

# The idiosyncrasies of place: geographic variation in the climate–distribution relationships of the American pika

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**Abstract.** Although climate acts as a fundamental constraint on the distribution of organisms, understanding how this relationship between climate and distribution varies over a species' range is critical for addressing the potential impacts of accelerated climate change on biodiversity. Bioclimatic niche models provide compelling evidence that many species will experience range shifts under scenarios of global change, yet these broad, macroecological perspectives lack specificity at local scales, where unique combinations of environment, biota, and history conspire against generalizations. We explored how these idiosyncrasies of place affect the climate–distribution relationship of the American pika (*Ochotona princeps*) by replicating intensive field surveys across bioclimatic gradients in eight U.S. national parks. At macroecological scales, the importance of climate as a constraint on pika distribution appears unequivocal; forecasts suggest that the species' range will contract sharply in coming decades. However, the species persists outside of its modeled bioclimatic envelope in many locations, fueling uncertainty and debate over its conservation status. Using a Bayesian hierarchical approach, we modeled variation in local patterns of pika distribution along topographic position, vegetation cover, elevation, temperature, and precipitation gradients in each park landscape. We also accounted for annual turnover in site occupancy probabilities. Topographic position and vegetation cover influenced occurrence in all parks. After accounting for these factors, pika occurrence varied widely among parks along bioclimatic gradients. Precipitation by itself was not a particularly influential predictor. However, measures of heat stress appeared most influential in the driest parks, suggesting an interaction between the strength of climate effects and the position of parks along precipitation gradients. The combination of high elevation, cold temperatures, and high precipitation lowered occurrence probabilities in some parks, suggesting an upper elevational limit for pikas in some environments. Our results demonstrate that the idiosyncrasies of place influence both the nature and strength of the climate–distribution relationship for the American pika. Fine-grained, but geographically extensive, studies replicated across multiple landscapes offer insights important to assessing the impacts of climate change that otherwise may be masked at macroecological scales. The hierarchical approach to modeling provides a coherent conceptual and technical framework for gaining these insights.

**Key words:** American pika; Bayesian hierarchical model; climate change; conservation; national parks; occupancy; *Ochotona princeps*; place-based contingencies; presence–absence; sign surveys; turnover.

## INTRODUCTION

The relationship between climate and the distribution of organisms is of central importance to ecology. The fact that climate constrains species' ranges has long been appreciated (e.g., Andrewartha and Birch 1954), but is of renewed importance in the current era of accelerated climate change, which increasingly is seen as the primary

threat to biodiversity and ecosystem function in many regions of the globe in the coming decades (IPCC 2007). Understanding and forecasting the effects of climate change on biota and other natural resources has become an overriding concern for conservation biologists and managers of parks and protected areas (Millar et al. 2007, Heller and Zavaleta 2009, Littell et al. 2011). In the western United States, where the conservation reserve system is disproportionately representative of high-elevation ecosystems (e.g., Wiens et al. 2011), it is especially important to describe patterns of distribution for high-elevation biota along bioclimatic gradients and to project how those distributions are likely to change. Projections made at macroecological scales using climate

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niche models show that many species are likely to lose ground or shift distribution poleward or upward in elevation during this century (Thomas et al. 2004, Thuiller et al. 2005, Lawler et al. 2009). Indeed, many species have already begun to shift their distributions, with pronounced responses among range-restricted species including those in high-elevation mountainous terrain (Parmesan 2006). However, these broad macroecological perspectives lack specificity at local scales, where the unique combinations of environment, biota, and history conspire against generalizations (Pearson and Dawson 2003, Willis and Bhagwat 2009). Such “idiosyncrasies of place” (sensu Billick and Price 2010) can influence contemporary distribution patterns as much as or more than regional climatic factors alone. In particular, predictions of range contraction based on climate factors may be overstated when local environmental conditions experienced by individuals and populations are not considered (Mackey and Lindenmayer 2001, Pearson and Dawson 2003, Willis and Bhagwat 2009, Austin and Van Niel 2011). Identifying the idiosyncrasies of place and the contingencies that they create in otherwise predictable (or at least expected) climate–distribution relationships should reveal insights into the mechanisms underlying contemporary biogeographic patterns that are masked at coarse macroecological scales. These insights, in turn, can be used to improve models of future distributional change and the interpretations and assessments drawn from them.

An important example of where idiosyncrasies of place appear to be influential is in the interpretation of climate–distribution models developed for the American pika (*Ochotona princeps* Richardson 1828). This species has received considerable attention for its potential vulnerability to climate change in high-elevation ecosystems of the western United States and southwestern Canada (Beever et al. 2003, Krajick 2004, Smith et al. 2004). The status of the American pika was recently reviewed by the U.S. Fish and Wildlife Service, which found insufficient evidence for a threat of species extinction within the foreseeable future (Crist 2010). Subsequent studies have disagreed regarding the evidence for contemporary range contraction induced by accelerated climate change (Beever et al. 2010, 2011, Millar and Westfall 2010a, b, Wolf 2010). Range-wide studies using climate niche models indicate that the species is likely to experience substantial range contraction in the coming decades as temperatures increase and precipitation decreases (Galbreath et al. 2009, Calkins et al. 2012). At finer scales, evidence for contemporary range contraction has come primarily from the Great Basin (Beever et al. 2003, 2010, 2011, Wilkening et al. 2011), but in other regions the evidence is less clear (Moritz et al. 2008, Millar and Westfall 2010a, b, Erb et al. 2011) and there are numerous locations where the species persists outside of its modeled bioclimatic envelope (Beever et al. 2008, Simpson 2009, Millar and Westfall 2010a, Rodhouse et al. 2010, Manning and

Hagar 2011). Interestingly, when modeling ecological niches and predicting geographical distributions between the Last Glacial Maximum and the present in their longitudinal study of niche conservatism in mammals, Martínez-Meyer et al. (2004) found that models developed with mean annual precipitation and temperature inputs had the lowest predictivity for American pika distribution among the 23 species that they considered.

The American pika is an obligate denizen of sparsely vegetated talus and lava flows and reduces its exposure to hostile temperatures by remaining below the surface for long periods of time (MacArthur and Wang 1974, Smith and Weston 1990). This ability to behaviorally thermoregulate is affected by local habitat conditions and is a likely explanation for some of the variation observed in the species’ pattern of distribution along climate gradients. Several studies have found that substrate characteristics and topography can drive variation in distribution and demographic rates of the American pika (Kruezer and Huntly 2003, Millar and Westfall 2010a, Rodhouse et al. 2010) as well as of the congeneric collared pika (*Ochotona collaris*; Morrison and Hik 2007). If these local characteristics of sites mediate the impacts of climate, they will also substantially influence how predictive distribution models perform for this species. This is a particularly important consideration for the American pika, perhaps outweighing other considerations such as loss of talus and lava flow habitats (thought to be stable over ecological time scales), and species interactions, which have not been shown to strongly influence patterns of American pika occurrence (Smith and Weston 1990; but see Clinchy et al. 2002). Martínez-Meyer et al. (2004) and Calkins et al. (2012) recognized this problem in their attempts to model American pika range dynamics over time and acknowledged the need to incorporate more habitat-specific information.

In this study we explore how the idiosyncrasies of place affect the climate–distribution relationship of the American pika, and whether there are place-based contingencies that have broader significance for evaluating American pika vulnerability to accelerated climate change. Specifically, we ask whether the patterns of American pika distribution covary with climate consistently across the species’ range after accounting for local site characteristics. To examine this question, we replicated intensive field surveys during 2010–2011 across eight large U.S. National Park Service units from the Rocky Mountains to the Cascade Range. Using the data from these replicated surveys, we modeled pika site occurrence probabilities along regional bioclimatic and local topographic and vegetation gradients. Our study is both fine-grained and geographically extensive, representing a substantial portion of the species’ range and habitat types. Because over-winter mortality and annual turnover in pika territory occupancy can be high (Smith 1980, Peacock and Smith 1997, Kruezer and Huntly

2003), we explicitly addressed turnover dynamics by modeling occurrence probabilities in year 2, not only as a function of local site characteristics and regional climatic factors, but also conditioned on site occupancy in year 1.

We used a hierarchical approach to modeling and inference that reflects the hierarchy of our study design, in which plot observations are nested within parks. It provides a coherent conceptual and technical framework for handling the multiple sources of variation and error inherent in large-scale, replicated field studies (Cressie et al. 2009). Such an approach has been recommended for tackling the species distribution modeling problem, although it is not yet widely implemented (Mackey and Lindenmayer 2001, Pearson and Dawson 2003). Our models were structured so as to simultaneously estimate within-park regression coefficients for bioclimatic variables and global among-park means and variances (hyperparameters) for those variables, a strategy referred to as “partial pooling” of the data set and also known as multilevel or random-effects modeling (Gelman and Hill 2007). Partial pooling of data from multiple park landscapes provides a regional context for interpreting the estimated effect sizes for individual park study areas and provides a more complete accounting of uncertainty than if parks were analyzed separately (unpooled) or if among-park variation were ignored (completely pooled; Gelman and Hill 2007). It reflects our expectation that our plot-based observations of pika occurrence will be more similar within parks than among parks, and it provides an efficient and direct way to evaluate the variation in the climate–distribution relationships of the American pika across the eight park study areas.

## METHODS

### *Study areas*

Our research was conducted at randomly selected sites in eight U.S. National Park Service units in six states: Crater Lake National Park (CRLA) in Oregon, Craters of the Moon National Monument and Preserve (CRMO) in Idaho, Grand Teton National Park (GRTE) in Wyoming, Rocky Mountain National Park (ROMO) and Great Sand Dunes National Park and Preserve (GRSA) in Colorado, Lassen Volcanic National Park (LAVO) and Lava Beds National Monument (LBE) in California, and Yellowstone National Park (YELL) that spans portions of Montana, Idaho, and Wyoming (Fig. 1). These parks represent a substantial portion of the species’ range and provide a broad range of pika habitat types, including large basalt lava flows and montane talus and boulder fields. Sites surveyed ranged from 1249 to 3987 m in elevation and spanned a latitudinal range of more than 7 degrees (37.7–45.1° N) and a longitudinal range of more than 16 degrees (105.5–122.2° W). Long-term average annual precipitation of sites ranged from 23 to 308 cm and the average maximum July temperatures for sites ranged from 13.5°

to 29.8°C (both estimated from 1971–2000 PRISM data, *available online*).<sup>7</sup> See Table 1 for a comparison of park characteristics.

### *Sampling design*

We used the Generalized Random Tessellation-Stratified (GRTS) algorithm to generate a spatially balanced random sample of survey locations for each park (Stevens and Olsen 2004, Rodhouse et al. 2010, Jeffress et al. 2011). Spatially balanced designs allow sample unit additions and deletions while maintaining statistically valid scopes of inference across sample frames (Stevens and Olsen 2004). The random draw was done independently for each park from sampling frames of mapped potential pika habitat. Potential pika habitat maps were created in a GIS using existing talus and lava habitat map layers, vegetation maps, and aerial imagery (see Appendix A for individual park maps). Each park presented unique survey challenges, including habitat map inaccuracies, travel restrictions and hazards, and other constraints. Due to these challenges, surveys in six parks (CRLA, CRMO, GRTE, LBE, LAVO, and YELL) were restricted to areas of mapped potential habitat within 600–1000 m of roads and/or trails, stratified by elevation and, in the case of CRMO, by lava type (*pahoehoe* or *aa*), which was previously found to influence pika distribution in that park (Rodhouse et al. 2010). Additionally, in two parks (GRSA and ROMO), a travel cost–surface model was used to adjust sample unit inclusion probabilities by distance to roads and trails as well as terrain. For all parks, slopes >35° were excluded from sampling frames due to safety concerns. Although our sampling frames were biased toward roads and trails for practical reasons, previous investigations (Rodhouse et al. 2010) and exploratory analysis for this study found no evidence that pika occurrence probabilities were biased away from roads and trails (Appendix B).

### *Survey methods*

Using a modified version of the survey methods used by Rodhouse et al. (2010) and further developed by Jeffress et al. (2011), we surveyed 1172 sample units (hereafter “sites”) for signs of pika occupancy from late June to early November in 2010 and 2011, although specific dates varied by park. In 2011, we resurveyed 265 sites first surveyed in 2010 to provide information on annual turnover. Project resources prevented us from resurveying more sites. Table A1 in Appendix A provides a breakdown of surveys by park.

Sites were 12 m radius plots centered on the random location drawn from the GRTS algorithm. Mapping errors resulted in some sites being empty of targeted potential habitat, and we established a priori a minimum criterion that sites must contain  $\geq 10\%$  target habitat,

<sup>7</sup> [www.prism.oregonstate.edu](http://www.prism.oregonstate.edu)

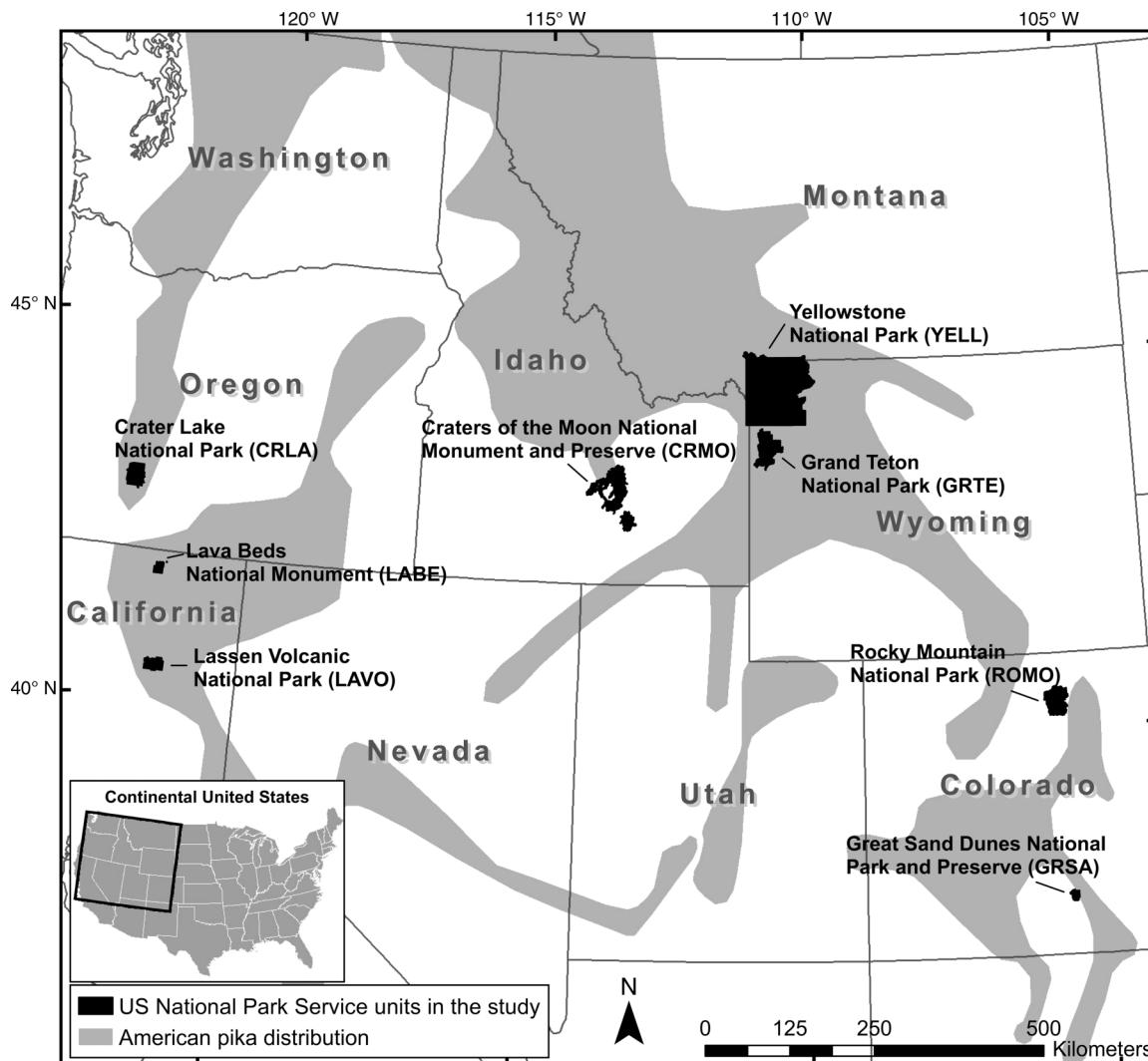


FIG. 1. Locations of the eight national park units in this study, in relation to the range of the American pika in the western United States (Beever and Smith 2011).

defined as creviced rock that could provide shelter for pikas. Sites that did not meet this criterion (e.g., scree slopes with no rocks >6 inches [15.24 cm] in diameter) were offset a random direction and distance ≤50 m from the original plot center (if sufficient target habitat was available within 50 m), or were dropped (if insufficient target habitat was available within 50 m) and replaced from the list of oversamples provided from the GRTS sample.

Sites were thoroughly searched for signs of current pika occupancy, beginning with a 5-min period of silent observation to increase opportunities for visual and aural detections, followed by a minimum of 15 minutes of active searching for pika sign. A site was considered occupied if any of the following were encountered within the plot: pika(s) seen or heard; fresh pika scat (round fecal pellets); and/or fresh pika “hay” (food cache). Scat

was considered fresh (<1 year old) if dark green or dark brown in color, containing greenish plant material when opened, and/or if cemented to a rock by urine or dried mucus in small groups of 2–50 pellets; in contrast, scat was considered >1 year old if grayish outside, lacking greenish color inside, and scattered (Nichols 2010, Rodhouse et al. 2010, Jeffress et al. 2011). Surveyors attended group training sessions designed to calibrate sign aging and other field methods at the start of each season and were provided with a detailed manual as well as photos of scat and hay of known age. Although old scat and hay have been noted to persist for very long times in arid and alpine environments, the indications of fresh pika sign (e.g., green color of plant tissue) have been shown to disappear from scat and hay of known age after several months (Nichols 2010).

TABLE 1. Comparison of climate variables (mean, with range in parentheses) at national park units where pika occupancy was studied; see Fig. 1 for full names of the parks.

National Park study unit	$T_{\max}$ (°C)	$T_{\min}$ (°C)	Warmest quarter (°C)	Precipitation (cm)	Elevation (m)
CRLA	19.8 (17.3 to 23.9)	-7.7 (-6.4 to -8.8)	10.5 (8.5 to 13.0)	156.7 (104.5-183.1)	2115 (1701-2530)
CRMO	28.9 (28.1 to 29.8)	-13.6 (-15.2 to -12.34)	17.4 (16.4 to 18.1)	32.7 (23.1-37.4)	1700 (1511-1833)
GRSA	18.6 (15.6 to 25.1)	-15.6 (-17.9 to -11.9)	9.2 (6.1 to 15.1)	86.2 (38.9-104.1)	3427 (2647-3987)
GRTE	19.0 (14.6 to 25.1)	-15.5 (-19.3 to -13.1)	8.4 (3.8 to 13.0)	171.9 (95.9-235.5)	2815 (2090-3635)
LABE	28.2 (26.9 to 28.8)	-5.4 (-6.5 to -4.1)	16.8 (15.2 to 17.7)	43.3 (31.2-58.0)	1463 (1249-1717)
LAVO	22.3 (18.1 to 25.5)	-6.5 (-8.9 to -5.1)	12.2 (7.6 to 14.9)	218.0 (85.0-308.4)	2282 (1731-3089)
ROMO	16.8 (13.5 to 24.8)	-16.0 (-18.4 to -9.8)	7.8 (5.9 to 14.1)	98.4 (45.2-130.8)	3462 (2572-3795)
YELL	21.6 (16.8 to 27.7)	-14.4 (-16.6 to -12.2)	11.0 (6.5 to 17.2)	94.5 (33.2-140.4)	2424 (1651-3088)

Given our reliance on multiple sources of conspicuous and persistent sign to determine occupancy, our use of trained and calibrated technicians, and previous findings of consistently high detectability (>90%) for similar pika sign surveys (Beever et al. 2008, Beever et al. 2010, Erb et al. 2011, Jeffress et al. 2011, Moyer-Horner et al. 2012) as well as from previous analyses of data from two park units included in this study (CRMO and LABE; Rodhouse et al. 2010; C. Ray *unpublished data*), we assumed that detectability was high (e.g., >90%). This allowed us to focus our resources on obtaining truly large and spatially extensive samples across all eight expansive park study areas rather than revisiting sites within seasons. Furthermore, when detectability exceeds 90%, the bias in estimated occurrence probabilities and in estimated effect sizes for covariates will be small (<1%; Royle and Dorazio 2008, Rodhouse et al. 2010). Lastly, given that the American pika is a highly philopatric species predisposed to generally very short dispersal distances of <300 m (Smith and Weston 1990) and infrequently over 1 km (Peacock 1997), we assumed closure within each summer survey period but allowed for turnover between years.

#### Site bioclimatic variables

We focused our attention on metrics reflecting heat and cold stress similar to those implicated in contemporary American pika range contraction in the Great Basin (Beever et al. 2003, 2010, 2011, Wilkening et al. 2011, Calkins et al. 2012) and considered elsewhere (Moritz et al. 2008, Millar and Westfall 2010a, Erb et al. 2011). Maximum temperature in July ( $T_{\max}$ ), generally the hottest month across our study area; minimum temperature in January ( $T_{\min}$ ), generally the coldest month across our study area; and annual precipitation (precip) were obtained from parameter-elevation regressions on independent slopes models (PRISM; see footnote 7), which provide grid-based estimates at 800-

m resolution for years 1971-2000 (Daly et al. 2008). We also compiled the mean temperature from the warmest three-month quarter of the year (warm.quarter) from the ANUSPLIN package, which provides grid-based estimates at ~1-km resolution for the years 1950-2000 (Hijmans et al. 2005; *available online*).<sup>8</sup> Our covariates represented potential measures of acute heat stress ( $T_{\max}$ ), chronic heat stress (warm.quarter), aridity (precip), and acute cold stress ( $T_{\min}$ ).

We further considered the elevation gradients in parks as alternative proxies for heat and cold stress. American pika occurrence patterns can vary strongly along elevational gradients (Hafner 1993, Galbreath et al. 2009, Rodhouse et al. 2010) and elevation may be a more parsimonious integrated measure of the combined effects on biota of temperature, atmospheric pressure, and clear-sky turbidity (Körner 2007). Given that the elevation effect can vary based on geographic location, we approximated the combined effects of climate using the residual of Hafner's (1993) "pika-equivalent elevation," which predicts the lower elevational limit of the American pika after adjusting for latitude and longitude as  $E(m) = 14\,087 - (56.6)^\circ N - (82.9)^\circ W$ . [For pikas, 14087 is the predicted minimum elevational limit at 0° N and 0° W. The rate (-56.6 m/degree) means that the predicted elevational limit will decrease 56.6 m per 1° increase in latitude. 56.6° is multiplied by the decimal degree latitude for the site (N) and that number is subtracted from the equation. The rate (-82.9 m/degree) means that the predicted elevational limit for pikas will decrease 82.9 m per 1° increase in longitude as one moves west. 82.9 is multiplied by the decimal degree longitude for the site (W) and that number is subtracted from the equation.] Our measure of residual elevation (resid.elev) was the observed elevation of the site, taken from 10-m digital elevation models available for each

<sup>8</sup> www.worldclim.org

park, minus the pika-equivalent minimum expected elevation,  $E(m)$ .

*Characterizing local site conditions*

Recognizing that slope and aspect will influence how pikas actually experience regional climate regimes, we estimated potential solar insolation (insol), a measure of topographic position, at sites as  $\text{sine}(\text{slope}) \times \text{cosine}(\text{aspect})$ . This ranged from  $-1$  to  $1$ , with steeper north-facing slopes represented with larger positive values (“northness”) and steeper south-facing slopes represented with larger negative values (“southness”). Previous studies have shown forb cover to correlate positively and graminoid cover to correlate negatively with site occurrence probabilities, patterns thought to reflect the quantity and quality of forage (Huntly et al. 1986, Dearing 1997, Rodhouse et al. 2010, Wilkening et al. 2011). Accordingly, graminoid (“gram”; including all rushes, sedges, and grasses encountered in plots) and forb foliar cover was estimated visually in plots and assigned to Daubenmire’s (1959) cover class scheme modified with the addition of 0%, trace (<1%), and 100% to discriminate better among sparsely vegetated sites, resulting in nine cover classes (Rodhouse et al. 2010, Jeffress et al. 2011). Quadratic terms ( $\text{gram}^2$  and  $\text{forb}^2$ ) were also included in models in order to test for an anticipated change in slope of occurrence probabilities in heavily vegetated sites.

The linear combination of graminoid and forb covariates also provided some indication of the influence of talus and lava substrate characteristics, with heavily vegetated sites expected to provide fewer subsurface cavities and passageways suitable for pika thermoregulation. Moreover, weasel predation is thought to be much higher in heavily vegetated talus (Smith and Gilpin 1997, Clinchy et al. 2002). Several studies have shown the importance of substrate characteristics in pika occurrence (Franken and Hik 2004, Millar and Westfall 2010a, Rodhouse et al. 2010), but across our eight park study areas, we were unable to develop suitable field measures of substrate that could be calibrated among observers, opting instead to rely on these measures of vegetation cover as proxies.

All input variables except graminoid and forb cover were mean-centered and divided by SD (i.e., standardized “Z scores”), improving computation and the interpretation of model intercepts (Gelman and Hill 2007). Interpretation of the model coefficients estimated from these variables is therefore made in terms of the influence on occurrence probability for each 1-unit change in SD. Graminoid and forb inputs, being ordinal, were centered at cover class 3 (1–5%), and these coefficients are interpreted in terms of a 1-unit change in cover class. This centering allows model intercepts to be interpreted as the estimated mean occurrence probability at average values of numeric covariates and at graminoid and forb cover of 1–5%.

*Model development*

We developed hierarchical logistic regression models using an autoregressive parameterization described by Royle and Dorazio (2008). This approach is convenient for incorporating temporal dependence with environmental predictors and for building the multilevel structure with probability models for both park-specific parameters and among-park hyperparameters. We denote our vector of pika occurrence observations as  $y_j(i,t)$ , for parks  $j = 1, \dots, 8$ , reflecting the fact that visits to site  $i$  at time  $t$  are nested within park  $j$ . Sites considered occupied based on the detection of fresh sign in year  $t$  were identified with a “1”; otherwise with “0.” We use  $\psi$  to represent the probability of pika occurrence, and  $X_k$  as vectors of site covariates, with  $k$  indexing the different covariates and corresponding  $\beta_k$  parameters. Climate parameters for each park are also indexed by  $j$ , indicating an additional level in the model hierarchy that enabled estimation of park-specific coefficients for climate variables. A probability model with hyperparameters mean  $\mu_\theta$  and variance  $\sigma_\theta^2$  was provided for each of these park-specific parameters, where  $\theta = \beta_{kj}$  and each parameter  $\beta_{kj} \sim \mathcal{N}(\mu_{\beta_{kj}}, \sigma_{\beta_{kj}}^2)$ . The hyperparameters provide estimates for the overall means and variances for respective climate parameters across all parks. The variance term  $\sigma_\theta^2$  provides an estimate of the among-park (geographic) variation in the climate–distribution relationships being modeled. If  $\sigma_\theta^2$  is at or near 0, and park-specific parameters all are estimated at or near  $\mu_\theta$ , then it indicates very little among-park variation.

Our logit-linear function for estimating the probability of occurrence in 2010 is

$$\text{logit}(\psi_{ij2010}) = a_j + \beta_1 X_1 + \dots + \beta_k X_k \tag{1}$$

and in 2011 is

$$\text{logit}(\psi_{ij2011}) = b_{1j} + b_{2j} y_j(i, 2010) + \beta_1 X_1 + \dots + \beta_k X_k. \tag{2}$$

This makes the model temporally dynamic, with  $\gamma_j = \text{logit}^{-1}(b_{1j})$  representing site colonization (probability that a site unoccupied in time 2010 becomes occupied in time 2011), and  $\phi_j = \text{logit}^{-1}(b_{1j} + b_{2j})$  in Eq. 3 representing site survival (probability that a site occupied in time 2010 is occupied in time 2011 as well; Royle and Dorazio 2008). We define turnover as the sum total of transition probabilities between occupied and unoccupied sites: the probability of an occupied site being a newly occupied one, or the probability of an unoccupied site being newly unoccupied (i.e.,  $\text{Pr}[y(i2010) = 0 | y(i2011) = 1]$  or  $\text{Pr}[y(i2010) = 1 | y(i2011) = 0]$ ). This is a derived parameter estimated from

$$\tau_j = \frac{\gamma_j(1 - \psi_{j2010})}{\gamma_j(1 - \psi_{j2010}) + \phi_j \psi_{j2010}} + \frac{(1 - \phi_j)\psi_{j2010}}{(1 - \phi_j)\psi_{j2010} + (1 - \gamma_j)(1 - \psi_{j2010})}. \tag{3}$$

Whereas Nichols et al. (1998) and Royle and Dorazio (2008) focused only on the first addend term in Eq. 3, we found this under-representative for parks where a considerable number of sites occupied in 2010 were observed to be unoccupied in 2011. Given that our study included only two years of surveys, our models generate only one set of dynamic parameters for each park.

We considered three models to evaluate the relative importance of climate and local site topography and vegetation conditions on pika occurrence probabilities. Each model had the same basic structure, varying only by substitution of climate or climate-proxy covariates that were highly correlated and therefore could not be included together in the same model. The covariates for model 1,  $\beta_{\text{model1}} = [\text{insol}, \text{gram}, \text{gram}^2, \text{forb}, \text{forb}^2, \text{resid.elev}_j]$  were altered for models 2 and 3 by replacing  $\text{resid.elev}_j$  with  $\beta_{\text{model2}} = [\dots, T_{\text{max}j}, T_{\text{min}j}, \text{precip}_j]$  and  $\beta_{\text{model3}} = [\dots, \text{warm.quarter}_j]$ . Note that the local site-specific variables solar insolation (insol) and the vegetation cover variables (gram and forb) are not indexed by  $j$ , thereby providing only single coefficients to represent the average estimated effect size of topography and vegetation cover over all eight parks. This strategy was chosen to focus attention on the variation in occurrence probabilities along regional climatic gradients, our primary goal, and after exploratory graphical analysis demonstrated that the range of insolation and vegetation cover values were well represented within each park, whereas some parks did not exhibit the full range of our bioclimatic variables (Fig. 2). We therefore anticipated strong park  $\times$  climate interactions, a further motivation for our multilevel modeling strategy.

#### *Bayesian analysis and model validation*

We used OpenBUGS 3.2.1 (Lunn et al. 2009), launched from R 2.14.1 (R Development Core Team 2011) with the R2OpenBUGS library (Sturtz et al. 2005) to implement Bayesian estimation of model parameters via Markov chain Monte Carlo (MCMC) samples of posterior distributions (see Supplement). We used independent vague normal distribution priors with mean 0 and variance 10 ( $N[0,10]$ ) on all mean parameters and hyperparameters and non-informative uniform priors ( $U[0,10]$ ) for variance hyperparameters (Gelman and Hill 2007, Royle and Dorazio 2008, Ntzoufras 2009). Posterior summaries were based on three chains of 4000 MCMC samples of the posterior distributions following an initial burn-in of 1000 MCMC iterations and thinning by a factor of 3. We assessed convergence of MCMC chains with trace plots and the Gelman-Rubin diagnostic,  $\hat{R}$ ; convergence was reached for all parameters according to the criteria  $|\hat{R} - 1| < 0.1$  (Ntzoufras 2009).

Bayesian posterior predictive  $P$  values were generated as a measure of the goodness of fit for the models (Ntzoufras 2009, Kéry and Schaub 2012). These were

estimated from the discrepancy between the sum of absolute values of model residuals from observed data and those from a simulated posterior predictive data set under the assumed model (Ntzoufras 2009, Kéry and Schaub 2012).  $P$  values near 0.5 indicate that the model generated data similar to the observations, providing a good fit to observed data, whereas  $P$  values near 0 or 1 indicate poor fit. Our  $P$  values ranged from 0.26 to 0.34, indicating adequate fit.

Statistical models differ in their power to explain and predict ecological phenomena (Shmueli 2010), and the measures of convergence, goodness of fit, and parameter uncertainty used to gain insight into explanatory performance do not reflect predictive performance. To evaluate the predictive performance of models, we used  $k$ -fold cross-validation with four unique subsets of holdout data ("folds") of equal size (293 sample units; 25% of the entire data set) to estimate the area under the curve (AUC) of the receiver operating characteristic (Fielding and Bell 1997, Wintle and Bardos 2006, Ntzoufras 2009). The receiver operating characteristic curve plots false-positive prediction rates against true-positive prediction rates. AUC scores range from 0.5 to 1.0 and represent the probability that a randomly selected site where the target species was encountered at least once during the study will have a higher occurrence probability than a site where the target species was not encountered at all. An AUC score of 0.5 indicates that a model discriminates among sites no better than random chance, whereas a score of 1.0 indicates that the model discriminates among sites perfectly. For each fold, models were fit to training data (879 sample units) and AUC was estimated from the holdout data. This ensured that each sample unit was used once for model building and once for model validation, but not both simultaneously, which would overestimate AUC. However, we report training data AUC for comparison with other recent studies. We used the ROCR library in R to estimate AUC (Sing et al. 2009).

To test for residual spatial autocorrelation, we estimated Moran's  $I$  coefficients with the APE (Analysis of Phylogenetics and Evolution) library in R (Paradis et al. 2004), using a weights matrix of inverse distances among sites. Given the philopatry and short dispersal distances typical for the species, distances  $>1000$  m were given 0 weight so as not to dampen any evidence for residual spatial autocorrelation. We did not anticipate that residual spatial autocorrelation would be present for this species and, in fact, Moran's  $I$  statistics were  $\leq 0.15$ , providing no evidence to the contrary.

#### RESULTS

We detected pikas at 44% of sites surveyed in 2010 and 33% of sites surveyed in 2011 (see Table A1 in Appendix A for raw survey results). The proportion of sites where fresh sign was encountered ranged from 0.07 in CRMO to 0.71 in GRSA. Of the 265 sites surveyed in

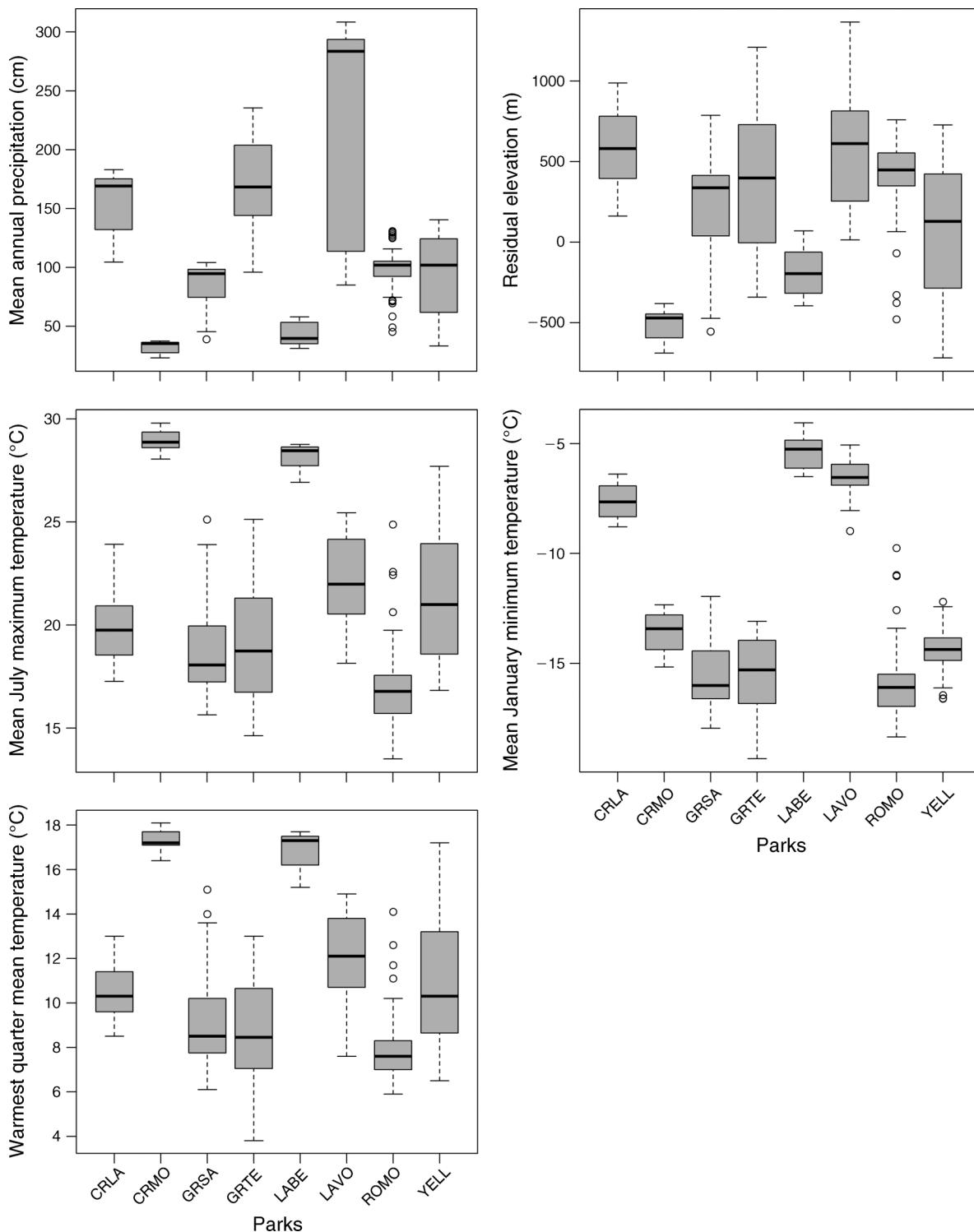


FIG. 2. Exploratory plots showing the range of values for climate variables in the surveyed sites of each park unit. These variables are abbreviated elsewhere as precip, resid.elev,  $T_{max}$ ,  $T_{min}$ , and warm.quarter. Park abbreviations correspond to those shown in Fig. 1. Plot components are as follows: the box represents the 25th to 75th percentile (lower and upper quartiles); the median (50th percentile) is represented by the bold black line; “whiskers” represent the boundaries of 1.5 times the interquartile range; open circles represent outliers.

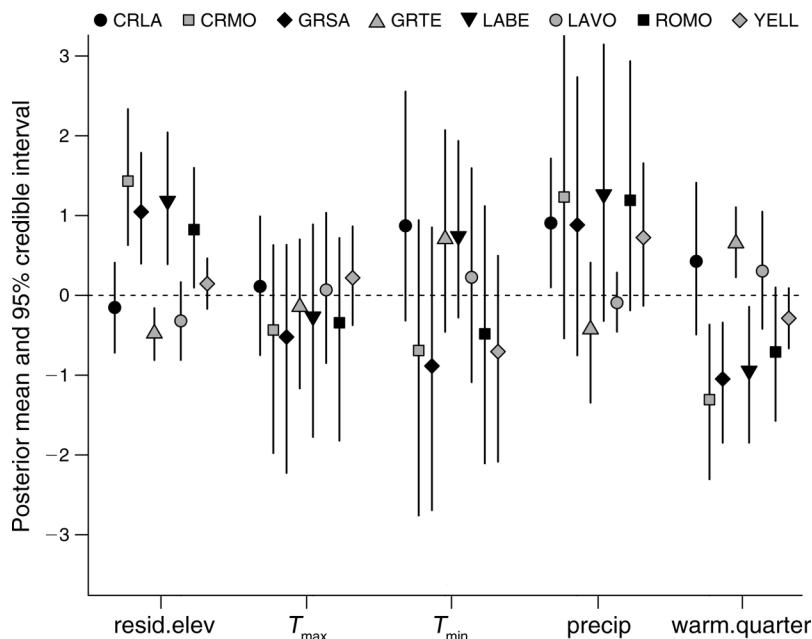


FIG. 3. Posterior means (symbols, coded by national park) and 95% Bayesian credible intervals for the five potential bioclimatic drivers evaluated in models. Residual elevation (resid.elev) was included in model 1. Maximum temperature ( $T_{max}$ ), minimum temperature ( $T_{min}$ ), and annual precipitation (precip) were included in model 2. The average temperature of the warmest three-month quarter of the year (warm.quarter) was included in model 3. Values above 0 indicate a positive association with pika occurrence; values below 0 are negatively associated. Posterior intervals that do not include 0 suggest a “clearer” signal for climate influences on local pika distribution than those with 0 near the estimated means. Both resid.elev and warm.quarter were estimated with more precision and reflected larger differences among parks than the did three metrics used in model 2.

both years, 65 (25%) changed occupancy status from 2010 to 2011. Pika presence was determined primarily through the discovery of indirect sign within survey plots, with fresh scat being the most common type of detection encountered (83% of occupied sites). Fewer occupied sites (<34%) had direct aural and/or visual detections reported, and only 9% of occupied sites had these direct detections as the sole indication of current occupancy. The lowest elevation survey site where fresh pika sign was found was 1259 m in LAVE and the highest elevation survey site where pikas were detected was 3987 m in GRSA. Old sign was found as low as 1252 m in LAVE.

Pika occurrence probabilities varied along bioclimatic gradients in ways expected in some parks and in ways unexpected in other parks. Several parks (e.g., GRSA and GRTE) were consistently estimated to have opposing climate–distribution relationships from one another (Fig. 3). This strong variation among parks resulted in hyperparameter means to be estimated near 0 with large variances ( $\sigma_0^2 \gg 0$ ) (Table 2). The magnitude of these variance estimates increased from a value of 0.59 for  $T_{max}$ , in which park-specific parameter estimates (i.e., the posterior mean point estimates) were most similar, to 1.16 for  $T_{min}$ , which had the most divergent (albeit imprecise) estimates. A close inspection of Fig. 3 shows how the drier parks (CRMO, GRSA, LAVE, ROMO, and YELL; Fig. 2) generally covaried together

in a positive direction for measures of heat stress (resid.elev,  $T_{max}$ , precip, and warm.quarter) and negatively for  $T_{min}$ , whereas the wetter parks (CRLA, GRTE, and LAVO; Fig. 2) tended to covary in opposite directions that are contrary to the general expectations of pika climate–distribution relationships. Parks with wider climatic gradients represented in Fig. 2 were estimated with greater precision in Fig. 3; in general, resid.elev and warm.quarter were better represented within parks and therefore were more precisely estimated than  $T_{max}$ ,  $T_{min}$ , and precip (Fig. 3).

Occurrence probabilities increased with residual elevation in CRMO, GRSA, LAVE, and ROMO, but decreased in GRTE and LAVO and, to lesser degree, in CRLA (Fig. 3). The same signal was also apparent from warm.quarter included in model 3, where the occurrence probabilities in CRMO, GRSA, LAVE, and ROMO trended negatively with chronic summer heat as expected, but, surprisingly, trended positively along that gradient in CRLA, GRTE and LAVO. YELL, which had the widest range of the residual elevation and warm-quarter gradients represented, was estimated precisely but near 0 for both of these covariates. The precision of the park coefficient estimates for the three bioclimatic variables from model 2 ( $T_{max}$ ,  $T_{min}$ , and precip) was very low, making it difficult to discern clear patterns. Precision was lowest for those parks with the narrowest gradients. LAVO, which had the widest range of

TABLE 2. Hyperparameter estimates for among-park means  $\mu_0$  and standard errors  $\sigma_0$  for climate parameters based on posterior summaries (mean, SD, and 2.5% and 97.5% percentiles for the credible interval, CRI) from three models fitted to pika population site occupancy surveys, 2010–2011.

Hyperparameter and model	Posterior mean	Posterior SD	95% CRI
<b>Model 1</b>			
$\mu(\text{resid.elev})$	0.45	0.39	−0.31, 1.27
$\sigma(\text{resid.elev})$	0.99	0.42	0.47, 1.98
<b>Model 2</b>			
$\mu(T_{\text{max}})$	−0.15	0.41	−1.07, 1.00
$\mu(T_{\text{min}})$	−0.02	0.57	−1.20, 1.00
$\mu(\text{precip})$	0.69	0.53	−0.24, 1.00
$\sigma(T_{\text{max}})$	0.59	0.45	0.02, 1.00
$\sigma(T_{\text{min}})$	1.16	0.68	0.15, 1.03
$\sigma(\text{precip})$	1.04	0.55	0.29, 1.00
<b>Model 3</b>			
$\mu(\text{warm.quarter})$	−0.35	0.41	−1.18, 0.46
$\sigma(\text{warm.quarter})$	1.02	0.43	0.46, 2.12

Notes: See *Methods* sections *Site bioclimatic variables*, *Characterizing local site conditions*, and *Model development* for descriptions of variables and models.

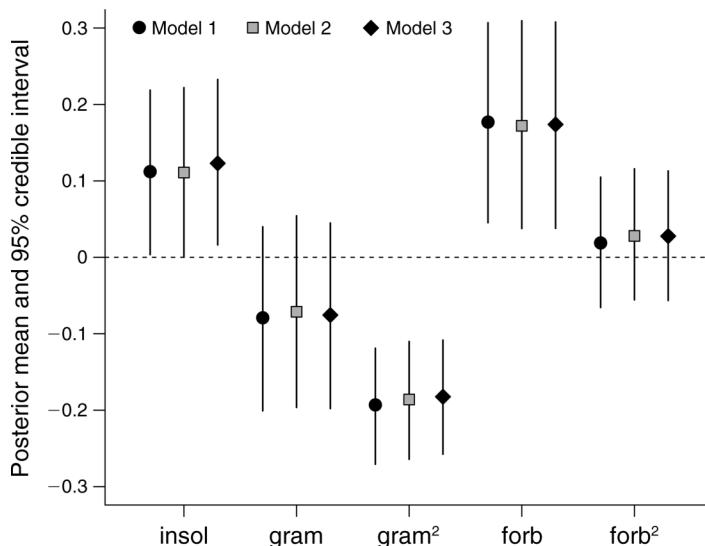
precipitation, was precisely estimated near 0 (Fig. 3). In general, occurrence probabilities increased along the precipitation gradient, with sites in GRTE and LAVO being the exceptions. These two parks included some of the highest and wettest sites. GRTE, which consistently has had much colder temperatures over the period of record than LAVO, exhibited these negative trends in pika occurrence most clearly.

Local site characteristics were clearly related to occurrence probabilities, as reflected in the posterior summaries of Fig. 4. There was no meaningful variation in these parameter estimates among the three models (Fig. 4). Pika occurrence probabilities increased with decreasing potential solar insolation (higher “northness” values) on cooler, north-facing slopes (Fig. 4). Pika occurrence probabilities were negatively associated with graminoid cover, and the posterior interval for  $\text{gram}^2$  indicated that the strength of this association increased

rapidly at high levels of graminoid cover. Conversely, forb cover was positively associated with pika site occurrence probabilities, with no indication of a nonlinear change in the slope of that relationship at higher levels of forb cover (Fig. 4).

After accounting for local site topographic and vegetation characteristics, regional climatic regimes, and site occupancy turnover between 2010 and 2011, average occurrence probabilities at average values of model inputs (due to centering) ranged from 0.35 to 0.72 in 2010 and from 0.39 to 0.72 in 2011 across the parks (Fig. 5; estimates reported from model 1). Turnover itself was similar among parks, near  $\sim 0.6$ , with overlapping credible intervals (Fig. 5). Our models predicted site occurrence probabilities reasonably well among the four validation folds, with AUC ranging from 0.93 to 0.95 for the training data and 0.70 to 0.72 for the holdout data. Notably, AUC did not vary among

FIG. 4. Posterior means and 95% Bayesian credible intervals for parameters of local site characteristics: insolation (insol), and the linear and quadratic parameters for graminoid (gram) and forb cover for each of the three models evaluated. Values above 0 indicate a positive association with pika occurrence; values below 0 are negatively associated. The positive effect sizes for insolation indicate that pika occurrence probabilities increase in cooler, north-facing sites. The strength of the negative relationship between pika occurrence and site graminoid cover increases sharply as graminoid cover increases, whereas there was evidence only for a strong positive, linear relationship between pika occurrence and forb cover.



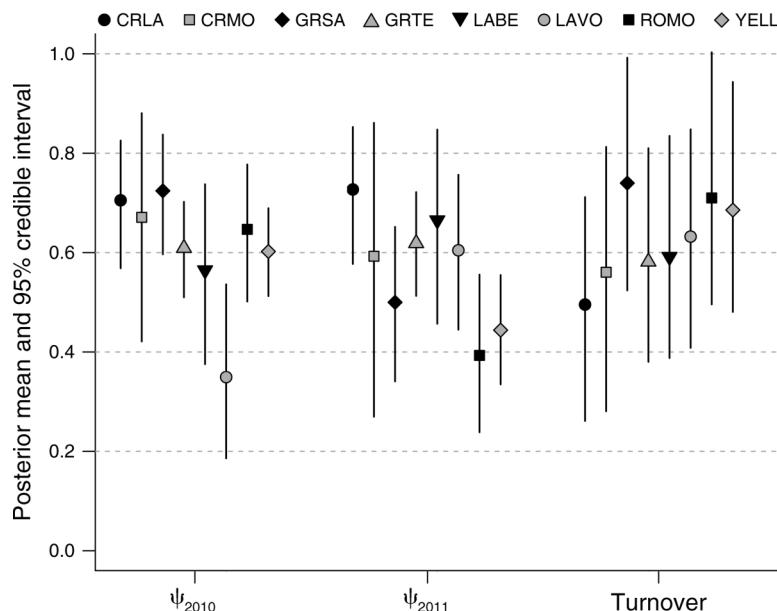


FIG. 5. Year 1 (2010) and year 2 (2011) occurrence probabilities, denoted by  $\psi$ , and estimated probabilities for site turnover (defined as the probability of an occupied site being a newly occupied site or conversely the probability of an unoccupied site being newly unoccupied) with 95% Bayesian credible intervals estimated from model 1.

the three models, indicating that the fitted values and residuals were very similar and that local-scale site characteristics (topography and vegetation) explained much of the variation in occurrence.

#### DISCUSSION

Although the search for generality has been an important approach in ecology, the investigation of geographic variation represents an alternative path of discovery that can reveal important insights about the mechanisms underlying patterns of distribution and abundance of organisms (Pulliam and Waser 2010). Our study of American pika distributions across multiple large landscapes yielded surprising insights about the circumstances—the idiosyncrasies of place (Billick and Price 2010)—under which this species is most strongly constrained by climatic factors, and by extension, most vulnerable to accelerated climate change. Our approach for generating these insights was to replicate intensive field surveys using a common protocol, mitigating the potential confounding of methodological differences that usually accompanies syntheses of broad geographic extent using contributed data sets from multiple teams (Pulliam and Waser 2010). Although the relationship between climate and distribution for pikas has been considered monotypic, defined by the species' sensitivity to extreme acute heat stress (MacArthur and Wang 1974, Smith 1974, Smith and Weston 1990), we found these anticipated relationships apparent only in the driest park study areas. In wetter parks we found apparently counterintuitive patterns in which occurrence probabilities actually increased with heat and decreased

with elevation. Yet precipitation itself was not a particularly influential predictor. The results of our study therefore suggest that the answer to the question “Where is the American pika most vulnerable to climate change?” will be “It depends...,” contingent on the particular combinations of local site characteristics, such as topography and vegetation, and regional climate regimes.

Increasing temperatures in the western United States are expected to have the largest impact on the distribution of the American pika in the future (Wolf et al. 2007). In our study, however, measures of acute ( $T_{max}$ ) and chronic (resid.elev and warm.quarter) heat stress were negatively correlated with distribution patterns only in four parks: CRMO, GRSA, LABE, and ROMO (Fig. 3). Yet those parks did not necessarily have the lowest elevational ranges or highest temperatures of our study areas. GRSA, for example, spanned the highest elevations of any of the study areas and was relatively cool, on average, over the period of record (Fig. 1), but site occurrence probabilities there clearly increased with residual elevation and decreased along the warm.quarter gradient (Fig. 3). Conversely, GRTE, which covers much of the same range of elevations and temperatures as GRSA, showed an opposite relationship with pika distribution patterns for the three measures of heat stress.

The most striking insight from our study was the mediating effect of precipitation. Precipitation alone was not a particularly informative predictor of site occupancy (Fig. 3). However, low mean annual precipitation was the common characteristic of the four parks where heat

stress clearly had a negative influence on pika occurrence probabilities, as well as a characteristic of YELL, where we found weaker evidence of the same kind of heat stress relationship (Figs. 2 and 3). High annual precipitation was the common feature of CRLA, GRTE, and LAVO, which all showed the counterintuitive positive relationship to measures of heat stress. This was most clearly exhibited for GRTE, which is also much colder during the winter than CRLA and LAVO (Fig. 2), providing compelling evidence for an upper elevational limit in high-elevation places that are cold and wet (and snowy). It is possible that this upper limit may continue to rise under continued warming trends and at some point may disappear entirely. However, based on our study, such an increase in occurrence probabilities would be contingent on not only a change in temperature but also a change in precipitation: if CRLA, GRTE, and LAVO get hotter and drier, then occurrence probabilities at high elevations would be expected to increase, but not necessarily if they only get hotter. Forecasting exactly how precipitation regimes will shift in the region remains difficult (Mote and Salathé 2010), and the moist-air maritime influences on CRLA and LAVO are likely to result in very different outcomes than in GRTE and other interior areas.

The influence of aridity on heat and cold stress is intuitive, but not readily apparent from unreplicated studies that focus only on one geographic region. However, Erb et al. (2011) identified aridity as a consistent characteristic of the small set of extirpated sites examined in their pika survey in the Southern Rocky Mountains, and aridity is a defining characteristic of the Great Basin, where evidence for recent range contraction has been most apparent (Beever et al. 2003, 2010, 2011, Wilkening et al. 2011). Beever et al. (2011) suggested that the absence of protective snowpack could increase cold stress on pikas in the Great Basin. We did not find clear evidence for a similar interaction between acute cold stress ( $T_{\min}$ ) and aridity, although we note that CRMO, GRSA, ROMO, and YELL all had posterior means for  $T_{\min}$  well below 0, suggesting a likely negative relationship with acute winter cold stress. These parks are both dry and cold. Conversely, CRLA, GRTE, and LAVO, the wettest parks in the study, showed an opposite positive relationship between pika occurrence and  $T_{\min}$ . It is evident that pikas will be more likely to persist in marginal conditions, such as at low elevations, in areas that experience greater amounts of precipitation or are generally more mesic, as is currently the case in places like the Columbia River Gorge (Simpson 2009). However, it is important to recognize that the potential for a cold-wet stress scenario exists in places like CRLA, GRTE, and LAVO, creating a “Goldilocks effect” of sorts that could squeeze pika populations from both the upper and lower ranges of climate–elevation gradients.

The importance of accounting for local environmental factors has been emphasized but is often not included in

species niche modeling and climate-change forecasting efforts (Mackey and Lindenmayer 2001, Pearson and Dawson 2003). Willis and Bhagwat (2009) reviewed several studies that reached very different conclusions about extinction risk across a range of taxa when local-scale factors were included. Their review underscored the important role of topographic heterogeneity in the persistence of biota during an era of accelerated climate change. Local factors are likely to be particularly important for the American pika because of its ability to use habitat features for behavioral thermoregulation. We found our measure of potential site insolation (insol) to be positively associated with site occupancy, where steeper north-facing slopes provide cooler, mesic conditions that enable pikas to better escape summer heat stress. We also found that occurrence covaried positively along the forb cover gradient and negatively along the graminoid gradient, with a particularly strong effect size estimated for high-graminoid sites ( $\text{gram}^2$ ). Previous studies have reported similar findings (Rodhouse et al. 2010, Wilkening et al. 2011) and these patterns may reflect a selection preference for forbs or an influence of microclimate on both vegetation and pikas. Although a generalist herbivore, the American pika has been reported to preferentially select forbs for haypiles, which are used for winter consumption (Huntly et al. 1986, Dearing 1997). Conversely, high levels of graminoid cover may reflect xeric site conditions (Wilkening et al. 2011). An abundance of graminoids may also indicate heavy soil development and infilling of talus and lava interstices, with a corresponding loss of thermal and predator escape habitat. Any of these scenarios is likely to result in lower site occupancy as both site fidelity and individual survival rates decline.

We explicitly modeled the dynamics of site occupancy among our park study areas and estimated the probability of site occupancy turnover, the summed probabilities of a site transitioning from occupied to unoccupied or unoccupied to occupied states, to be high ( $\sim 0.6$ ). High latent turnover among individuals and the fine grain of our study is the likely explanation for this, although we note that imperfect detection, if lower than we assumed, may also have inflated these estimates. However, pikas have been widely shown to suffer high over-winter mortality and territory turnover (Smith 1980, Southwick et al. 1986, Peacock 1997, Peacock and Smith 1997, Kruezer and Huntly 2003). For example, Peacock and Smith (1997) reported a 62% turnover among adults between two years of study, and Kruezer and Huntly (2003) reported a 100% disappearance rate in one meadow study area during a single winter. Turnover is an important source of error that, if left unaccounted for, could yield highly misleading results. Specifically, if turnover is high, then parameter estimates for site-specific predictors of occurrence, such as climate and topography, could be biased low, especially if turnover is nonrandomly associated with specific site environ-

mental characteristics. It is quite likely that the kinds of contingencies we identified acting on current site-occupancy states, such as the combinations of topographic heterogeneity, precipitation, and chronic heat stress, are also influencing variation in the rates of turnover over time. With longer time series of survey data, the autoregressive structure of our models can be augmented to address such a question. Furthermore, as studies of this nature are replicated across larger numbers of park landscapes and other study areas, the multilevel structure of the models can be used to better address the park-level climate interactions that were apparent from our analysis, but that were difficult to estimate directly with samples from only eight parks. Our modeling framework would be even more insightful with several dozen study areas, enabling park-level climate predictors, perhaps informed by ordination scoring of study areas along multiple climate axes, to be incorporated into hyperparameter (group-level) models. We suggest this hierarchical modeling approach to meta-analysis could be extremely powerful for improving our understanding of current pika distributions and our forecasts of distributional change over time, and we encourage future monitoring efforts to draw upon common methods such as the National Park Service protocol (Jeffress et al. 2011) to facilitate this.

During our study we discovered that characterizing talus and lava substrate during field surveys was not straightforward. Although we collected substrate information, we were unable to develop suitable field measures that could be calibrated among observers, yet this may in fact be the most important local feature that mediates the impacts of regional temperature regimes on pika demography and occurrence. Millar and Westfall (2010a) identified periglacial rock-ice features as having particularly high probabilities of pika occurrence. Similarly, Rodhouse et al. (2010) identified *pahoehoe* lava flows as having >10 times greater odds of pika occurrence than *aa* flows in CRMO. We believe that the strong negative quadratic relationship between graminoid cover and occurrence observed across all eight of our parks may reflect substrate habitat quality, because heavily vegetated sites will provide smaller and fewer interstices to escape hostile weather and predators. However, this is clearly confounded with other influences of graminoid cover, such as forage quality and overall site aridity. Based on our experience, we are skeptical that qualitative measures of substrate, such as the relative depth of talus crevices, can be reliably estimated by multiple observers and compared among studies. Therefore, we recommend that repeatable quantitative measures using high-resolution remotely sensed imagery, such as from laser altimetry (Vierling et al. 2008), be explored. This will be particularly important to analyses applied across multiple large landscapes.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Maps of the park potential pika habitat and sampling frame with survey locations and results, and summary of occupancy survey results by park ([Ecological Archives A023-044-A1](#)).

### Appendix B

Exploratory plots showing the relationship between site occurrence probabilities and site distances to nearest roads for each park unit ([Ecological Archives A023-044-A2](#)).

### Supplement

OpenBUGS code for hierarchical multi-park distribution models ([Ecological Archives A023-044-S1](#)).