressing the biogeography of this species, suggests that this apparent extension of the pika's envelope can be explained by access to high-quality forage, or by access to the microclimates that produce high-quality forage. Further characterization of the microclimates in this complex landscape will be needed to determine whether the dimensions of the bioclimatic envelope must be adjusted to explain the occurrence of pikas at this range margin.

Understanding anomalous extensions of a species' bioclimatic envelope will aid in projecting effects of climate change and guiding conservation efforts (Pearson and Dawson 2003, Smith and Nagy 2015). Failing to recognize that a species' occurrence is mediated by a microclimate will result in over-predicting species presence or persistence. Accurate projection also involves accurately characterizing relationships between climate and microclimate (Franklin et al. 2013), especially for microclimatic specialists such as the many burrowing and saxicolous animals. We have outlined some of the challenges involved in characterizing species-relevant microclimates (Potter et al. 2013) in lava bed landscapes. Further study of the American pika in these habitats could elucidate important mechanisms underlying species persistence in anomalous circumstances.

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