

Geographical variation in the influence of habitat and climate on site occupancy turnover in American pika (*Ochotona princeps*)

Thomas J. Rodhouse¹  | Mackenzie R. Jeffress² | Kirk R. Sherrill³ |
Sean R. Mohren⁴ | Nancy J. Nordensten⁵ | Michael L. Magnuson⁶ |
Donelle Schwalm⁷ | Jessica A. Castillo⁷ | Matthew Shinderman⁸ | Clinton W. Epps⁷

¹National Park Service Upper Columbia Basin Network, Oregon State University-Cascades, Bend, Oregon

²Nevada Department of Wildlife, Elko, Nevada

³National Park Service, Fort Collins, Colorado

⁴Crater Lake National Park, Crater Lake, Oregon

⁵Lava Beds National Monument, Tulelake, California

⁶Lassen Volcanic National Park, Mineral, California

⁷Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon

⁸Human and Ecosystem Resilience and Sustainability Lab, Oregon State University-Cascades, Bend, Oregon

Correspondence

Thomas J. Rodhouse, National Park Service, Oregon State University-Cascades Suite 105, 497 SW Century Drive, Bend, OR, 97702.

Email: Tom_Rodhouse@nps.gov

Present addresses

Nancy J. Nordensten, US Forest Service, 7887 Hwy 50, Pollock Pines, California 95726
and

Jessica A. Castillo, Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544

Funding information

Rocky Mountain Cooperative Ecosystem Studies Unit, Grant/Award Number: H1200090004; US Geological Survey Park-Oriented Biological Support, Grant/Award Number: G11AC20397; US National Park Service Climate Change Response Program, Grant/Award Number: 163377; Pacific Northwest Cooperative Ecosystem Studies Unit, Grant/Award Number: H8W07060001 and H8W07110001

Editor: Michael McCarthy

Abstract

Aim: Environmental changes that amplify rates of site or patch occupancy turnover can increase risks of decline in spatially structured populations. We asked whether local habitat and meso-scale climate influenced site occupancy turnover rates in four American pika (*Ochotona princeps*) metapopulations. We focused on winter cold stress, which is a proposed driver of American pika extinction risk but has been rarely studied.

Location: Oregon, Northern California, and Idaho.

Methods: We developed Bayesian hierarchical multiseason site occupancy models that accounted for both false-negative and false-positive survey detection errors to explore the winter stress turnover hypothesis. We used remotely sensed meso-scale (1 km) snowpack and temperature data and fine-grained local habitat attributes as covariates to model site persistence and colonization rates.

Results: The estimated magnitude of imperfect detection was greater than previously reported for the species. After accounting for imperfect detection, we found no evidence of declines in site occupancy over the 5-year study period, but our

models provided evidence that pika site occupancy turnover can be high (>50% between some years) and apparently exacerbated by winter cold stress, summer heat stress and variation in site habitat quality. However, strength of evidence varied among metapopulations, suggesting influential local contingencies, as reported previously for the species.

Main conclusions: Our empirical results suggest that the American pika may be vulnerable to wintertime turnover, negatively exacerbated by climatic events, with implications for future persistence given forecasted snowpack declines across the species' range. Our models suggest a more nuanced dynamism to persistence and extinction risk than the simple scenario of inexorable, monotonic range contraction offered by static range-wide distribution models, and we suggest several ways to strengthen these insights with future studies.

KEYWORDS

Bayesian hierarchical model, climate change, extinction, site occupancy dynamics, snowpack decline, turnover

1 | INTRODUCTION

Accelerated climate change is implicated in a growing list of contemporary range contractions and extinctions across multiple taxa (Chen, Hill, Ohlemüller, & Thomas, 2011; Parmesan, 2006; Root, Price, Hall, & Schneider, 2003; Walther et al., 2002). Forecasts suggest that substantial losses in global biodiversity will occur over the next several decades (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; IPCC, 2013; Jetz, Wilcove, & Dobson, 2007; Thomas et al., 2004). Losses are expected to be particularly high for dispersal-limited species in montane environments (Guralnick, 2007; Lawler et al., 2009; Parmesan, 2006; Williams, Henry, & Sinclair, 2015). Studies of these systems that develop mechanistic insights into specific climate-related processes contributing to extinction risk are needed to advance the science of climate change impacts on biota and to inform effective conservation and adaptation strategies (Chen et al., 2011; Parmesan, 2006). Much of the evidence for climate change-induced range shifts comes from comparisons of historic, current and future distributions via predictive models (e.g., bioclimatic niche models; Guisan & Thuiller, 2005; Martinez-Meyer, Peterson, & Hargrove, 2004; Pearson & Dawson, 2003; Pacifici et al., 2015). These models describe broad-scale and temporally static patterns (i.e., assume equilibrium between species ranges and environmental predictors; Guisan & Thuiller, 2005), providing evidence of net changes. However, they are limited in their ability to reveal how climate and other factors influence the dynamic processes of local extirpation and persistence that drive the observed net changes in distributions and, ultimately, range-wide extinction (Anderson et al., 2009). But, with recent developments in the class of dynamic distribution models referred to as multiseason occupancy models (MacKenzie, Nichols, Knutson, & Franklin, 2003; Royle & Dorazio, 2008), explicit study of the dynamic rates

of distributional change—the rates of turnover in site occupancy—is possible (Chandler et al., 2015; Eaton, Hughes, Hines, & Nichols, 2014; Fernandez-Chacon et al., 2014). A particularly important aspect of this modelling framework is the ability to account for imperfect detection with datasets developed from surveys of sites replicated within and among seasons (Bailey, MacKenzie, & Nichols, 2014; Guillera-Arroita, 2017; Guillera-Arroita, Ridout, & Morgan, 2010; MacKenzie & Royle, 2005). This replication allows detection probabilities to be estimated. Without this capability, it is impossible to distinguish true rates of annual turnover from apparent turnover confounded by imperfect detection (Kery, Spillmann, Truong, & Holderegger, 2006; Risk, de Valpine, & Beissinger, 2011; Ruiz-Gutierrez & Zipkin, 2011).

Turnover in occupancy of habitat patches or sites by a species can result from both intrinsic (e.g., demographic stochasticity) and extrinsic factors (e.g., climate-driven environmental stochasticity). When turnover is asynchronous and recolonization is sufficient to replace extirpated sites, populations persist, but when extrinsic factors exacerbate turnover, directional (deterministic) changes can result. In dispersal-limited organisms occupying patchy habitats, extrinsic factors that elevate occupancy turnover rates can drive populations towards extinction, particularly when sufficiently widespread to induce synchronicity, such as land use change and climate and weather events (Elkin & Possingham, 2008; Fleishman, Ray, Sjögren-Gulve, Boggs, & Murphy, 2002; Gaggiotti & Hanski, 2004; Hanski, 1998; Heino, Kaitala, Ranta, & Lindström, 1997).

The growing need and opportunity to examine site occupancy dynamics requires more explicit consideration of mechanisms influencing local extirpation. For instance, while there is considerable evidence of rapid range shifts along elevational gradients in mountain systems (Sekercioglu et al., 2008; Lawler et al., 2009; Wilson et al., 2005), contributions of declining mountain snowpack and other

factors correlated with elevation are not as well understood (Jackson, Betancourt, Booth, & Gray, 2009; Williams et al., 2015). Declining snowpack is particularly important for understanding climate-induced extinction risk. Snowpack reflects ocean-atmosphere and topographic interactions that are subject to high spatial and temporal variability (Bennie et al., 2013; Daly, Conklin, & Unsworth, 2010; Jackson et al., 2009; Williams et al., 2015), and declines can have acute and counter-intuitive impacts (e.g., by exposing heat-sensitive animals to winter cold stress; Guralnick, Erb, & Ray, 2011; Williams et al., 2015). Snowpack declines are occurring rapidly in many mountainous regions of the world (Barnett, Adam, & Lettenmaier, 2005), particularly in regions influenced by oscillating ocean-atmosphere interactions, such as in western North America (e.g., Pacific-decadal oscillation; Kapnick & Hall, 2012; Lute, Abatzoglou, & Hegewisch, 2015; Mote, Hamlet, Clark, & Lettenmaier, 2005). While the impacts of snowpack declines are intuitive and evident for ecosystem services such as water storage (Berghuijs, Woods, & Hrachowitz, 2014), drought and fire (Gergel, Nijssen, Abatzoglou, Lettenmaier, & Stumbaugh, 2017), the potential impacts on faunal extinction risk are less so (Jackson et al., 2009; Williams et al., 2015).

In this study, we develop a suite of multiseason site occupancy models to examine how, after accounting for both false-negative and false-positive (Chambert, Miller, & Nichols, 2015) detection errors, spatial variation in wintertime depth of snowpack and cold temperatures influence rates of site occupancy turnover in the American pika (*Ochotona princeps*). The American pika is a highly territorial, philopatric and dispersal-limited montane lagomorph that occupies patchy talus and lava-flow habitat in western North America (Peacock, 1997; Smith & Ivins, 1983; Smith & Weston, 1990). It exhibits high rates of overwinter mortality and metapopulation-type dynamics in some areas (Kruezer & Huntly, 2003; Smith & Nagy, 2015). The species is thought to be undergoing contraction in some portions of its range due to accelerated warming (Beever, Brussard, & Berger, 2003; Beever et al., 2016) and in general is thought to be range-restricted by summer heat stress (Galbreath, Hafner, & Zamudio, 2009; Wilkening, Ray, Beever, & Brussard, 2011). However, it continues to exhibit enigmatic persistence in apparently inhospitable locations (Beever, Wilkening, McIvor, Weber, & Brussard, 2008; Jeffress, Van Gunst, & Millar, 2017; Millar & Westfall, 2010; Millar, Westfall, & Delany, 2013; Ray, Beever, & Rodhouse, 2016; Rodhouse et al., 2010; Shinderman, 2015; Smith & Nagy, 2015; Smith, Nagy, & Millar, 2016), fuelling ongoing investigations into its vulnerability to contemporary climate change (Calkins, Beever, Boykin, Frey, & Anderson, 2012; Schwalm et al., 2016).

Another hypothesis proposes that declining snowpack and exposure to cold temperatures and freezing rain also contribute to American pika extinction risk (Beever, Ray, Mote, & Wilkening, 2010; Guralnick et al., 2011). Variation in snowpack is implicated in mortality rates for the American pika (Kruezer & Huntly, 2003) as well as for its close congener the collared pika (*O. collaris*; Franken & Hik, 2004; Morrison & Hik, 2007). We test this hypothesis with Bayesian hierarchical multiseason occupancy models fit to datasets collected over 5 years (2010–2014) at ~150 sites in each of four US national

parks (Jeffress et al., 2011). The study was replicated in four park study areas along a temperature-moisture gradient, an approach designed to reveal important place-based contingencies (Billick & Price, 2010; Castillo et al., 2016; Jeffress, Rodhouse, Ray, Wolff, & Epps, 2013; Schwalm et al., 2016) and test the generalizability of hypothesized climatic controls on pika distribution dynamics. Our analysis is contextualized by knowledge about pika dispersal and gene flow obtained simultaneously during our study in these same four parks (Castillo et al., 2016). We focus on both acute and chronic winter impacts using daily temperature and snow depth data measured at meso-scales (~1 km) that reflect threshold-type conditions and seasonal mean conditions. In a specific manner, we asked whether rates of turnover in site occupancy of the American pika covaried with the 5-year plot average of (a) number of days during January–March (winter) with no snow and minimum temperatures below -5°C , (b) mean winter snow depth and (c) mean minimum winter temperature. We contrasted these models with one for heat stress that included as a covariate (d) mean maximum summer temperature (June–August). In each of these models, we also included site-level forb % cover as an influential local-scale indication of habitat condition (Erb, Ray, & Guralnick, 2014; Jeffress et al., 2013; Ray et al., 2016; Rodhouse et al., 2010; Wilkening et al., 2011). We also examined the potential influences of site topographic position (insolation) and relative habitat patch size via a metric informed by genetic analyses of average dispersal distances estimated for each study area (Castillo et al., 2016; Schwalm et al., 2016). Accounting for these additional environmental factors enhanced our ability to elucidate the relative strength of climatic winter stress relative to summer heat stress and local site habitat quality conditions. Our study provides a uniquely replicated, fine-grained perspective on the mechanics of population persistence and extirpation in mountain ecosystems experiencing rapid climate change.

2 | METHODS

2.1 | Study areas

Following methods developed by Rodhouse et al. (2010), Jeffress et al. (2011, 2013) and Ray et al. (2016), and described also by Schwalm et al. (2016), we conducted site occupancy surveys at randomly selected long-term monitoring sites in four US National Park units in three states: Crater Lake National Park (CRLA) in the Cascade Range of southern Oregon, Craters of the Moon National Monument and Preserve (CRMO) in the Snake River Plain in central Idaho, and Lassen Volcanic National Park (LAVO) and Lava Beds National Monument (LABE), both in the southern end of the Cascade Range in northern California (Figure 1).

The four parks provided a range of pika habitat types, including montane talus slopes and boulder fields in CRLA and LAVO and low-elevation basalt lava flows in CRMO and LABE (see Jeffress et al., 2013 and Appendix S1 for detailed maps). The four parks varied climatically along a warm-dry to cool-wet continuum (see descriptions by Jeffress et al., 2013 and Schwalm et al., 2016 and Figure 2):



FIGURE 1 Map of the four national park study areas located within the north-western United States across gradients of substrate types, elevations and climates. The pika distribution map was provided by The International Union for Conservation of Nature (IUCN)

CRMO and LAVO were considerably hotter in summer and drier in winter than CRLA and LAVO, experiencing only ephemeral snowpacks; CRLA and LAVO are higher in elevation and experienced deep and persistent snowpacks, and LAVO averaged colder than CRLA in winter (Figure 2).

Each park supports spatially structured American pika populations that exhibit metapopulation-type characteristics. Maps in Appendix S1 illustrate the highly patchy distribution of rock (talus and lava) substrate that the species inhabited within each park, with mainland-island spatial patterns evident in CRMO, mapped in detail by Rodhouse et al. (2010), and a continuum of clumpy to completely fragmented patterns in the other parks. Castillo, Epps, Davis, and Cushman (2014), Castillo et al. (2016) used genetic

techniques to provide estimates of average intergenerational dispersal distances for pikas in each of the studied parks that ranged from ~1 to 4.5 km, and of functional connectivity among patches that revealed dispersal and gene flow to be strongly influenced by landscape features.

2.2 | Site occupancy surveys

We established our survey design framework with circular plots 452 m² in area (12 m radii) randomly distributed across each park's mapped and accessible portions of suitable habitat (Rodhouse et al., 2010; Jeffress et al., 2011, 2013; Ray et al., 2016; Appendix S1). We scaled our plots so as to correspond approximately with published

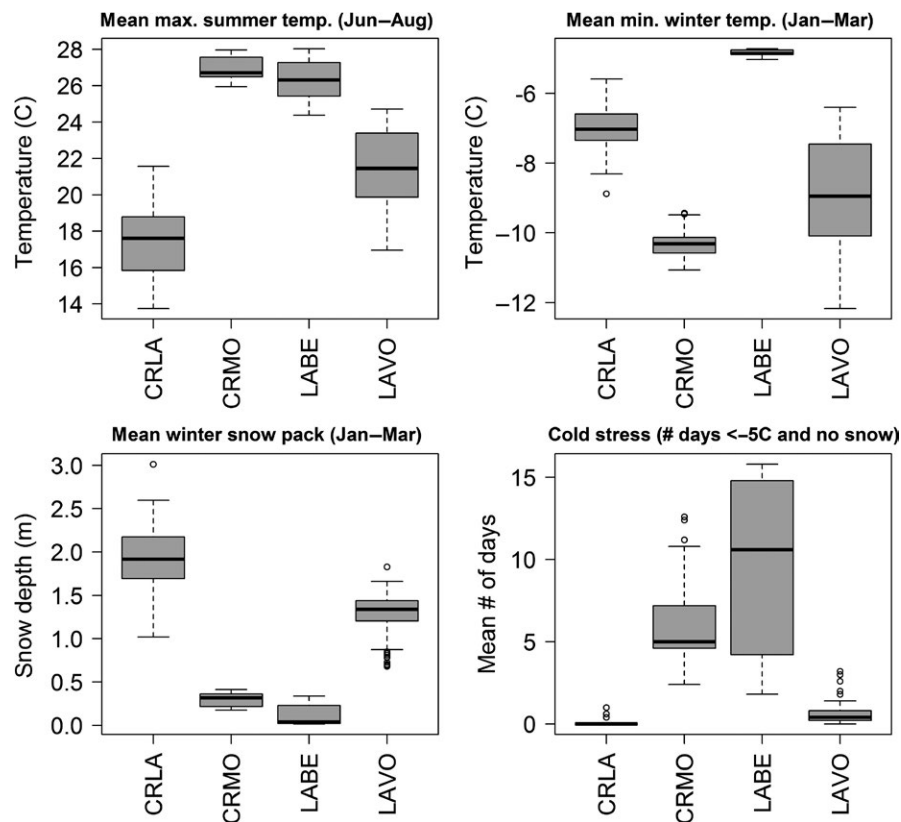


FIGURE 2 Variation in contemporary climatic regimes among the four study areas, with Crater Lake National Park (CRLA) and Lassen Volcanic National Park (LAVO) being generally more mesic and less extreme than Craters of the Moon National Monument & Preserve (CRMO) and Lava Beds National Monument (LAVE). CRMO and LAVE exhibit strikingly different winter temperature patterns, however

pika territory sizes and scale of foraging and dispersal activity (Smith & Weston, 1990; Smith & Nagy, 2015). We made a within-season (summer) species-level closure assumption, required for occupancy modelling studies in general (but note some accommodation for violation of this assumption when occupancy is interpreted as use; MacKenzie et al., 2006), and for our study a plausible one given the sedentary and centrally placed foraging behaviour of pikas.

Randomization of plot locations was carried out with the Generalized Random Tessellation-Stratified (GRTS) algorithm (Stevens & Olsen, 2004), which provided for spatially balanced random sampling of and corresponding scope of inference across each park's mapped and accessible pika habitat (sampling frames included in Appendix S1). We conducted occupancy surveys annually in each plot during snow-free summer and autumn periods (June–November). Sample sizes varied during the first 2 years of study as sampling frame errors (e.g., mapping errors) and other logistical challenges were resolved, but stabilized at ~100 plots per park; ~150 plots per park were visited at least once during the 5-year study and included in modelling (Table 1). Within-season revisits (second visits) to ~30% of plots were performed each year to provide information for estimating detection probabilities (Table 1).

We surveyed for fresh, active sign of pika occupancy within each plot by recording encounters with active animals visible or audible within established plot boundaries, or when fresh hay piles (food caches) and fresh scat were found. These indirect signs have been routinely used for ascertaining pika presence (Beever et al., 2003; Erb, Ray, & Guralnick, 2011; Jeffress et al., 2013; Millar & Westfall, 2010; Ray et al., 2016; Rodhouse et al., 2010; Shinderman, 2015;

TABLE 1 Summary of American pika survey activity in each of the four studied parks during 2010–2014

Park	2010	2011	2012	2013	2014
Total number of sites surveyed					
CRLA	85	107	145	100	100
CRMO	56	135	146	103	103
LAVE	101	102	100	100	100
LAVO	76	112	75	103	103
Total number of sites revisited					
CRLA	50	30	30	41	30
CRMO	50	35	30	20	29
LAVE	50	0	30	14	50
LAVO	41	30	0	21	20
Proportion of sites with fresh sign (detections)					
CRLA	0.65	0.63	0.54	0.60	0.71
CRMO	0.21	0.07	0.16	0.08	0.21
LAVE	0.24	0.29	0.40	0.45	0.61
LAVO	0.14	0.42	0.21	0.43	0.43

Note. Parks included in the study were Crater Lake National Park (CRLA), Craters of the Moon National Monument & Preserve (CRMO), Lava Beds National Monument (LAVE) and Lassen Volcanic National Park (LAVO).

Smith & Nagy, 2015), and estimates of detectability of pikas with sign surveys are generally thought to be high (Beever et al., 2008; Beever, Ray, Wilkening, Brussard, & Mote, 2011; Erb et al., 2011; Ray et al., 2016; Rodhouse et al., 2010). Fresh, actively maintained hay

piles are conspicuous and easily identified when found among rock interstices. However, consistent ageing of scat can be problematic—old sign can persist in situ for many years (Millar et al., 2014; Nichols, 2010), creating opportunities for false-positive detection errors to occur when old sign is assigned fresh status. This type of observation error is thought to be rare because indications of fresh scat (e.g., green when opened) fade quickly over a period of weeks (Millar et al., 2014; Nichols, 2010), although this assumption has not been formally tested and could bias occupancy models (Bailey et al., 2014; Chambert et al., 2015; McClintock, Bailey, Pollock, & Simons, 2010; Miller et al., 2013; Royle & Link, 2006). Field observers adhered to a common protocol used in all four park study areas (Jeffress et al., 2011) and were consistently trained and calibrated together during group sessions conducted by the authors of this study.

2.3 | Local and synoptic influences: model covariates

At each plot, we visually assessed forb cover (referred to as FORB when discussing modelling methods and results) and other vegetation and rock physiognomic cover types using a modified Daubenmire (1959) cover classification strategy with eight categories ranging from 0%, trace (<1%), 1%–5%, 5%–25%, 25%–50%, 50%–75%, 75%–95%, 100% (Jeffress et al., 2011, 2013; Rodhouse et al., 2010). We used a 10-m digital elevation model to extract plot slope and aspect and construct a measure of topographic position (insolation or heat loading, referred to as INSOLATION), calculated as $\sin(\text{slope}) \times \cos(\text{aspect})$, which varied from -1 to 1 and captured the gradient steep south to flat to steep north slopes (Jeffress et al., 2013; Schwalm et al., 2016). We used a metric of patch area and habitat connectivity constructed by Castillo et al. (2016) and Schwalm et al. (2016) that was calculated as the % of mapped rock habitat within circles centred on plots with radii corresponding to average intergenerational pika dispersal distances determined by Castillo et al. (2016:1667, referred to here as %HABITAT). The radii used for each park were 1.2 km for CRMO, 2.5 km for CRLA, 3.5 km for LABE and 4.5 km for LAVO (Castillo et al., 2016; Schwalm et al., 2016). Schwalm et al. (2016) found this metric to be useful in some parks for predicting distributional changes over time, and Stewart et al. (2015) also successfully used a similar approach but with an arbitrary fixed radius of 1 km.

Snow depth (referred to as SNOW) and mean minimum (winter; T_{MIN}) and maximum (summer; T_{MAX}) temperatures were obtained from the publically available Snow Data Assimilation System (SNODAS; NOHRSC, 2004) and the Daymet daily surface weather and climatological summaries (Thornton, Thornton, Wei, Vose, & Boyer, 2017). Both datasets are provided as spatial grids at 1 km resolution, and processed and compiled with the National Park Service NPScape Climate Grid Analysis Toolset (Monahan, Gross, Svancara, & Philippi, 2012). Our measure of acute cold stress (COLD) was compiled for each plot via overlay with gridded data as mean counts of days with no snow and minimum temperatures $< -5^{\circ}\text{C}$ over the 5-year period. Because so few days met these conditions in CRLA

and LAVO, due to maritime climatic influences and persistent deep snowpack, we could only use this measure for CRMO and LABE. Snow depth and chronic cold stress and heat stress were compiled as 3-month means, also averaged over the 5-year study period for each plot (January–March and June–August, respectively).

2.4 | Statistical analysis

We used the multiseason occupancy methods developed by MacKenzie et al. (2003), Royle and Kéry (2007), and Royle and Dorazio (2008) and previously applied for pikas in eight parks, including our four study areas, by Jeffress et al. (2013). Following Chambert et al.'s (2015) site-confirmation design, we extended our detection model to account for both false-negative and false-positive errors in which fresh scat was considered as an ambiguous detection method vulnerable to both types of errors, and all other sign types were considered unambiguous and vulnerable only to false-negative error.

We used Royle and Dorazio's (2008) autoregressive parameterization to construct additive models on the logit scale for covariates to influence dynamic occupancy parameters (see Jeffress et al., 2013). Because these models involve many parameters and separability, identifiability and convergence can be difficult to achieve in some circumstances, we used a step-wise procedure to assemble models for testing hypotheses. First, we considered models with local influences FORB, INSOLATION and %HABITAT only. In each park, FORB emerged as the most influential covariate with posteriors $\neq 0$ (see Section 3). We retained only FORB for subsequent models that included meso-scale winter and summer stress variables, which were each modelled separately because of cross-correlation. Mean climatic (stress) conditions were constructed as 5-year means for each site so that a single vector could be included as a covariate (e.g., SNOW was constructed as a single vector with n elements each compiled as 5-year means from a matrix of t annual 3-month winter snow depth averages). In general, American pika sign surveys have been shown to yield high levels of detectability and we maintained a simple pooled structure for each park wherein all detection probabilities were assumed constant and averaged over the 5-year study period. However, in CRMO, model convergence was improved for some models when year-specific detection probabilities were allowed (see Section 3).

We used OpenBUGS 3.2.3 (Lunn, Spiegelhalter, Thomas, & Best, 2009), launched from R 3.2.3 (R Development Core Team, 2015) with the R2OpenBUGS library (Sturtz, Ligges, & Gelman, 2005) to implement Bayesian estimation of model parameters via Markov chain Monte Carlo (MCMC) samples of posterior distributions. We used independent vague $N(0,10)$ priors on all logit-scale parameters and $U(0,1)$ priors for parameters bounded by 0 and 1 on the probability scale (Ntzoufras, 2009; Royle & Dorazio, 2008). Posterior summaries were based on 10,000 MCMC samples of the posterior distributions from 3 chains run simultaneously, thinned by a factor of 3, following an initial burn-in of 5,000 MCMC iterations. 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

TABLE 2 Summary of apparent (naïve, not accounting for imperfect detection) American pika site occupancy turnover patterns in the 4 study parks, 2010–2014

	ϕ	γ	ϵ
CRLA			
2010–2011	23	3	3
2011–2012	49	4	15
2012–2013	48	11	3
2013–2014	54	15	3
CRMO			
2010–2011	4	1	1
2011–2012	7	11	2
2012–2013	7	1	12
2013–2014	8	14	0
LABE			
2010–2011	6	5	7
2011–2012	7	9	4
2012–2013	31	14	9
2013–2014	39	22	6
LAVO			
2010–2011	3	6	2
2011–2012	11	3	17
2012–2013	11	21	5
2013–2014	23	16	17

Notes. Site survival or persistence (ϕ) is the number of sites that remained apparently occupied (based on detections) from 1 year to the next. Site colonization (γ) is the number of sites that apparently transitioned from unoccupied to occupied from 1 year to the next. Site extinction (ϵ) is the number of sites that apparently transitioned from occupied to unoccupied from 1 year to the next.

$|\hat{R} - 1| < 0.1$ (Ntzoufras, 2009). Given our goals to explain empirical patterns rather than predict to unsurveyed locations (see Shmueli, 2010), we did not formally evaluate predictive power of the models (e.g., with receiver operating characteristic) and other potential problems such as residual spatial autocorrelation but note that these concerns were addressed after the first 2 years of our study by Jeffress et al. (2013; e.g., Moran's $I \sim 0$). We did, however, perform Bayesian posterior predictive checks on all models using the discrepancies of observed detections and the posterior predictions of detections (but not directly on site occupancy as it is only a partially observed state when the observation process is imperfect; Zipkin, Campbell Grant, & Fagan, 2012).

3 | RESULTS

3.1 | Imperfect detection, site occupancy, and turnover

Naïve site occupancy (raw proportion of sites with detections) and turnover rates varied among years and among parks with no apparent among-park temporal trend or regional synchronicity (Table 2). For

example, numbers of vacated plots (apparent local extinction, ϵ) were high in both CRLA and LAVO from 2011 to 2012, but only CRMO in 2012–2013 and only LAVO in 2013–2014 (Table 2). Site occupancy was steady for CRLA but varied widely in the other parks, especially in CRMO where surveys yielded very few detections (<10%) in 2011 and 2013 (Table 1). Site occupancy appeared to trend positively over the 5 years in LABE but not in the other parks. However, imperfect detection was evident for all park surveys (Figure 3a). The probability of detection ranged from 0.30 to 0.65 for the unambiguous methods, from 0.70 to 0.90 for the ambiguous method (fresh scat), and was notably higher in CRLA than in other parks (Figure 3a). False-positive error rates using fresh scat ranged from 0.03 to 0.10 (Figure 3a). We considered year-specific detection probabilities to help some of the CRMO models to converge, and these annual probabilities ranged from 0.30 to 0.75 and 0.30 to 0.83, respectively.

After accounting for imperfect detection, patterns of site occupancy and mean annual turnover, site occupancy probabilities changed: positive trends emerged in all 5 parks, most notably in LABE and LAVO (Figure 3b), as did asynchronous rates of turnover probability evident from the raw detection patterns (Figure 3c). Annual variation in site occupancy and corresponding rates of turnover were very low for CRLA and CRMO relative to LABE and LAVO. Colonization rates exceeded extinction rates in most transitions (between years) in CRMO, LABE and LAVO, most notably in LABE and LAVO where mean probabilities of colonization exceeded 50% between 2010 and 2011 (Figure 3c). Two transitions with relatively high rates of site extinction probability were evident in CRLA (between 2010–2011 and 2011–2012) and LAVO (2011–2012 and 2013–2014; Figure 3c).

3.2 | Local influences on turnover

Models fit with local-scale site covariates FORB, INSOLATION and %HABITAT parameterized to influence both the estimated probabilities of site persistence and colonization consistently showed a strong relationship (high precision and lower credible interval >0) between turnover and forb cover (FORB; Figure 4). Forb cover positively influenced colonization in all four parks, most strongly in CRLA, CRMO and LAVO. Counter-intuitively, forb cover negatively influenced site persistence in CRLA, CRMO and LABE, but was a positive influence on persistence in LAVO. There was no clear evidence of relationships between INSOLATION and % HABITAT and turnover rates except in CRMO where % habitat appeared to positively influence site persistence (Figure 4).

3.3 | Meso-scale influences on turnover

After accounting for imperfect detection and local forb cover, mean # of days with no snow and very cold (<−5°C) temperatures (COLD) negatively influenced site persistence in CRMO and site colonization in LABE (Figure 5). As noted in Methods, few days met this criterion in CRLA and LAVO. In a corresponding manner, snow depth (SNOW) was a positive influence on site persistence in CRMO and in LAVO (but note the wide credible interval that includes 0) and on colonization

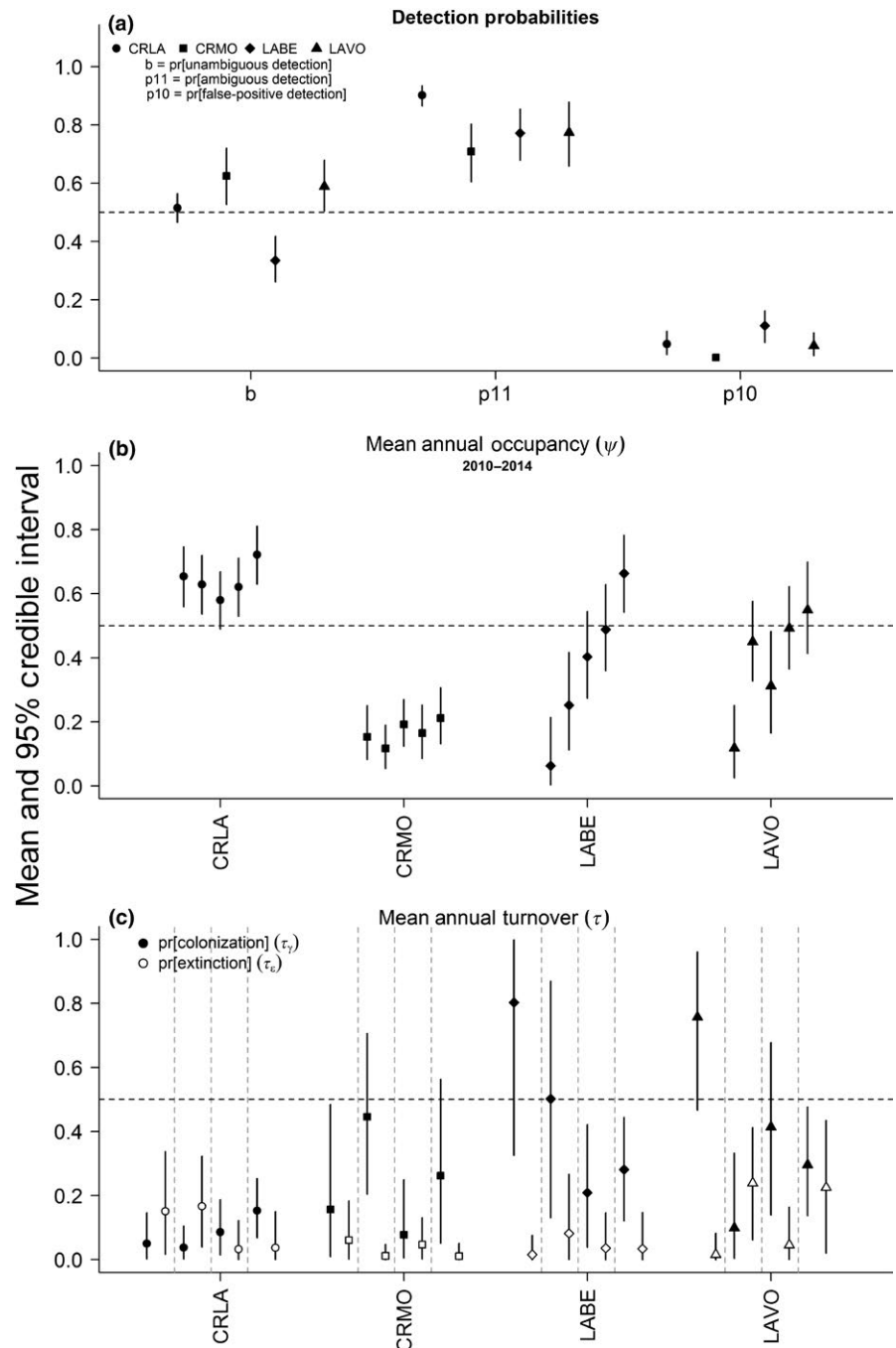


FIGURE 3 (a) Estimated probabilities of detection, including both ambiguous ($p11$ from fresh scat) and unambiguous (b from haypiles and direct animal encounters) detection probabilities (1—false-negative error) and false-positive error ($p10$ from old scat erroneously recorded as fresh); (b) mean annual probabilities of occupancy, after accounting for imperfect detection and at average local site environmental and synoptic climatic conditions (due to centring of model covariates); and (c) probabilities of site turnover for each yearly (wintertime) transition between summer surveys, where vertical dashed grey lines demarcate pairs of annual transition probabilities (from left to right 2010–2011, 2011–2012, 2012–2013, 2013–2014). Notation in (a) follows standards established by Chambert et al. (2015)

in LABE, but was not apparently influential in CRLA (Figure 6). TMIN positively influenced site colonization in CRLA, not in LABE, and, counter-intuitively, negatively influenced site persistence in LAVO, possibly also in CRMO but with high uncertainty (Figure 7). At last, summer heat stress (TMAX) negatively influenced site persistence in CRMO and LAVO but not in the other parks (Figure 8).

4 | DISCUSSION

Accelerated climate changes are already evident in the mountains of western North America, with steady declines in snowpack and

warming temperatures recorded in many basins (Barnett et al., 2005; Kapnick & Hall, 2012; Mote et al., 2005) and corresponding changes in distributions and abundances of some organisms (Brodie & Post, 2010; Brown, Hannah, & Milner, 2007; Epps, McCullough, Wehausen, Bleich, & Rechel, 2004; McKelvey et al., 2011; Williams et al., 2015). Our study considers whether American pika site occupancy dynamics covary with contemporary climatic patterns and whether those dynamics are consistent with winter cold stress and summer heat stress hypotheses to explain apparent contraction in some portions of the species' range (Beever et al., 2010; Galbreath et al., 2009; Guralnick et al., 2011; Wilkening et al., 2011). We found that site turnover can be higher when sites are exposed to cold stress

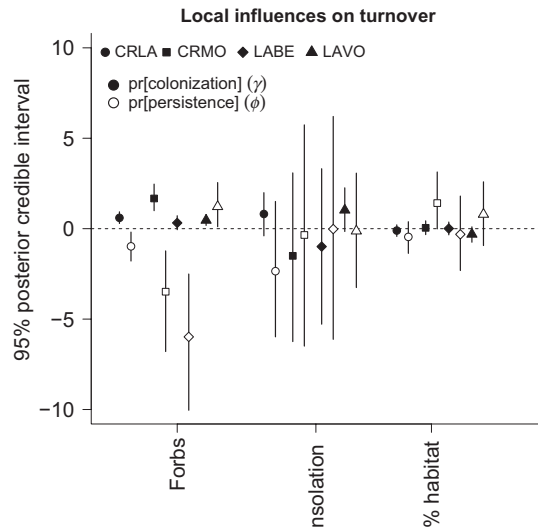


FIGURE 4 Estimated effect sizes of local site (plot) environmental conditions on American pika site occupancy turnover probabilities among the four park study areas. Forbs (plot forb cover) were consistently influential in all parks, whereas insolation (topographic position) and % habitat (% of mapped rock habitat within average dispersal radii defined for each park with molecular genetic techniques) were not apparently influential to turnover

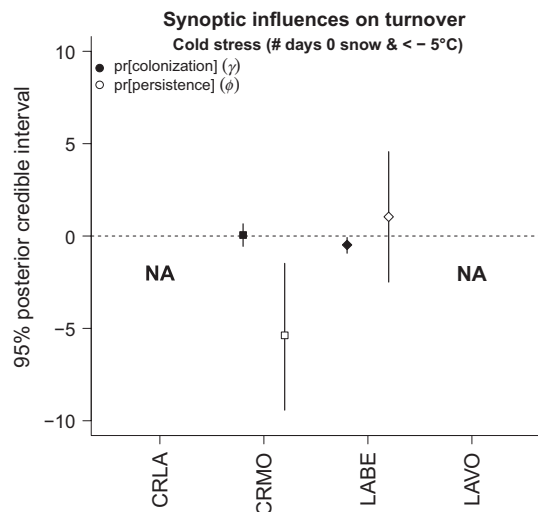


FIGURE 5 Estimated effect sizes of the mean number of acute cold stress days during winter (January–March) on American pika site occupancy turnover probabilities for two parks. Two other parks, Crater Lake National Park (CRLA) and Lassen Volcanic National Park (LAVO), had such deep and persisting snowpacks that this measure of cold stress was uninformative

without an insulating snow blanket (e.g., estimated persistence probability declined to ~ 0 in CRMO in sites experiencing 1 SD more cold, snow-free days, Figure 5). However, our results were highly variable among parks, suggesting influential local contingencies, as has been reported previously for the species (Castillo et al., 2016; Jeffress et al., 2013; Schwalm et al., 2016). The influences of winter stress were most evident in our two low-elevation parks, CRMO and LABE,

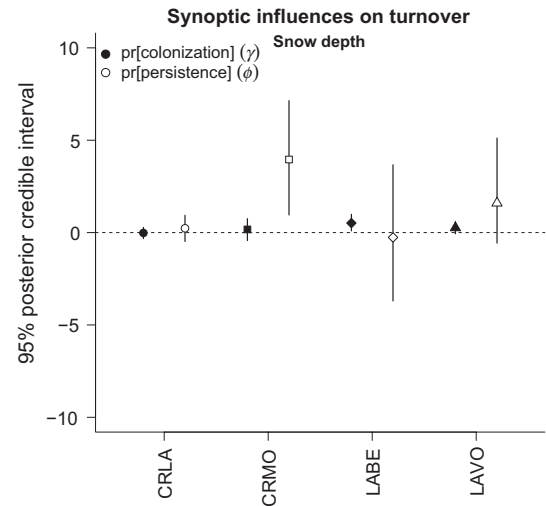


FIGURE 6 Estimated effect sizes of average snow depth during winter (January–March) on American pika site occupancy turnover probabilities among the four park study areas

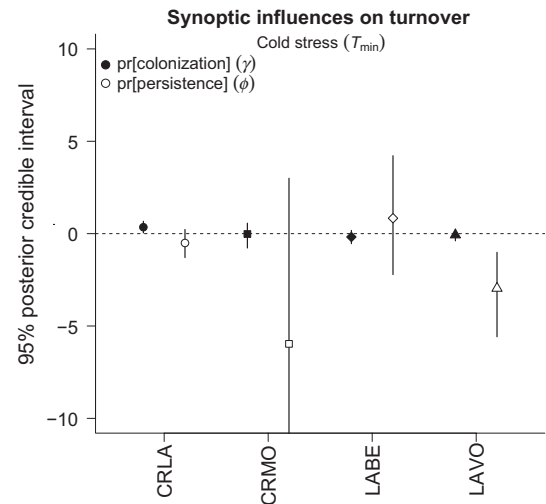


FIGURE 7 Estimated effect sizes of cold temperatures during winter (mean minimum temperatures during January–March) on American pika site occupancy turnover probabilities among the four park study areas

where snowpack is ephemeral. Lack of snow and the combination of lack of snow and cold temperatures reduced probability of site occupancy persistence in CRMO and reduced site colonization probability in LABE. CRLA and LAVO routinely experience deep and persistent maritime snowpack that mitigates this kind of stress under the current climate regime, and our constructed acute cold stress variable was uninformative for those parks. Cold temperature (TMIN), by itself, was less informative (credible intervals centred on zero), but there was clear positive influence of warmer winter minimum temperatures on site colonization in CRLA and a strong, counter-intuitive, reduction in persistence in LAVO with warmer winter minimums, possibly reflecting the broader range and greater heterogeneity of winter temperatures in LAVO compared to the other parks (Figure 2).

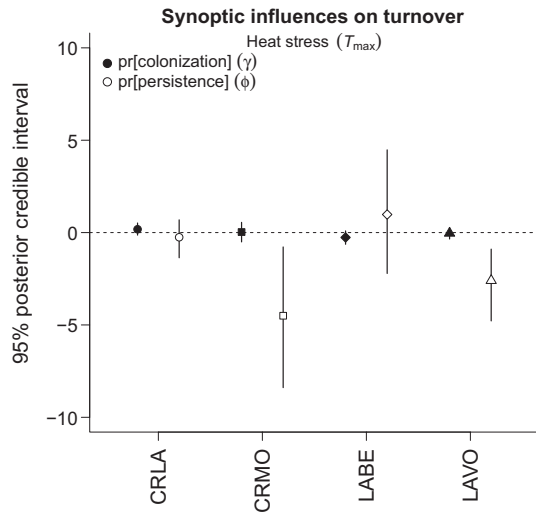


FIGURE 8 Estimated effect sizes of high temperatures during summer (mean maximum temperatures during June–August) on American pika site occupancy turnover probabilities among the four park study areas

We found evidence that summer heat stress negatively influenced site persistence and exacerbated turnover rates in CRMO and LAVO (e.g., chances of persistence declined to ~15% in LAVO in sites experiencing 1 SD higher mean maximum temperatures, Figure 8). Contrary to expectation, there was no discernible influence of heat stress on turnover in LAVE, the lowest-elevation park among the four. In general, evidence for heat stress as a driver of contemporary American pika site occupancy patterns and range contraction has been equivocal and our study underscores the highly contingent nature of the heat stress phenomenon on the species' contemporary and future biogeography. Range-wide species distribution models and inspections of historically occupied sites arrayed along elevational gradients have provided evidence of contraction (Beever et al., 2003; Moritz et al., 2008; Calkins et al., 2012; Stewart et al., 2015; 2017; Beever et al., 2016). But, finer-grained studies and those that have been replicated across multiple large landscapes using random sampling have presented evidence of enigmatic persistence in unusually low and hot locations, or otherwise have not found a consistent heat stress signal in their analyses (Erb et al., 2011; Jeffress et al., 2013, 2017; Millar & Westfall, 2010; Millar et al., 2018; Ray et al., 2016; Rowe et al., 2015; Schwalm et al., 2016; Shinderman, 2015; Smith & Nagy, 2015). Most pertinent to our study was Smith and Nagy's (2015) conclusion that heat stress apparently did not contribute to metapopulation dynamics in their long-term study of pikas in a California ore dump. They did not consider the possible effects of winter cold stress, however. It is increasingly clear that thermal buffering of the rock subsurface microclimatic environments where pikas live, and the subsequent opportunities this creates for behavioural thermoregulation, explains much of the enigmatic persistence in low-elevation sites (Hall, Chalfoun, Beever, & Loosen, 2016; Henry, Henry, & Russello, 2012; Millar, Westfall, & Delaney, 2016; Rodhouse, Hovland, & Jeffress, 2017; Varner & Dearing, 2014; Wilkening et al., 2011). In at least two

of our studied parks (CRMO and CRLA), talus and lava rock substrates stabilized subsurface temperatures in summer and winter (Rodhouse et al., 2017). It is difficult to measure subsurface temperatures across large landscapes with many replicate sites, in part because of finely-grained microclimate heterogeneity (Rodhouse et al., 2017), but doing so could provide future opportunities to directly examine microclimatic influences on site occupancy dynamics.

Coarse-grain range-wide approaches to estimating climate-driven changes in distribution have limited value for some species, especially given the importance of local-scale habitat conditions to site occupancy patterns (Schwalm et al., 2016; Willis & Bhagwat, 2009). For example, site-level forb cover, which could be an above-ground indication of persistent rock subsurface ice and water (Erb et al., 2011; Millar & Westfall, 2010), has been a consistently positive predictor of pika site occupancy across multiple studies (Erb et al., 2014; Jeffress et al., 2013; Ray et al., 2016; Rodhouse et al., 2010; Wilkening et al., 2011). Consistent with these prior findings, our study revealed that forb cover positively influenced site colonization in all parks. However, site persistence was actually lower in high forb cover sites in three parks. This is interesting because it suggests forb-rich sites that provide growing-season forage and possibly reflect more mesic microclimates attract but also lose more immigrants. Clinchy, Haydon, and Smith (2002) anticipated such an outcome and suggested ephemeral colonization could result from, among several possibilities, higher rates of dispersal but lower rates of juvenile survival, even in sites with beneficial habitat attributes. This is a compelling possibility given the territoriality and philopatry exhibited by American pikas and reports that most individuals dispersing within pika metapopulations are juveniles (Peacock & Smith, 1997). An additional possibility that has not yet been explored is the connection between winter forage quantity and quality and site persistence and turnover. The low detections of active food caching behaviour (hay-piling) in some study areas (Ray et al., 2016; Rodhouse et al., 2010; Shinderman, 2015) could be another indication of vulnerability in an era of increasingly variable snowpack and cold weather events.

We found no evidence that topographic position (INSOLATION) and habitat connectivity (%HABITAT) influenced turnover. However, topographic position explained variation in site occupancy when only 2 years of survey data for multiple (8) study areas were pooled into a single model (see Jeffress et al., 2013). We have also found connectivity to be useful for pika distribution models using a random forest approach (Schwalm et al., 2016). These methodological differences and others (e.g., no consideration of imperfect detection) and our emphasis on dynamic rates of site turnover likely account for some of this discrepancy. Of connectivity, an additional consideration is that our random sampling study design was uninformative about neighbourhood effects. Random sampling designs reduce spatial autocorrelation and parameter estimation bias from lack of independence, but also prevent us from fully specifying the spatially auto-correlated site recolonization process (MacKenzie et al., 2018). Given the importance of nonrandom pathways of dispersal to pika metapopulation dynamics and gene flow (Castillo et al., 2016; Clinchy et al., 2002; Peacock & Smith, 1997; Smith & Nagy, 2015),

it is not surprising that our %HABITAT metric was uninformative. We suspect that other autocorrelation metrics based on Euclidean distance (MacKenzie et al., 2018:307) will be uninformative for this same reason, as indicated by our previous inspections of residual spatial autocorrelation using Moran's I (Jeffress et al., 2013). A modification of our sampling approach to account better for the clustered spatial patterns of habitat and individual movement would be required to describe the broad range of metapopulation-type dynamics likely to be exhibited across study areas when configuration of rock patch structure varies from mainland-island to completely fragmented (Appendix S1). Alternatives such as adaptive cluster sampling (Thompson, 2002) coupled with the directional spatial autoregressive occupancy models used recently with grid-based (lattices) survey designs to model biological invasions (Bled, Royle, & Cam, 2011) could be useful for these kinds of questions.

Our results provide empirical evidence that the American pika may indeed be vulnerable to wintertime site turnover, negatively exacerbated by the synchronicity of climatic conditions, with implications for future persistence given the forecasts of continued snowpack declines across the species' range (Gergel et al., 2017; Lute et al., 2015). Yandow et al. (2015) also reported evidence from the mountains of Wyoming that pika scat density patterns varied in ways consistent with the cold-stress hypothesis, but Smith and Millar (in press) found no evidence of population decline in the mountains of California following a year of extreme snow drought. However, the strength of evidence for cold stress- and low snowpack-induced site occupancy turnover provided by our analysis must be considered within the context of the considerable uncertainties in some of our estimated parameter spaces (e.g., Figures 5–7). This is in part a result of our Bayesian hierarchical inferential paradigm which accounts for more uncertainty than is typical with frequentist maximum-likelihood approaches (Cressie, Calder, Clark, Ver Hoef, & Wile, 2009), particularly when also accounting for imperfect detection (Guillera-Aroita, 2017), and also our highly replicated multipark study design. Two other likely influences on uncertainty include the smoothing effect of using low-resolution (meso-scale) climate data averaged over months and the decoupling of regional climate and weather from the local conditions actually experienced by individual animals (Jackson et al., 2009). Studies of American pika subsurface rock microhabitats provide particularly good examples of this decoupling (Millar et al., 2016). In more general context, in topographically heterogeneous mountain systems, decoupling results in discrepancies between broad-scale forecasts of loss and enigmatic local-scale persistence that can compromise the efficiency of local-scale conservation strategies developed in response to broad-scale forecasts. This is a persistent challenge for climate science that underscores the tremendous need for studies that collect microclimate information across broad geographic extents.

Our study revealed that the detection probabilities of indirect sign surveys of American pikas are much more heterogeneous than has been assumed (Jeffress et al., 2013; Wilkening et al., 2011) and should be examined more closely in future occupancy studies. Of the few pika studies that have explicitly estimated detection probabilities (Beever et al., 2008, 2010; Erb et al., 2011; Moyer-Horner,

Smith, & Belt, 2012; Ray et al., 2016; Rodhouse et al., 2010), methodological and study design differences prevent meaningful comparisons and none but the present study actually accounted for imperfect detection in analyses. For example, Rodhouse et al. (2010) and Ray et al. (2016) provided single-season detection estimates based on the same fixed-radius (12 m radii) plot dimensions we used, but, after demonstrating ~90% detectability, did not include imperfect detection in subsequent analyses (under the rationale that it was high enough). Our small but nontrivial false-positive error estimates from using fresh scat as an indication of site occupancy suggest that such sign should be used only when detection errors can be accounted for. False-positive error estimates of similar magnitude to our results have repeatedly been shown to bias occupancy parameters (McClintock et al., 2010; Miller et al., 2015). It is possible that the species-level closure assumption for within-season replicate surveys was violated (e.g., summer weasel predation nonrandomly emptying sites between surveys, Clinchy et al., 2002), which, if widespread, could bias detection and turnover probabilities. The sedentary nature of the species and large sample sizes should mitigate this, but it is nonetheless a consideration.

At last, we reflect on the implications of our study for elevated extinction risk among pika metapopulations exposed to changing climatic regimes. We found no evidence of short-term contemporary declines in site occupancy. In fact, increases were evident in all four parks, particularly in LBE and LAVO. However, CRMO had very low (<20%) net occupancy rates, suggesting that metapopulation may be at elevated risk of extirpation (precarious metapopulation persistence *sensu* Thomas & Hanski, 2004) simply because chances of synchronous extinctions among all remaining territories is higher, particularly if our inferences about turnover probabilities exacerbated by cold and heat stress in that park prove to be accurate. Castillo et al. (2016) found evidence that gene flow was relatively high among the extant sites in the vast lava flow expanses of CRMO and Schwalm et al. (2016) integrated that information into bioclimatic niche models forecasting long-term persistence in CRMO under some climate change scenarios. However, Castillo (unpublished data) found markedly lower genetic diversity (allelic richness) among CRMO animals compared with animals sampled in the nearest (~20 km) rocky habitats in the mountains north of the park's lava flows, suggesting potential genetic isolation and relatively small effective population size. In contrast to CRMO, the three other study areas, most notably CRLA, appear to have much greater elasticities in their pika metapopulations. Schwalm et al. (2016) found surprisingly low chances of long-term persistence in CRLA under some climate change scenarios in large part due to landscape barriers to dispersal (gene flow, Castillo et al., 2016) and positive feedback looping with climate change. In addition, our study suggests that below-average snowpack and cold temperatures and above-average summer heat may stress these metapopulations and reverse current positive trends in site occupancy patterns. Ongoing monitoring of pika occupancy in these four parks will enable testing of these hypotheses about park-wide metapopulation persistence.

ACKNOWLEDGEMENTS

M. Hovland, E. Authier, D. Popp and K. Irvine provided helpful comments during preparation of the manuscript. The Crater Lake Science and Learning Center and the parks involved in the study provided additional personnel, materials and logistical support. Funding was provided to Oregon State University Fisheries & Wildlife Department and Oregon State University-Cascades Campus Human & Ecosystem Resilience & Sustainability Lab by the US National Park Service's Upper Columbia Basin Network Inventory and Monitoring Program and the US National Park Service's Climate Change Response Program (via PMIS #163377), facilitated by the Pacific Northwest Cooperative Ecosystem Studies Unit (cooperative agreements H8W07060001 and H8W07110001) and Rocky Mountain Cooperative Ecosystem Studies Unit (cooperative agreement H1200090004) and by the US Geological Survey Park-Oriented Biological Support (POBS) program (grant #G11AC20397).

ORCID

Thomas J. Rodhouse  <http://orcid.org/0000-0001-5953-9113>

REFERENCES

- Anderson, B. J., Akçakaya, H. R., Araújo, M. B., Fordham, D. A., Martinez-Meyer, E., Thuiller, W., & Brook, B. W. (2009). Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B*, 276, 1415–1420. <https://doi.org/10.1098/rspb.2008.1681>
- Bailey, L. L., MacKenzie, D. I., & Nichols, J. D. (2014). Advances and applications of occupancy models. *Methods in Ecology and Evolution*, 5, 1269–1279. <https://doi.org/10.1111/2041-210X.12100>
- Barnett, T. P., Adam, J. C., & Lettenmaier, D. P. (2005). Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature*, 438, 303–309. <https://doi.org/10.1038/nature04141>
- Beever, E. A., Brussard, P. F., & Berger, J. (2003). Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. *Journal of Mammalogy*, 84, 37–54. [https://doi.org/10.1644/1545-1542\(2003\)084\[0037:POAEAI\]2.0.CO;2](https://doi.org/10.1644/1545-1542(2003)084[0037:POAEAI]2.0.CO;2)
- Beever, E. A., Perrine, J. D., Rickman, T., Flores, M., Clark, J. P., Waters, C., ... Collins, G. H. (2016). Pika (*Ochotona princeps*) losses from two isolated regions reflect temperature and water balance, but reflect habitat area in a mainland region. *Journal of Mammalogy*, 97, 1495–1511. <https://doi.org/10.1093/jmammal/gyw128>
- Beever, E. A., Ray, C., Mote, P. W., & Wilkening, J. L. (2010). Testing alternative mechanisms of climate stress in the ecoregional collapse of an alpine mammal. *Ecological Applications*, 20, 164–178. <https://doi.org/10.1890/08-1011.1>
- Beever, E. A., Ray, C., Wilkening, J. L., Brussard, P. F., & Mote, P. W. (2011). Contemporary climate change alters the pace and drivers of extinction. *Global Change Biology*, 17, 2054–2070. <https://doi.org/10.1111/j.1365-2486.2010.02389.x>
- Beever, E. A., Wilkening, J. L., Mclvor, D. E., Weber, S. S., & Brussard, P. F. (2008). American pikas (*Ochotona princeps*) in northwestern Nevada: A newly discovered population at a low-elevation site. *Western North American Naturalist*, 68, 8–14. [https://doi.org/10.3398/1527-0904\(2008\)68\[8:APOPIN\]2.0.CO;2](https://doi.org/10.3398/1527-0904(2008)68[8:APOPIN]2.0.CO;2)
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15, 265–377.
- Bennie, J., Hodgson, J. A., Lawson, C. R., Holloway, C. T. R., Roy, D. B., Brereton, T., ... Wilson, R. J. (2013). Range expansion through fragmented landscapes under a variable climate. *Ecology Letters*, 16, 921–929. <https://doi.org/10.1111/ele.12129>
- Berghuijs, W. R., Woods, R. A., & Hrachowitz, M. (2014). A precipitation shift from snow towards rain leads to a decrease in streamflow. *Nature Climate Change*, 4, 583–586. <https://doi.org/10.1038/nclimate2246>
- Billick, I., & Price, M. V. (2010). Idiosyncrasy of place: Challenges and opportunities. In I. Billick, & M. V. Price (Eds.), *The ecology of place: Contributions of place-based research to ecological understanding* (pp. 63–67). Chicago, IL: The University of Chicago Press. <https://doi.org/10.7208/chicago/9780226050447.001.0001>
- Bled, F., Royle, J. A., & Cam, E. (2011). Hierarchical modeling of an invasive spread: The Eurasian collared-dove *Streptopelia decaocto* in the United States. *Ecological Applications*, 21, 290–302. <https://doi.org/10.1890/09-1877.1>
- Brodie, J. F., & Post, E. (2010). Nonlinear responses of wolverine populations to declining winter snowpack. *Population Ecology*, 52, 279–287. <https://doi.org/10.1007/s10144-009-0189-6>
- Brown, L. E., Hannah, D. M., & Milner, A. M. (2007). Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. *Global Change Biology*, 13, 958–966. <https://doi.org/10.1111/j.1365-2486.2007.01341.x>
- Calkins, M. T., Beever, E. A., Boykin, K. G., Frey, J. K., & Anderson, M. C. (2012). Not-so-splendid isolation: Modeling climate-mediated range collapse of a montane mammal *Ochotona princeps* across numerous ecoregions. *Ecography*, 35, 780–791. <https://doi.org/10.1111/j.1600-0587.2011.07227.x>
- Castillo, J. A., Epps, C. W., Davis, A. R., & Cushman, S. A. (2014). Landscape effects on gene flow for a climate-sensitive montane species, the American pika. *Molecular Ecology*, 23, 843–856. <https://doi.org/10.1111/mec.12650>
- Castillo, J. A., Epps, C. W., Jeffress, M. R., Ray, C., Rodhouse, T. J., & Schwalm, D. (2016). Replicated landscape genetic and network analyses reveal wide variation in functional connectivity for American pikas. *Ecological Applications*, 26, 1660–1676. <https://doi.org/10.1890/15-1452.1>
- Chambert, T., Miller, D. A. W., & Nichols, J. D. (2015). Modeling false positive detections in species occurrence data under different study designs. *Ecology*, 96, 332–339. <https://doi.org/10.1890/14-1507.1>
- Chandler, R. B., Muths, E., Sigafus, B. H., Schwalbe, C. R., Jarchow, C. J., & Hossack, B. R. (2015). Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. *Journal of Applied Ecology*, 52, 1325–1333. <https://doi.org/10.1111/1365-2664.12481>
- Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026. <https://doi.org/10.1126/science.1206432>
- Clinchy, M., Haydon, D. T., & Smith, A. T. (2002). Pattern does not equal process: What does patch occupancy really tell us about metapopulation dynamics? *The American Naturalist*, 159, 351–362. <https://doi.org/10.1086/338990>
- Cressie, N., Calder, C. A., Clark, J. S., Ver Hoef, J. M., & Wikle, C. K. (2009). Accounting for uncertainty in ecological analysis: The strengths and limitations of hierarchical statistical modeling. *Ecological Applications*, 19, 553–570. <https://doi.org/10.1890/07-0744.1>
- Daly, C., Conklin, D. R., & Unsworth, M. H. (2010). Local atmospheric decoupling in complex topography alters climate change impacts. *International Journal of Climatology*, 30, 1857–1864.
- Daubenmire, R. F. (1959). A canopy-coverage method of vegetation analysis. *Northwest Science*, 33, 43–64.
- Eaton, M. J., Hughes, P. T., Hines, J. E., & Nichols, J. D. (2014). Testing metapopulation concepts: Effects of patch characteristics and neighborhood occupancy on the dynamics of an endangered lagomorph. *Oikos*, 123, 662–676. <https://doi.org/10.1111/oik.01008>

- Elkin, C. M., & Possingham, H. (2008). The role of landscape-dependent disturbance and dispersal in metapopulations persistence. *American Naturalist*, 172, 563–575. <https://doi.org/10.1086/590962>
- Epps, C. W., McCullough, D., Wehausen, J. D., Bleich, V. C., & Reche, J. L. (2004). Effects of climate change on population persistence of desert-dwelling mountain sheep in California. *Conservation Biology*, 18, 102–113. <https://doi.org/10.1111/j.1523-1739.2004.00023.x>
- Erb, L. P., Ray, C., & Guralnick, R. (2011). On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*). *Ecology*, 92, 1730–1735. <https://doi.org/10.1890/11-0175.1>
- Erb, L. P., Ray, C., & Guralnick, R. (2014). Determinants of pika population density vs. occupancy in the Southern Rocky mountains. *Ecological Applications*, 24, 429–435. <https://doi.org/10.1890/13-1072.1>
- Fernandez-Chacon, A., Stefanescu, C., Genovart, M., Nichols, J. D., Hines, J. E., Paramo, F., ... Oro, D. (2014). Determinants of extinction-colonization dynamics in Mediterranean butterflies: The role of landscape, climate and local habitat features. *Journal of Animal Ecology*, 83, 276–285. <https://doi.org/10.1111/1365-2656.12118>
- Fleishman, E., Ray, C., Sjögren-Gulve, P., Boggs, C. L., & Murphy, D. D. (2002). Assessing the roles of patch quality, area, and isolation in predicting metapopulations dynamics. *Conservation Biology*, 16, 706–716. <https://doi.org/10.1046/j.1523-1739.2002.00539.x>
- Franken, R. J., & Hik, D. S. (2004). Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of colored pikas *Ochotona collaris*. *Journal of Animal Ecology*, 73, 889–896. <https://doi.org/10.1111/j.0021-8790.2004.00865.x>
- Gaggiotti, O. E., & Hanski, I. (2004). Mechanisms of extinction. In I. Hanski, & O. Gaggiotti (Eds.), *Ecology, genetics, and evolution in meta-populations* (pp. 337–366). Burlington, MA: Elsevier Academic Press. <https://doi.org/10.1016/B978-012323448-3/50016-7>
- Galbreath, K. E., Hafner, D. J., & Zamudio, K. R. (2009). When cold is better: Climate-driven elevation shifts yield complex patterns of diversification and demography in an alpine specialist (American pika, *Ochotona princeps*). *Evolution*, 63, 2848–2863. <https://doi.org/10.1111/j.1558-5646.2009.00803.x>
- Gergel, D. R., Nijssen, B., Abatzoglou, J. T., Lettenmaier, D. P., & Stumbaugh, M. R. (2017). Effects of climate change on snowpack and fire potential in the western USA. *Climatic Change*, 141, 287–299. <https://doi.org/10.1007/s10584-017-1899-y>
- Guillera-Aroita, G. (2017). Modelling of species distributions, range dynamics and communities under imperfect detection: Advances, challenges and opportunities. *Ecography*, 40, 281–295. <https://doi.org/10.1111/ecog.02445>
- Guillera-Aroita, G., Ridout, M. S., & Morgan, B. J. T. (2010). Design of occupancy studies with imperfect detection. *Methods in Ecology and Evolution*, 1, 131–139. <https://doi.org/10.1111/j.2041-210X.2010.00017.x>
- Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8, 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Guralnick, R. (2007). Differential effects of past climate warming on mountain and flatland species distributions: A multispecies North American mammal assessment. *Global Ecology and Biogeography*, 16, 14–23. <https://doi.org/10.1111/j.1466-8238.2006.00260.x>
- Guralnick, R., Erb, L., & Ray, C. (2011). Mammalian distributional responses to climatic changes: A review and prospectus. In J. Balant, & E. Beever (Eds.), *Ecological consequences of climate change: Mechanisms, conservation, and management* (pp. 85–103). Boca Raton, FL: CRC Press. <https://doi.org/10.1201/b11179>
- Hall, L. E., Chalfoun, A. D., Beever, E. A., & Loosen, A. E. (2016). Microrefuges and the occurrence of thermal specialists: Implications for wildlife persistence amidst changing temperatures. *Climate Change Responses*, 3, 8. <https://doi.org/10.1186/s40665-016-0021-4>
- Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396, 41–49. <https://doi.org/10.1038/23876>
- Heino, M., Kaitala, V., Ranta, E., & Lindström, J. (1997). Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings of the Royal Society B: Biological Sciences*, 264, 481–486. <https://doi.org/10.1098/rspb.1997.0069>
- Henry, P., Henry, A., & Russello, M. A. (2012). Variation in habitat characteristics of American pikas along an elevation gradient at their northern range margin. *Northwest Science*, 86, 346–350. <https://doi.org/10.3955/046.086.0410>
- Intergovernmental Panel on Climate Change (IPCC). (2013). Summary for policymakers. In S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Avery, M. Tignor, & H. L. Miller (Eds.), *Climate change 2007: The physical science basis. Contribution of Working Group 1 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1–18). New York, NY: Cambridge University Press.
- Jackson, S. T., Betancourt, J. L., Booth, R. K., & Gray, S. T. (2009). Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences*, 106, 19685–19692. <https://doi.org/10.1073/pnas.0901644106>
- Jeffress, M. R., Apel, J., Garrett, L. K., Holm, G., Larson, D., Nordensten, N., & Rodhouse, T. J. (2011). *Monitoring the American pika (Ochotona princeps) in the Pacific West Region – Crater Lake National Park, Craters of the Moon National Monument and Preserve, Lassen Volcanic National Park, and Lava Beds National Monument: Narrative Version 1.0. Natural Resource Report NPS/UCBN/NRR-2011/336*. Fort Collins, CO: National Park Service.
- Jeffress, M. R., Rodhouse, T. J., Ray, C., Wolff, S., & Epps, C. (2013). The idiosyncrasies of place: Geographic variation in the climate-distribution relationships of the American pika. *Ecological Applications*, 23, 864–878. <https://doi.org/10.1890/12-0979.1>
- Jeffress, M. R., Van Gunst, K. J., & Millar, C. I. (2017). A surprising discovery of American pika sites in the northwestern Great Basin. *Western North American Naturalist*, 77, 252–268. <https://doi.org/10.3398/064.077.0213>
- Jetz, W., Wilcove, D. S., & Dobson, A. P. (2007). Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, 5, e157. <https://doi.org/10.1371/journal.pbio.0050157>
- Kapnick, S., & Hall, A. (2012). Causes of recent changes in western North American snowpack. *Climate Dynamics*, 38, 1885–1899. <https://doi.org/10.1007/s00382-011-1089-y>
- Kery, M., Spillmann, J. H., Truong, C., & Holderegger, R. (2006). How biased are estimates of extinction probability in revisitation studies. *Journal of Ecology*, 94, 980–986. <https://doi.org/10.1111/j.1365-2745.2006.01151.x>
- Kruezer, M. P., & Huntly, N. J. (2003). Habitat-specific demography: Evidence for source-sink population structure in a mammal, the pika. *Oecologia*, 134, 343–349. <https://doi.org/10.1007/s00442-002-1145-8>
- Lawler, J. J., Shafer, S. L., White, D., Kareiva, P., Maurer, E. P., Blaustein, A. R., & Bartlein, P. J. (2009). Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, 90, 588–597. <https://doi.org/10.1890/08-0823.1>
- Lunn, D., Spiegelhalter, D., Thomas, A., & Best, N. (2009). The BUGS project: Evolution, critique, and future directions. *Statistics in Medicine*, 28, 3049–3067. <https://doi.org/10.1002/sim.3680>
- Lute, A. C., Abatzoglou, J. T., & Hegewisch, K. C. (2015). Projected changes in snowfall extremes and interannual variability of snowfall in the western United States. *Water Resources Research*, 51, 960–972. <https://doi.org/10.1002/2014WR016267>
- MacKenzie, D. I., Nichols, J. D., Knutson, M. G., & Franklin, A. B. (2003). Estimating site occupancy, colonization and local extinction when species are detected imperfectly. *Ecology*, 84, 2200–2207. <https://doi.org/10.1890/02-3090>
- MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Hines, J. E., & Bailey, L. L. (2006). *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence*. San Diego, CA: Elsevier.

- MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Hines, J. E., & Bailey, L. L. (2018). *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence*, 2nd ed. San Diego, CA: Elsevier.
- MacKenzie, D. I., & Royle, J. A. (2005). Designing occupancy studies: General advice and allocating survey effort. *Journal of Applied Ecology*, 42, 1105–1114. <https://doi.org/10.1111/j.1365-2664.2005.01098.x>
- Martinez-Meyer, E., Peterson, A. T., & Hargrove, W. W. (2004). Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecology and Biogeography*, 13, 305–314. <https://doi.org/10.1111/j.1466-822X.2004.00107.x>
- McClintock, B. T., Bailey, L. L., Pollock, K. H., & Simons, T. R. (2010). Unmodeled observation error induces bias when inferring patterns and dynamics of species occurrence via aural detections. *Ecology*, 91, 2446–2454. <https://doi.org/10.1890/09-1287.1>
- McKelvey, K. S., Copeland, J. P., Schwartz, M. K., Littell, J. S., Aubry, K. B., Squires, J. R., ... Mauger, G. S. (2011). Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological Applications*, 21, 2882–2897. <https://doi.org/10.1890/10-2206.1>
- Millar, C. I., Delaney, D. L., Hersey, K. A., Jeffress, M. R., Smith, A. T., Van Gunst, K. J., & Westfall, R. D. (2018). Distribution, climatic relationships, and status of American pikas (*Ochotona princeps*) in the Great Basin, USA. *Arctic, Antarctic, and Alpine Research*, 50, e1436296.
- Millar, C. I., Heckman, C., Swanston, C., Schmidt, K., Westfall, R. D., & Delany, D. L. (2014). Radiocarbon dating of American pika fecal pellets provides insights into population extirpations and climate refugia. *Ecological Applications*, 24, 1748–1768. <https://doi.org/10.1890/13-0520.1>
- Millar, C. I., & Westfall, R. D. (2010). Distribution and climate relationships of American pika (*Ochotona princeps*) in the Sierra Nevada and Western Great Basin, USA; Periglacial landforms as refugia in warming climates. *Arctic, Antarctic, and Alpine Research*, 42, 76–88. <https://doi.org/10.1657/1938-4246-42.1.76>
- Millar, C. I., Westfall, R. D., & Delaney, D. L. (2016). Thermal components of American pika habitat—how does a small lagomorph encounter climate? *Arctic, Antarctic, and Alpine Research*, 48, 327–343. <https://doi.org/10.1657/AAAR0015-046>
- Millar, C. I., Westfall, R. D., & Delany, D. L. (2013). New records of marginal locations for American pika (*Ochotona princeps*) in the western Great Basin. *Western North American Naturalist*, 73, 457–476. <https://doi.org/10.3398/064.073.0412>
- Miller, D. A. W., Nichols, J. D., Gude, J. A., Rich, L. N., Podrutzny, K. M., Hines, J. E., & Mitchell, M. S. (2013). Determining occurrence dynamics when false positives occur: Estimating range dynamics of wolves from public survey data. *Plos One*, 8, e65808. <https://doi.org/10.1371/journal.pone.0065808>
- Monahan, W. B., Gross, J. E., Svancara, L. K., & Philippi, T. (2012). *A guide to interpreting NPScape data and analyses*. Natural Resource Technical Report NPS/NRSS/NRTR–2012/578. Fort Collins, CO: National Park Service.
- Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C., & Beissinger, S. R. (2008). Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, 322, 261–264. <https://doi.org/10.1126/science.1163428>
- Morrison, S. F., & Hik, D. S. (2007). Demographic analysis of a declining pika *Ochotona collaris* population: Linking survival to broad-scale climate patterns via spring snowmelt patterns. *Journal of Animal Ecology*, 76, 899–907. <https://doi.org/10.1111/j.1365-2656.2007.01276.x>
- Mote, P. W., Hamlet, A. F., Clark, M. P., & Lettenmaier, D. P. (2005). Declining mountain snowpack in western North America. *Bulletin of the American Meteorological Society*, 86, 39–49. <https://doi.org/10.1175/BAMS-86-1-39>
- Moyer-Horner, L., Smith, M. M., & Belt, J. (2012). Citizen science and observer variability during American pika surveys. *Journal of Wildlife Management*, 76, 1472–1479. <https://doi.org/10.1002/jwmg.373>
- National Operational Hydrologic Remote Sensing Center (NOHRSC). (2004). *Snow data assimilation system (SNODAS) Data Products at NSIDC, Version 1*. Boulder, CO: NOHRSC.
- Nichols, L. B. (2010). Fecal pellets of American pikas (*Ochotona princeps*) provide a crude chronometer for dating patch occupancy. *Western North American Naturalist*, 70, 500–507.
- Ntzoufras, I. (2009). *Bayesian modeling using WinBUGS*. Hoboken, NJ: John Wiley and Sons. <https://doi.org/10.1002/9780470434567>
- Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., ... Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, 5, 215–225. <https://doi.org/10.1038/NClimate2448>
- Parnesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Peacock, M. M. (1997). Determining natal dispersal patterns in a population of North American pikas (*Ochotona princeps*) using direct mark-resight and indirect genetic methods. *Behavioral Ecology*, 8, 340–350. <https://doi.org/10.1093/beheco/8.3.340>
- Peacock, M. M., & Smith, A. T. (1997). The effect of habitat fragmentation on dispersal patterns, mating behavior, and genetic variation in a pika (*Ochotona princeps*) metapopulation. *Oecologia*, 112, 524–533. <https://doi.org/10.1007/s004420050341>
- Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography*, 12, 361–371. <https://doi.org/10.1046/j.1466-822X.2003.00042.x>
- R Development Core Team. (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Ray, C., Beever, E. A., & Rodhouse, T. J. (2016). Distribution of a climate-sensitive species at an interior range margin. *Ecosphere*, 7, e01379. <https://doi.org/10.1002/ecs2.1379>
- Risk, B. B., de Valpine, P., & Beissinger, S. R. (2011). A robust-design formulation of the incidence function model of metapopulation dynamics applied to two species of rails. *Ecology*, 92, 462–474. <https://doi.org/10.1890/09-2402.1>
- Rodhouse, T. J., Beever, E. A., Garrett, L. K., Irvine, K. M., Jeffress, M. R., Muntz, M., & Ray, C. (2010). Distribution of American pikas in a low-elevation lava landscape: Conservation implications from the range periphery. *Journal of Mammalogy*, 91, 1287–1299. <https://doi.org/10.1644/09-MAMM-A-334.1>
- Rodhouse, T. J., Hovland, M., & Jeffress, M. R. (2017). Variation in subsurface thermal characteristics of microrefuges used by range core and peripheral populations of the American pika (*Ochotona princeps*). *Ecology and Evolution*, 7, 1514–1526. <https://doi.org/10.1002/ece3.2763>
- Root, T. L., Price, J. T., Hall, J. R., & Schneider, S. H. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, 421, 57. <https://doi.org/10.1038/nature01333>
- Rowe, K. C., Rowe, K. M. C., Tingley, M. W., Koo, M. S., Patton, J. L., Conroy, C. J., ... Moritz, C. (2015). Spatially heterogeneous impact of climate change on small mammals of montane California. *Proceedings of the Royal Society B*, 282, 20141857.
- Royle, J. A., & Dorazio, R. M. (2008). *Hierarchical modeling and inference in ecology*. London, England: Elsevier.
- Royle, J. A., & Kéry, M. (2007). A Bayesian state-space formulation of dynamic occupancy models. *Ecology*, 88, 1813–1823. <https://doi.org/10.1890/06-0669.1>
- Royle, J. A., & Link, W. A. (2006). Generalized site occupancy models allowing for false positive and false negative errors. *Ecology*, 87, 835–841. [https://doi.org/10.1890/0012-9658\(2006\)87\[835:GSOMAF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[835:GSOMAF]2.0.CO;2)
- Ruiz-Gutierrez, V., & Zipkin, E. F. (2011). Detection biases yield misleading patterns of species persistence and colonization in fragmented landscapes. *Ecosphere*, 2, 61. <https://doi.org/10.1890/ES10-00207.1>
- Schwalm, D., Epps, C. W., Rodhouse, T. J., Monahan, W. B., Castillo, J. A., Ray, C., & Jeffress, M. R. (2016). Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: A place-based approach. *Global Change Biology*, 22, 1572–1584. <https://doi.org/10.1111/gcb.13189>

- Şekercioğlu, Ç. H., Schneider, S. H., Fay, J. P., & Loarie, S. R. (2008). Climate change, elevational range shifts, and bird extinctions. *Conservation Biology*, 22, 140–150. <https://doi.org/10.1111/j.1523-1739.2007.00852>
- Shinderman, M. (2015). American pika in a low-elevation lava landscape: Expanding the known distribution of a temperature-sensitive species. *Ecology and Evolution*, 5, 3666–3676. <https://doi.org/10.1002/ece3.1626>
- Shmueli, G. (2010). To explain or to predict? *Statistical Science*, 25, 289–310. <https://doi.org/10.1214/10-ST5330>
- Smith, A. T., & Ivins, B. L. (1983). Colonization in a pika population: Dispersal vs philopatry. *Behavioral Ecology and Sociobiology*, 13, 37–47. <https://doi.org/10.1007/BF00295074>
- Smith, A. T., & Nagy, J. D. (2015). Population resilience in an American pika (*Ochotona princeps*) metapopulation. *Journal of Mammalogy*, 96, 394–404. <https://doi.org/10.1093/jmammal/gyv040>
- Smith, A. T., Nagy, J. D., & Millar, C. I. (2016). Behavioral ecology of American pikas (*Ochotona princeps*) at Mono Craters, California: Living on the edge. *Western North American Naturalist*, 76, 459–484. <https://doi.org/10.3398/064.076.0408>
- Smith, A. T., & Millar, C. I. (In press). *American pika (Ochotona princeps) population survival in winters with low or no snowpack*. *Western North American Naturalist*.
- Smith, A. T., & Weston, M. L. (1990). *Ochotona princeps*. *Mammalian Species*, 352, 1–8. <https://doi.org/10.2307/3504319>
- Stevens, D. L., & Olsen, A. R. (2004). Spatially balanced sampling of natural resources. *Journal of the American Statistical Association*, 99, 262–278. <https://doi.org/10.1198/016214504000000250>
- Stewart, J. A. E., Perrine, J. D., Nichols, L. B., Thorne, J. H., Millar, C. I., Goehring, K. E., ... Wright, D. H. (2015). Revisiting the past to foretell the future: Summer temperature and habitat area predict pika extirpations in California. *Journal of Biogeography*, 42, 880–890. <https://doi.org/10.1111/jbi.12466>
- Stewart, J. A. E., Wright, D. H., & Heckman, K. A. (2017). Apparent climate-mediated loss and fragmentation of core habitat of the American pika in the northern Sierra Nevada, California, USA. *PLoS One*, 12, e0181834. <https://doi.org/10.1371/journal.pone.0181834>
- Sturtz, S., Ligges, U., & Gelman, A. (2005). R2WinBUGS: A package for running WinBUGS from R. *Journal of Statistical Software*, 12, 1–16.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ... Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427, 145–148. <https://doi.org/10.1038/nature02121>
- Thomas, C. D., & Hanski, I. (2004). Metapopulation dynamics in changing environments: Butterfly responses to habitat and climate change. In I. Hanski, & O. E. Gaggiotti (Eds.), *Ecology, genetics, and evolution of meta-populations*. Amsterdam, The Netherlands: Elsevier Academic Press.
- Thompson, S. K. (2002). *Sampling*, 2nd ed. New York, NY: John Wiley & Sons.
- Thornton, M. M., Thornton, P. E., Wei, Y., Vose, R. S., & Boyer, A. G. (2017). *Daymet: Station-level inputs and model predicted values for North America, Version 3*. Oak Ridge, TN: ORNL DAAC.
- Varner, J., & Dearing, M. D. (2014). The importance of biologically relevant microclimates in habitat suitability assessments. *PLoS ONE*, 9, e104648. <https://doi.org/10.1371/journal.pone.0104648>
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., ... Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395. <https://doi.org/10.1038/416389a>
- Wilkening, J. L., Ray, C., Beever, E. A., & Brussard, P. F. (2011). Modeling contemporary range retraction in Great Basin pikas (*Ochotona princeps*) using data on microclimate and microhabitat. *Quaternary International*, 235, 77–88. <https://doi.org/10.1016/j.quaint.2010.05.004>
- Williams, C. M., Henry, H. A. L., & Sinclair, B. J. (2015). Cold truths: How winter drives responses of terrestrial organisms to climate change. *Biological Reviews*, 90, 214–235. <https://doi.org/10.1111/brv.12105>
- Willis, K. J., & Bhagwat, S. A. (2009). Biodiversity and climate change. *Science*, 326, 806–807. <https://doi.org/10.1126/science.1178838>
- Wilson, R. J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R., & Monserrat, V. J. (2005). Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, 8, 1138–1146. <https://doi.org/10.1111/j.1461-0248.2005.00824.x>
- Yandow, L. H., Chalfoun, A. D., & Doak, D. F. (2015). Climate tolerances and habitat requirements jointly shape the elevational distribution of the American pika (*Ochotona princeps*) with implications for climate change effects. *PLoS One*, 10, e0131082. <https://doi.org/10.1371/journal.pone.0131082>
- Zipkin, E. F., Campbell Grant, E. H., & Fagan, W. F. (2012). Evaluating the predictive abilities of community occupancy models using AUC while accounting for imperfect detection. *Ecological Applications*, 22, 1962–1972. <https://doi.org/10.1890/11-1936.1>

BIOSKETCH

Tom Rodhouse is an ecologist with the US National Park Service vital signs monitoring program and Oregon State University courtesy graduate faculty member. He approaches questions from a biogeographical perspective and uses species distribution models and related tools to help protected-area decision-makers make strategic conservation decisions. Tom and his co-author Matt Shinderman direct the Human & Ecosystem Resilience & Sustainability Lab on the OSU-Cascades Campus to facilitate collaborative interagency co-production of applied conservation science. You can visit their University laboratory website here: <https://osucascades.edu/HERS> and Tom's National Park Service website here: <https://science.nature.nps.gov/im/units/ucbn/>.

Author contributions: T.J.R., M.R.J., S.R.M., N.J.N., M.L.M. and C.W.E. conceived of the ideas and planned the study. M.R.J., S.R.M., N.J.N. and M.L.M. collected the data. M.S. tested study ideas and methodology in a replicate study area and provided feedback for study refinement. K.R.S. analysed climate data. D.S., J.A.C. and C.W.E. analysed and interpreted genetic data and developed the genetic distance radii for use with the INSOLATION and %HABITAT metrics. T.J.R. performed the modelling and led manuscript writing. All other authors helped write, edit and refine the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Rodhouse TJ, Jeffress MR, Sherrill KR, et al. Geographical variation in the influence of habitat and climate on site occupancy turnover in American pika (*Ochotona princeps*). *Divers Distrib*. 2018;24:1506–1520. <https://doi.org/10.1111/ddi.12791>