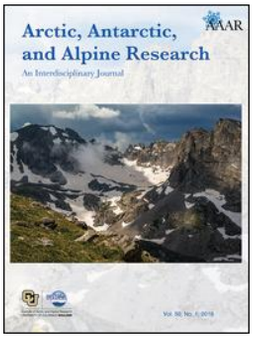

Taylor & Francis
Taylor & Francis Group

Arctic, Antarctic, and Alpine Research
An Interdisciplinary Journal

ISSN: 1523-0430 (Print) 1938-4246 (Online) Journal homepage: http://www.tandfonline.com/loi/uaar20

Distribution, climatic relationships, and status of American pikas (Ochotona princeps) in the Great Basin, USA

Constance I. Millar, Diane L. Delany, Kimberly A. Hersey, Mackenzie R. Jeffress, Andrew T. Smith, K. Jane Van Gunst & Robert D. Westfall

To cite this article: Constance I. Millar, Diane L. Delany, Kimberly A. Hersey, Mackenzie R. Jeffress, Andrew T. Smith, K. Jane Van Gunst & Robert D. Westfall (2018) Distribution, climatic relationships, and status of American pikas (Ochotona princeps) in the Great Basin, USA, Arctic, Antarctic, and Alpine Research, 50:1, e1436296

To link to this article: https://doi.org/10.1080/15230430.2018.1436296

This article not subject to U.S. copyright law.

View supplementary material

Published online: 30 Apr 2018.

Submit your article to this journal

Article views: 209

View related articles

View Crossmark data

Full Terms & Conditions of access and use can be found at
http://www.tandfonline.com/action/journalInformation?journalCode=uaar20

ARCTIC, ANTARCTIC, AND ALPINE RESEARCH
2018, VOL. 50, NO. 1, e1436296 (19 pages)
https://doi.org/10.1080/15230430.2018.1436296

Taylor & Francis
Taylor & Francis Group

OPEN ACCESS Check for updates

Distribution, climatic relationships, and status of American pikas (*Ochotona princeps*) in the Great Basin, USA

Constance I. Millar[a], Diane L. Delany[a], Kimberly A. Hersey[b], Mackenzie R. Jeffress[c], Andrew T. Smith[d], K. Jane Van Gunst[e], and Robert D. Westfall[a]

[a]USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA; [b]Utah Division of Wildlife, Salt Lake City, Utah, USA; [c]Nevada Department of Wildlife, Elko, Nevada, USA; [d]School of Life Sciences, Arizona State University, Tempe, AZ, USA; [e]Nevada Department of Wildlife, Winnemucca, Nevada, USA

ABSTRACT

To advance understanding of the distribution, climatic relationships, and status of American pikas (*Ochotona princeps*) in the Great Basin, United States, we compiled 2,387 records of extant pika sites surveyed since 2005, 89 records of documented extirpated sites (resurvey of historic sites), and 774 records of sites with old sign only. Extant sites extended across five degrees latitude and ten degrees longitude, encompassed six subregions, traversed forty mountain ranges, spanned 2,378 m in elevation (1,631–4,009 m), and comprised three of five currently described pika subspecies. A climate envelope for extant sites using the PRISM climate model expands the range of temperature and precipitation values that have been previously described. Extirpated and old-sign sites were mostly found within the geographic and climatic space of extant sites, but often in warmer and drier portions. Considerable overlap of extirpated, old, and extant groups within the same climate space suggests that nonclimatic factors have also contributed to population losses. The broad distribution and enlarged climate envelope of extant pika sites indicate that despite some localized extirpations, pika populations are persisting across Great Basin mountains, and appear to be able to tolerate a broader set of habitat conditions than previously understood.

ARTICLE HISTORY
Received 13 June 2017
Accepted 8 January 2018

KEYWORDS
American pika; climate change; Great Basin; geographic distribution; *Ochotona princeps*; population extirpation; population occurrence

Introduction

American pikas (*Ochotona princeps*) have been widely reported as vulnerable to contemporary climate change (Appendix 1). These small lagomorphs, distributed across montane regions of western North America, thermoregulate poorly, have high resting and low lethal body temperatures, do not hibernate, and show minimal physiological resilience to temperature extremes and chronic stress (Smith and Weston 1990). Pikas are behaviorally solitary and patchily distributed in disjunct talus fields, which under even the best of conditions support low population numbers. Dependence on talus patches, coupled with the potential for local metapopulation dynamics (Smith and Gilpin 1997; Smith and Nagy 2015), have been considered additional risk factors for pikas under accelerating climate change.

Trends of extirpation during prehistoric times provide temporal context for modern population vulnerabilities. Prehistoric records of pikas in the Great Basin (GB) portion of the range document millennial scale population losses correlated with Late Pleistocene and Holocene warming (Grayson 2005). Rising modern temperatures prompt a similar concern for climatic impacts, with an expectation that pika populations will retreat to higher elevations for suitable habitat, eventually running out of space.

Scientific evidence in support of this scenario, however, is inconsistent. In the GB, resurveys of historic sites document a steep extirpation curve in recent decades at low elevations and other marginal sites where temperature is typically warmest (Beever et al. 2011, 2016; Stewart et al. 2015). In addition, extirpation at some northwestern GB sites has been assumed when only old sign was found during single-visit surveys (Jeffress, Van Gunst, and Millar 2017). In other time-series studies of this region, however, population status does not correlate consistently with temperature or elevation (Millar et al. 2014a; Smith and Nagy 2015;

CONTACT Constance I. Millar cmillar@fs.fed.us
Supplemental data for this article can be accessed here.

This article not subject to U.S. copyright law.
This is an Open Access article distributed under the terms of the Creative Commons Attribution License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Stewart and Wright 2012). Surveys in parts of the western GB (Massing 2012; Millar and Westfall 2010; Millar, Westfall, and Delany 2013; Stewart et al. 2015) documented the locally widespread presence of pikas, including sites at low and climatically marginal GB sites, which suggest thermal tolerance (Beever et al. 2008; Collins and Bauman 2012; Jeffress, Van Gunst, and Millar 2017; Millar, Westfall, and Delany 2013; Smith, Nagy, and Millar 2016).

Differing methods used for data collection and analyses may contribute to the inconsistency of the earlier findings. Because the primary objective of many pika studies in the GB was to resurvey twentieth-century historic sites, study locations were limited by their availability and distribution, and documented historic sites do not necessarily represent the range of occupied sites. In addition, studies based on surveys of modern (nonhistoric) sites have focused on limited portions of the GB pika range. Finally, some monitoring efforts used rapid-assessment surveys, which have an increased likelihood for introducing error in population status compared with traditional methods that are more time consuming (Smith, Nagy, and Millar 2016). Taken together, a widely held assumption in scientific and public understanding is that pikas have become rare (especially in the GB), pikas are limited to a few high and cool elevations, a significant portion of GB pika sites have become extirpated, and that the species is at risk of extinction. In many ways, the American pika has become an icon of climate-change vulnerability (see Appendix 1).

Because these perceptions of American pika vulnerability are based on a small number of sites and in limited portions of the GB, we sought to systematically document the range of known pika occurrence locations across the GB. To provide temporal, geographic, and climatic context for evaluating the conditions and potential vulnerability of GB pikas, we compiled known published and unpublished surveys of modern occupied sites, documented extirpated sites, and old-sign-only sites across the hydrographic GB. We interrogated the resulting databases to answer the following questions and to provide a more comprehensive understanding of the status of pikas in the GB:

(1) What is the geographic distribution of extant pika populations in the GB?
(2) What are the prevailing climatic conditions at extant and relict pika locations?
(3) Do the geographic and climatic values for the extant sites differ from those of twentieth- and twenty-first-century extirpation sites and sites with only old sign?
(4) How do the new data on the geographic and climatic limits of extant pika populations across the GB affect and/or change our understanding of the status and vulnerability of pikas in the GB relative to climate?

Methods

The study covered the hydrographic Great Basin, United States, where all surface waters drain to interior basins. We derived the perimeter and interior watershed boundaries from the National Hydrography Dataset (Levels 2, 3, and 4 HUC; USGS, The National Map, accessed March 11, 2016). This range includes parts of California, Oregon, Nevada, and Utah (Figure 1).

Extant pika sites

From published literature and unpublished inventories, we compiled records of extant (i.e., occupied) locations for American pika populations within the GB. We included a few records that were outside the hydrographic GB but less than 5 km from the boundary; these were in areas where the GB boundary was topographically indistinct and records were otherwise sparse or absent. These records represent a mix of survey methods based on the source of the data (see Appendix 2 for protocols). For previously unpublished records, we only included those where expert surveyors had conducted the surveys. Given recently reported population declines, we accepted only sites that were documented as extant in 2005 or later (most recent, spring 2017). We felt that this threshold was necessary to accept a record as current. While recognizing that this was a qualitative decision, we based it on published records (Beever et al. 2011), wherein repeat observations showed losses during time periods greater than about a decade. Our choice of 2005 was further based on published analyses (Stewart et al. 2015) that considered records older than 2000 (approximately fifteen years prior to analysis) as "historic." We defined a talus as "extant" when one or more of several commonly used criteria for the presence of pikas was noted: sightings, vocalizations, fresh pellets (in combination with other signs), and current-year haypiles (winter caches of vegetation). Unpublished inventories included records of sites observed by one of the authors or provided by state Natural Heritage or wildlife offices. We did not include records from a paper published late in our manuscript revision period (Stewart, Wright, and Heckman 2017). Extant locations reported in that paper are, however, already represented by records in our database. Given the methods of observation, and recognizing the population ecology and behavior of the species (Smith and Nagy 2015), we assume that most if not all of the extant sites we compiled to represent self-sustaining local populations.

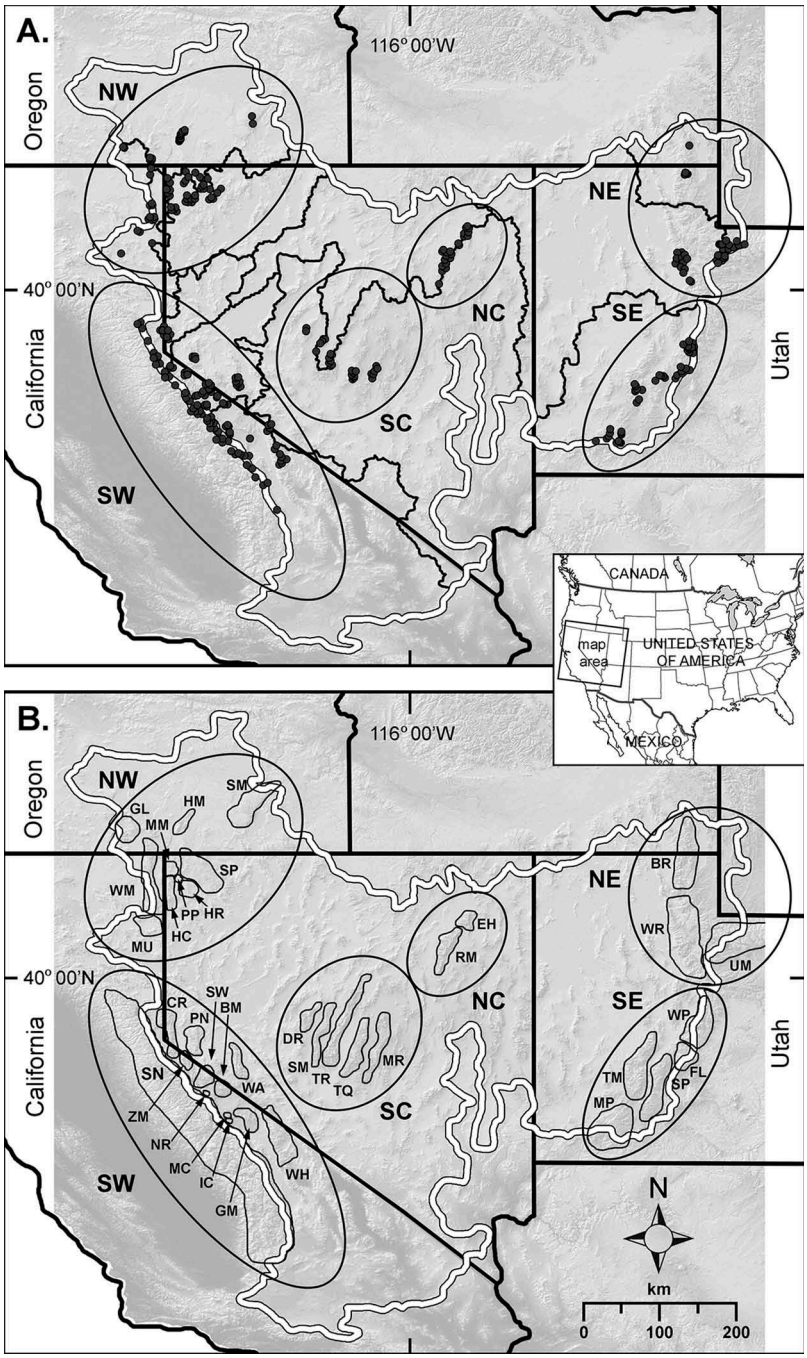

Figure 1. The hydrographic Great Basin. (A) Great Basin perimeter and subwatershed boundaries with six subregions (bold lines) used to assess extant American pika sites (black dots). More than one observation record is included in most dots at this scale. (B) Mountain ranges mentioned in the text where extant pika sites occur (not all ranges are shown). Codes for mountain ranges: *Northwest subregion*: GL, Glass Mountains; HM, Hart Mountains; HC, Hayes Canyon Range; HR, High Rock; MU, Madeline Uplands; MM, Mosquito Mountains; PP, Painted Point Range; SP, Sheldon Plateau; SM, Steens Mountains; WM, Warner Mountains. *Southwest subregion*: BM, Bodie Mountains; CR, Carson Range; GM, Glass Mountains; IC, Inyo Craters; MC, Mono Craters; NR, New Range; PN, Pine Nut Mountains; SN, Sierra Nevada; SW, Sweetwater Mountains; WA, Wassuk Mountains; WH, White Mountains; ZM, Zunnamed Mountains. *North Central subregion*: EH, East Humboldt Range; RM, Ruby Mountains. *South Central subregion*: DR, Desatoya Range; MR, Monitor Range; SM, Shoshone Mountains; TR, Toiyabe Range; TQ, Toquima Range. *Northeast subregion*: BR, Bear River Mountains; UM, Uinta Mountains; WR, Wasatch Range. *Southeast subregion*: FL, Fish Lake Plateau; MP, Markagunt Plateau; SP, Sevier Plateau; TM, Tushar Mountains; WP, Wasatch Plateau.

Definitions of individual sites varied among the studies, and included detections a few meters apart (e.g., Nevada Department of Wildlife), occurrence sites ≥50 m apart (e.g., Millar and Westfall 2010), and areas within a 1–3 km radius (e.g., Beever et al. 2016). We screened for redundancy and removed duplicate

records. Remaining records were compiled into a single database with associated geographic information (mountain range, location, latitude, longitude, elevation, aspect). In a few cases, coordinates listed in original publications were in error by a degree or more; these we corrected and noted in Appendices 3–5. Aspects for extant records, if not documented in the original database, were estimated by intersecting locations with 30 m tiles in geographic information systems (GIS; ESRI 2015). Two methods for quantifying aspect were used: aspect degrees transformed to cosine, and aspect degrees binned into one of eight 45° ordinal categories (N, NE, E, SE, etc.). When elevation data were not given in published or unpublished records, they were estimated from 30 m digital elevation models (DEM) in GIS. We included elevation and aspect because these have been used as proxies for climate in other pika studies. Other environmental factors—such as geomorphic setting; talus substrate, size, and connectivity; or vegetation characteristics—while relevant, could not be included because of heterogeneity of methods used in previous studies and, thus, our inability to quantify these variables.

To avoid overrepresentation from closely adjacent observations, we established in GIS a 50 m buffer around the location of each record. This distance was used as a conservative haypile nearest-neighbor distance, representing an individual animal territory (Smith and Weston 1990). Records that overlapped 50 m buffers were combined into "50 m buffer clusters," which in some cases resulted in larger polygons (as in Jeffress, Van Gunst, and Millar 2017).

Extirpated and old pika sites

We also compiled records of sites that were documented as extirpated or contained only old sign. For this we used published literature and unpublished inventories where observations or publications dated from 2005 or later. For the extirpated dataset we included only records for which a resurvey had been conducted, the repeat surveys were conducted at five or more years apart, and both the most recent and the penultimate surveys indicated no sign of pika occurrence.

We compiled a third dataset from published and unpublished sources dated from 2005 or later. This included records in which surveyors reported only old pika sign at a site, based either on single-visit surveys or on resurveys that did not meet the previous criteria. "Old" pika sign (i.e., older than the current year) was characterized by small, decomposing pellets, decomposing haypiles, and/or old urine stains, coupled with no observation of live animals. We treated redundancies, calculated 50 m buffer clusters, and estimated elevation and aspect for extirpated sites and old pika sites in the same way as for sites in the extant group. We refer to extirpated and old sites collectively as "relict sites."

Geographic and climatic data analysis

To better understand the role of geography and climate in pika occurrence across the GB, we compared these variables for extant and relict pika sites. Analyses were nested by geographic scale. The broadest level was the hydrographic GB. Based on GB geography and bioclimatic zonation, we partitioned pika sites into six subregions within the GB (Figure 1). These are described as: (1) Southwest (SW) = Sierra Nevada, White Mountains, and adjacent minor ranges; (2) Northwest (NW) = northeast California, northwest Nevada, and south-central Oregon; (3) North Central (NC) = northeast Nevada; (4) South Central (SC) = central Nevada; (5) Northeast (NE) = northern Utah (Uinta Mountains, Wasatch Range, Bear River Mountains); and (6) Southeast (SE) = southern Utah. For analyses within subregions, we assessed differences in pika populations among mountain ranges. Elevation spans within ranges are reported as indicators of habitat breadth used locally by pikas.

To assess differences among slope aspects within and between the three groups (extant, extirpated, and old), we applied a nominal logistic two-level hierarchical analysis of variance (ANOVA), assessing differences among subregions and among mountain ranges within subregions (JMP 12.2; SAS Institute 2015). The units of analysis for elevation and aspect were the 30 m DEM tiles. Differences in elevation among subregions and mountain ranges were tested in a two-level nested ANOVA, with ranges in subregions as a random effect. We evaluated climate relationships for the three datasets using the 800 m (30 arc-sec) PRISM climate model (Daly, Neilson, and Phillips 1994). Units of analyses for climate were the 800 m PRISM tiles. Although surface-air temperatures, as modeled by PRISM, do not represent microclimatic conditions encountered among habitat components of American pikas, some of which appear decoupled from surface air (Millar, Westfall, and Delany 2016), talus surface temperatures do correlate with surface-air temperatures as measured by PRISM. We used PRISM values to characterize the overall environmental contexts of pika

sites at local to subregional to GB scales, and to compare with the local climatic conditions described in other pika studies, without intending to imply that these represent the specific conditions encountered by pikas. We selected climate variables that others have used (Beever et al. 2010, 2011; Millar and Westfall 2010; Wilkening et al. 2011) to discriminate between extant and extirpated pika sites, and from those determined variables that best predicted pika population status in our datasets (see the list of variables in Table 4). We excluded winter precipitation as a variable, because in the GB it is highly correlated with annual precipitation.

Summary statistics were compiled for the GB and for each subregion. We assessed correlations between elevation and climate by computing elevation means for digital elevation model tiles, then computed climate and elevation means for PRISM tiles. Climate differences in extant locations among subregions and ranges in individual subregions were assessed by discriminant (canonical) analysis. Differences in climate between extant and relict locations and among subregions were tested with a two-factor multivariate analysis of variance (MANOVA), including two-way interactions. Correlations, discriminant analysis, nested ANOVA and MANOVA, and tests of significance (F statistics, t tests) were performed in JMP (JMP 12.2; SAS Institute 2015). Distributions for the ANOVA and MANOVA analyses showed values close to normality; for the discriminant analysis, after excluding a few (~6) outliers, residuals for the first canonical vector were not significantly different from normality.

Results

Distribution and climate relationships of extant sites

We compiled 2,387 individual pika records from published and unpublished sources (Tables 1 and 2; Appendix 3). Combining closely adjacent records yielded 1,320 50 m buffer clusters. Pika records were distributed across forty mountain ranges, including the large Sheldon Plateau, Nevada, which contains many poorly distinguished mountain groups (Table 2). All six subregions were represented, with the smallest number of records in the SE (63) and the largest in the NW (958). Elevations of extant sites across the entire GB ranged from 1,631 m to 4,009 m (a span of 2,378 m; $\bar{x}$ = 2,569 m). Mean elevation in the NW subregion (2,039 m) was significantly lower ($p < 0.001$) than in the remaining five subregions ($\bar{x}$ = 2,990 m), which did not differ significantly from one another. Elevation

Table 1. Distribution of American pika sites in the hydrographic Great Basin.

			Pika Record Elevations (m)			
Subregions	Number of Records	Number of Mountain Ranges	Mean	Minimum	Maximum	Span
1. Extant Sites						
Northwest	958	12	2,039	1,631	3,208	1,577
Southwest	928	13	2,832	1,827	4,009	2,182
North Central	111	2	2,999	2,323	3,436	1,113
South Central	170	5	3,007	2,461	3,503	1,042
Northeast	157	3	2,955	2,377	3,650	1,273
Southeast	63	5	3,111	2,325	3,477	1,152
Total	**2,387**	**40**	**2,577**	**1,631**	**4,009**	**2,378**
2. Extirpated Sites						
Northwest	26	8	1,929	1,615	2,560	945
Southwest	57	5	2,764	2,113	3,106	993
North Central	None					
South Central	6	5	2,507	2,160	2,886	726
Northeast	None					
Southeast	None					
Total	**89**	**18**	**2,420**	**1,615**	**3,106**	**1,491**
3. Historic Resurvey Subset						
Extant	48	15	2,584	1,872	3,368	1,496
Extirpated	23	15	2,196	1,615	2,753	1,138
Total	**71**	**24**	**2,458**	**1,615**	**3,368**	**1,753**
4. Old Sites						
Northwest	661	15	1,966	1,628	2,598	970
Southwest	76	7	2,532	2,104	3,085	981
North Central	None					
South Central	16	2	2,737	2,483	3,267	784
Northeast	11	3	2,781	2,463	3,169	706
Southeast	10	4	3,099	2,656	3,435	779
Total	**774**	**31**	**2,054**	**1,628**	**3,435**	**1,807**

Notes. 1. Extant sites. 2. Extirpated sites, twentieth and twenty-first century. 3. Subset of records that derive from historic resurvey locations. 4. Old sites, from single survey observations or limited range resurveys.

Table 2. Mountain ranges within Great Basin subregions that contain extant pika sites.

Subregions	Mountain Ranges	State	Number of Pika Records	Pika Sites: Elevation (m) Mean	Minimum	Maximum	Span
Northwest	Cascade Range	CA	4	1,651	1,631	1,676	45
	Glass Mountains	OR	9	2,271	2,228	2,413	185
	Hart Mountains	OR	110	1,978	1,809	2,240	431
	Hays Canyon Range	NV	104	2,046	1,924	2,211	287
	High Rock	NV	301	1,930	1,768	2,100	332
	Madeline Uplands	CA	6	2,221	1,848	2,411	563
	Massacre Rim	NV	23	1,876	1,838	2,021	183
	Mosquito Mountains	NV	108	1,905	1,807	1,973	166
	Painted Point Range	NV	22	1,823	1,769	2,005	236
	Sheldon Plateau	NV	248	1,963	1,813	2,204	391
	Steens Mountains	OR	2	2,394	2,031	2,757	726
	Warner Mountains	CA/OR	21	2,418	1,766	3,208	1,442
Southwest	Bodie Mountains	CA/NV	18	2,644	2,545	2,761	216
	Carson Range	CA/NV	22	2,863	2,599	3,190	591
	Glass Mountains	CA	1	3,395	NA	NA	NA
	Inyo Craters	CA	11	2,540	2,471	2,984	513
	Mono Craters	CA	23	2,283	2,055	2,573	518
	New Range	CA	9	2,644	2,469	2,865	396
	Pine Grove Hills	NV	4	2,853	2,815	2,913	98
	Pine Nut Mountains	CA/NV	22	2,731	2,567	2,873	306
	Sierra Nevada	CA/NV	613	2,984	1,827	3,953	2,126
	Sweetwater Mountains	CA/NV	65	2,977	2,310	3,348	1,038
	Wassuk Mountains	NV	36	3,064	2,891	3,397	506
	White Mountains	CA/NV	91	3,279	2,442	4,009	1,543
	Zunnamed Mountains	CA	13	2,582	2,366	2,716	350
North Central	East Humboldt Range	NV	41	3,039	2,688	3,334	646
	Ruby Mountains	NV	70	2,958	2,323	3,436	1,113
South Central	Desatoya Range	NV	2	2,655	2,461	2,849	388
	Monitor Range	NV	33	3,152	2,652	3,285	633
	Shoshone Mountains	NV	52	2,730	2,546	2,879	333
	Toiyabe Range	NV	35	3,003	2,652	3,503	851
	Toquima Range	NV	48	3,192	2,861	3,492	631
Northeast	Bear River Mountains	UT	10	2,701	2,554	2,955	401
	Uinta Mountains	UT	43	3,056	2,377	3,650	1,273
	Wasatch Range	UT	104	3,107	2,611	3,549	938
Southeast	Fish Lake Plateau	UT	9	3,218	2,894	3,452	558
	Markagunt Plateau	UT	19	2,785	2,325	3,342	1,017
	Sevier Plateau	UT	5	3,171	2,978	3,276	298
	Tushar Mountains	UT	13	3,200	2,927	3,477	550
	Wasatch Plateau	UT	17	3,183	3,209	3,333	124
40 Ranges			**2,387**	**2,577**	**1,631**	**4,009**	**2,378**

spans were greatest in the SW subregion and least in the SC. The subset of extant records that derived from published historic resurveys had a mean elevation of 2,584 m and range of 1,872–3,368 m (Table 1).

Although extant pika sites were found on all aspects, there was a slight excess of northerly aspects (Table 3). The ANOVA yielded significant ($p < 0.0001$) differences in aspect among subregions and among ranges within subregions; differences among subregions and ranges in subregions were significant ($p > 0.001$), although the chi-square for ranges was much larger than that for subregions. North aspects had the largest percentage of extant sites, particularly in the central subregions, followed by northeast and northwest aspects. Southerly and eastward aspects had the lowest representation. These patterns were relatively consistent across subregions, with exceptions for the southwesterly aspects, where the NE and SE subregions had more than twice the percentage of extant sites than other subregions.

Extant pika sites intersected with 782 PRISM climate tiles. Discriminant analysis of the extant sites identified the six subregions as distinct groups (Figure 2). The first three canonical vectors described 93 percent of the variation (v1, 66%; v2, 19%; v3, 8%), with canonical correlations (goodness of fit) of 0.99, 0.97, and 0.92 for v1, v2, and v3, respectively (Table 4). Canonical scores of vector 1 were highly correlated with summer precipitation (sum of July, August, and September values) and winter maximum temperature (Tmax; sum of December, January, and February values) among subregions, and moderately to weakly correlated with winter and summer minimum temperature (Tmin). Vector 2 was highly correlated with summer Tmax and annual and September Tmin among subregions, and moderately correlated with annual Tmax and winter and summer Tmin. Vector 3 was moderately correlated with July dewpoint temperature, a measure of humidity, among subregions. Ranges in subregions had

Table 3. Percent occurrence of slope aspects of pika sites by subregion.

	%N	%NE	%E	%SE	%S	%SW	%W	%NW
1. Extant Sites Subregion								
Northwest	17	6	9	13	9	7	23	17
Southwest	17	15	9	14	16	9	8	12
North Central	28	18	10	5	7	2	15	14
South Central	26	23	14	15	12	2	4	4
Northeast	13	14	6	10	12	16	11	18
Southeast	12	13	3	15	12	18	12	15
Means	**19**	**15**	**9**	**12**	**11**	**9**	**12**	**13**
2. Extirpated Sites Subregion[1]								
Northwest	32	23	5	9	5	9		18
Southwest	39	8	12	2	8	14	8	8
Means	**37**	**13**	**10**	**4**	**7**	**13**	**6**	**11**
3. Old Sites Subregion[2]								
Northwest	11	9	7	8	13	22	13	18
Southwest	33	5	9	5	8	13	14	14
South Central	7	67	0	13	7	0	7	0
Northeast	33	25	0	17	17	0	8	0
Southeast	0	43	14	29	0	0	0	14
Means	**17**	**30**	**6**	**14**	**9**	**7**	**8**	**9**

Notes. [1]South Central subregion not included as there were only a few records.
[2]No old sites in North Central subregions.

Table 4. Correlations among climate variables and vectors (CV 1–3) from discriminant analyses. Correlations overall (across subregions) and for individual subregions (among ranges within subregions), with percent of total variation explained by the canonical vectors and overall canonical correlations. CV3 values are not shown for the SC and SE subregions because their contributions were minor.

	Subregions			Northwest			Southwest			North Central	South Central		Northeast		Southeast	
	CV1	CV2	CV3	CV1	CV2	CV3	CV1	CV2	CV3	CV1	CV1	CV2	CV1	CV2	CV1	CV2
Annual precipitation	−0.55	−0.54	−0.45	0.95	0.03	0.04	−0.70	−0.21	−0.56	−0.90	0.17	−0.95	1.00	−0.02	−0.40	−0.83
July precipitation	−0.89	−0.33	0.24	0.82	−0.06	0.35	0.68	−0.56	0.36	−0.36	0.77	−0.57	−0.80	0.60	−0.35	0.55
August precipitation	−0.93	−0.25	0.18	0.49	−0.60	0.45	0.92	−0.03	0.22	0.00	0.84	−0.46	−0.48	0.88	−0.93	−0.11
September precipitation	−0.97	−0.13	−0.15	0.77	0.37	0.27	−0.49	−0.02	−0.74	−0.67	0.85	−0.50	0.66	0.75	0.31	−0.87
July dewpoint temperature	−0.23	0.16	−0.78	−0.73	−0.30	−0.32	−0.63	−0.13	−0.43	−0.68	−0.25	0.80	−0.37	−0.93	−0.06	0.99
Annual Tmax	0.49	0.63	0.14	−0.84	−0.17	−0.11	−0.45	0.47	0.33	0.40	−0.27	0.83	−0.92	−0.40	−0.03	0.93
December Tmax	0.93	−0.09	0.06	−0.74	−0.08	0.09	−0.55	0.37	0.26	0.59	−0.08	0.89	−0.99	0.16	0.02	0.95
January Tmax	0.93	−0.04	0.04	−0.75	−0.06	0.23	−0.51	0.35	0.21	0.47	0.06	0.90	−0.97	−0.23	0.08	0.95
February Tmax	0.82	0.25	0.04	−0.71	−0.11	0.09	−0.60	0.36	0.19	0.55	−0.19	0.87	−0.98	−0.20	0.01	0.96
July Tmax	0.01	0.84	0.30	−0.86	−0.21	−0.17	−0.26	0.60	0.39	0.21	−0.21	0.85	−0.79	−0.61	0.04	0.89
August Tmax	0.09	0.88	0.26	−0.87	−0.21	−0.13	−0.33	0.59	0.39	0.34	−0.21	0.85	−0.65	−0.76	−0.18	0.84
September Tmax	0.32	0.81	0.07	−0.84	−0.16	−0.02	−0.49	0.52	0.34	0.26	−0.42	0.76	−0.87	−0.49	−0.04	0.90
Annual Tmin	0.15	0.88	0.10	−0.59	−0.02	0.09	−0.34	0.77	−0.09	0.00	−0.42	0.74	0.96	−0.29	0.01	0.90
December Tmin	0.76	0.57	0.08	−0.21	0.34	0.37	−0.34	0.79	−0.29	0.06	−0.27	0.80	0.98	−0.21	−0.10	0.94
January Tmin	0.69	0.64	0.10	−0.45	0.37	0.25	−0.20	0.86	−0.23	0.28	−0.29	0.81	0.98	−0.21	0.02	0.91
February Tmin	0.49	0.77	0.12	−0.51	0.16	0.08	−0.27	0.82	−0.09	0.00	−0.35	0.77	0.97	−0.23	−0.01	0.93
July Tmin	−0.70	0.67	0.07	−0.54	−0.30	0.08	−0.19	0.79	−0.02	−0.12	−0.55	0.65	0.94	−0.35	0.09	0.77
August Tmin	−0.63	0.75	0.06	−0.56	−0.15	0.16	−0.37	0.79	−0.12	−0.21	−0.52	0.68	0.97	−0.25	0.00	0.83
September Tmin	−0.33	0.85	0.08	−0.06	0.26	0.28	−0.28	0.82	−0.20	−0.04	−0.48	0.70	0.95	−0.32	−0.10	0.85
Percent explained	**66**	**19**	**8**	**49**	**27**	**14**	**44**	**24**	**14**	**100**	**63**	**28**	**68**	**32**	**67**	**27**
Canonical correlations	**0.99**	**0.97**	**0.92**	**0.99**	**0.99**	**0.97**	**0.9**	**0.84**	**0.76**	**0.96**	**0.99**	**0.99**	**0.98**	**0.96**	**0.99**	**0.98**

considerable heterogeneity in the strengths of correlations, especially in the importance of summer precipitation, and in winter and summer Tmax.

Scatter plots of PRISM tile values from records across the entire GB provide estimates of the outer limits of climate values for locations where pika sites occurred, as well as the distribution of values within the climate envelope (Figures 2, 3). As canonical vector correlations with climate (Table 4, Figure 2) indicate, the NW and SW subregions had the warmest winters and the lowest summer precipitation, while the NE and SE subregions had the coolest winters, highest summer Tmin, and the highest summer precipitation. Most of the high summer precipitation sites (extant and old) in Figure 3 derive from the eastern subregions, and these high values distinguish Utah sites from the rest of the GB. The SC subregion was most related to the SW subregion in climate, differentiated by the SC subregion having cooler winters, warmer summers, and greater summer precipitation. The NC subregion was intermediate among the subregions in many climate variables.

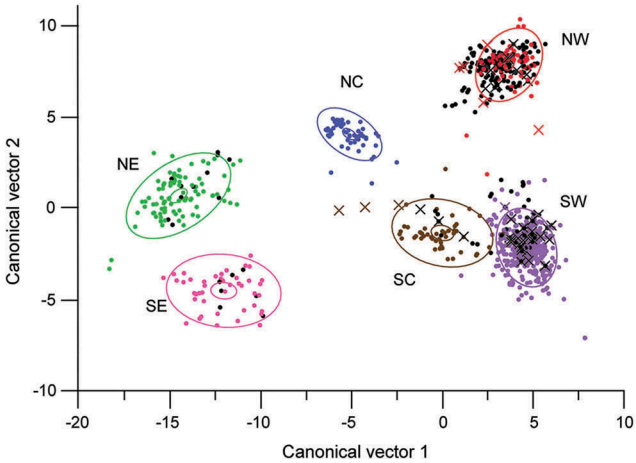

Figure 2. Discriminant analysis of American pika locations in the hydrographic Great Basin. Dots are PRISM tiles containing pika sites; overlapping sites are contained in many of the single dots. Extant sites are shown by subregion and in color: Northeast = green; Southeast = pink; North Central = blue; South Central = brown; Northwest = red; Southwest = purple. Larger ellipsoids indicate 50 percent concentration of the subregional points; smaller (inner) ellipsoids indicate 95 percent confidence intervals of the subregional means. Extirpated sites are shown as crosses; old sites are shown as black dots. For extirpated sites, all those that lie within the area of ellipsoids derive from that subregion; for sites that lie outside the ellipsoid, the color of the crosses indicates the subregion to which they belong.

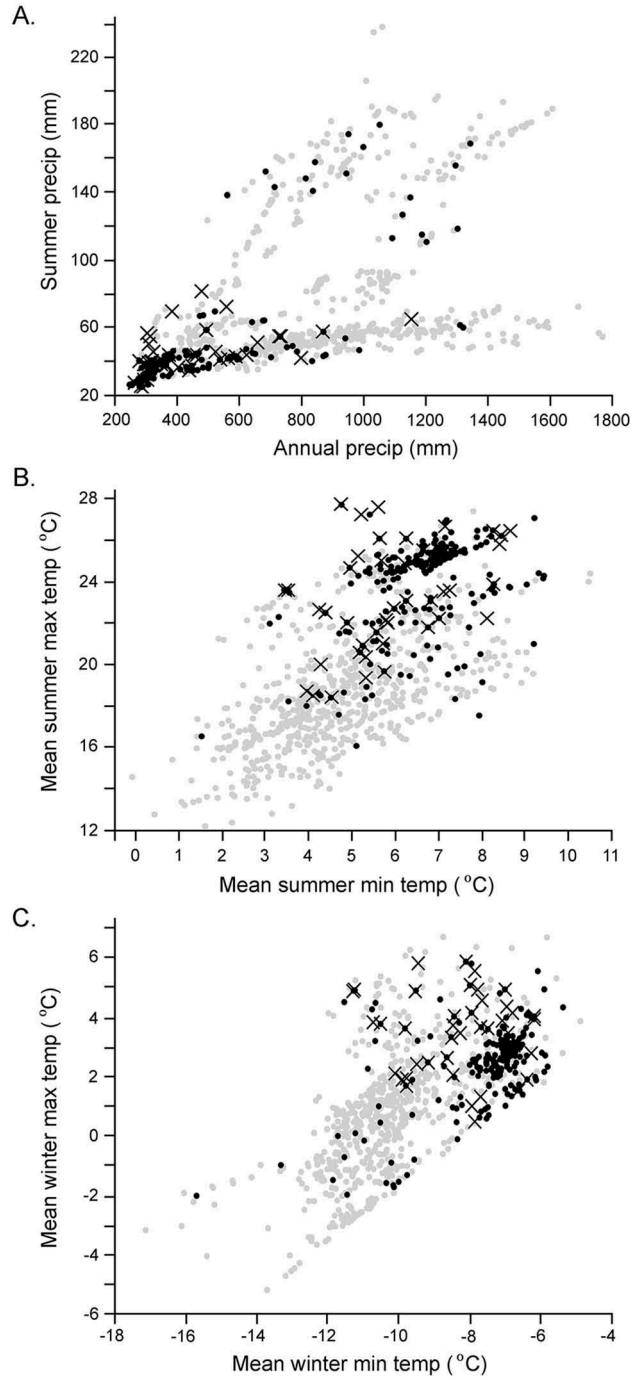

Figure 3. Scatter plots showing range of mean climate values for extant (grey dots), extirpated (black crosses), and old (black dots) Great Basin sites, as represented by PRISM tiles that include the sites. (A) Annual precipitation versus summer precipitation. (B) Summer minimum temperature versus summer maximum temperature. (C) Winter minimum temperature versus winter maximum temperature.

Northern subregions tended to have warmer summer Tmax and warmer annual, winter, and summer Tmins (compare Figure 2 and CV2 in Table 4). These patterns were reflected in the subregional mean values for the PRISM climate data (Table 5), which also underscored the range of July humidities (dewpoint temperature), which were lowest in the central subregions (NC, SC) and highest in the northern subregions (NE, NW).

Elevation and climate variables at extant sites were predictably correlated; that is, precipitation variables were positively correlated with elevation, and temperature variables were negatively correlated with elevation (Table 6). Correlations were mostly high and relatively similar across subregions. Sites in the SC region had more high correlations ($r > 0.90$) than other subregions, notably in annual, winter, and summer Tmin. The few low correlations in absolute value were annual precipitation and September precipitation in the SW, NC, and NE subregions; winter and September Tmin in the NW subregion; July precipitation in the SE subregion; and July dewpoint temperature in the NC subregion.

Discriminant analysis within the six subregions revealed strong climate differentiation among mountain ranges in all but the SW subregion, where there was considerable overlap among ranges (Figure 4). Canonical correlations were high for the first two vectors in all subregions and the first two vectors accounted for 68–100 percent of the variation (Table 4). Summer precipitation was highly differentiated among ranges in

Table 5. Summary of subregional mean climatic data from PRISM climate model (1981–2010 normals, Daly, Neilson, and Phillips 1994). For overall means and range of values, boldface is annual, light shading is summer, and dark shading is winter.

	Subregional Means						Overall		
							Means	Ranges	
	Northwest	Southwest	North Central	South Central	Northeast	Southeast		Min	Max
A. Extant Sites									
Annual precipitation (mm)	408	855	951	605	1,186	837	**819**	**259**	**1,787**
July precipitation (mm)	11	16	20	32	38	44	21	5	66
August precipitation (mm)	12	15	23	32	47	61	23	8	85
September precipitation (mm)	16	23	41	28	73	54	31	9	99
Annual temperature (°C)	5.6	2.9	2.3	3.0	2.2	2.9	**3.1**	**−2.4**	**8.5**
July dewpoint temperature (°C)	0.5	−0.6	−3.3	−4.1	1.5	−0.3	−0.6	−6.3	4.2
Annual maximum temperature (°C)	12.2	9.2	7.9	9.5	7.9	9.1	**9.4**	**2.7**	**16.6**
December maximum temperature (°C)	1.6	1.5	−1.8	0.9	−2.2	−0.4	0.6	−5.2	6.2
January maximum temperature (°C)	2.0	1.7	−1.6	1.1	−1.9	−0.4	0.9	−4.9	6.6
February maximum temperature (°C)	3.1	1.7	−0.5	1.2	−0.7	0.7	1.4	−5.6	7.3
July maximum temperature (°C)	25.7	19.5	20.4	22.3	20.5	21.0	20.9	13.3	28.4
August maximum temperature (°C)	25.2	19.2	20.2	21.5	19.8	19.9	20.4	12.9	28.5
September maximum temperature (°C)	20.8	15.6	15.4	15.5	14.7	15.6	16.3	8.0	24.4
Annual minimum temperature (°C)	−1.1	−3.4	−3.2	−3.4	−3.5	−3.2	**−3.1**	**−9.1**	**1.1**
December minimum temperature (°C)	−7.4	−9.6	−10.7	−9.7	−11.7	−11.3	−9.7	−16.9	−4.8
January minimum temperature (°C)	−7.2	−9.8	−10.7	−9.7	−11.7	−11.3	−9.8	−16.8	−4.8
February minimum temperature (°C)	−7.2	−10.5	−10.7	−10.3	−11.7	−11.1	−10.2	−17.5	−5.2
July minimum temperature (°C)	7.6	5.6	7.3	6.2	7.7	7.5	6.5	1.6	12.5
August minimum temperature (°C)	7.3	5.2	7.0	5.7	7.1	6.8	6.0	0.9	11.8
September minimum temperature (°C)	3.8	1.9	2.7	2.1	2.8	2.9	2.4	−2.7	7.2
B. Extirpated Sites									
Annual precipitation (mm)	575	429		423			**457**	**265**	**1,157**
July precipitation (mm)	12	13		20			14	5	24
August precipitation (mm)	13	13		24			14	6	29
September precipitation (mm)	19	14		22			17	10	31
Annual temperature (°C)	5.8	4.8		6.0			**5.3**	**2.8**	**7.5**
July dewpoint temperature (°C)	1.1	−0.8		−1.5			−0.4	−4.2	3.0
Annual maximum temperature (°C)	12.5	12.2		12.6			**12.5**	**8.9**	**15.8**
December maximum temperature (°C)	2.2	3.6		2.4			3.0	−0.2	5.3
January maximum temperature (°C)	2.6	3.7		2.6			3.2	0.3	5.9
February maximum temperature (°C)	3.8	3.9		3.4			3.9	1.2	6.7
July maximum temperature (°C)	25.4	23.3		26.1			24.7	19.7	29.1
August maximum temperature (°C)	25.0	23.0		25.2			24.2	19.2	28.7
September maximum temperature (°C)	20.7	19.2		19.8			20.0	15.6	24.4
Annual minimum temperature (°C)	−0.8	−2.6		−0.7			**−1.7**	**−4.2**	**0.7**
December minimum temperature (°C)	−7.1	−9.2		−8.2			−8.4	−11.5	−6.5
January minimum temperature (°C)	−6.9	−9.1		−7.9			−8.3	−11.5	−6.3
February minimum temperature (°C)	−6.7	−9.3		−7.8			−8.2	−10.9	−5.7
July minimum temperature (°C)	7.8	7.0		9.6			7.6	5.1	10.9
August minimum temperature (°C)	7.3	5.9		8.8			6.8	4.1	9.7
September minimum temperature (°C)	4.3	2.5		4.9			3.3	0.2	5.6
C. Old Sites									
Annual precipitation (mm)	351	607		559	1,141	797	**451**	**248**	**1,345**
July precipitation (mm)	10	12		21	34	43	13	5	51
August precipitation (mm)	11	13		23	40	60	15	6	66
September precipitation (mm)	14	19		20	64	52	19	10	78
Annual temperature (°C)	6.0	4.8		4.6	3.0	3.1	**5.5**	**−0.4**	**8.1**
July dewpoint temperature (°C)	0.6	−0.3		−3.1	2.4	0.0	0.4	−5.8	4.1
Annual maximum temperature (°C)	12.7	12.0		10.9	8.5	9.4	**12.2**	**6.7**	**15.6**
December maximum temperature (°C)	1.9	3.4		1.4	−1.9	−0.2	1.9	−2.8	5.5
January maximum temperature (°C)	2.3	3.5		1.6	−1.5	−0.1	2.2	−2.4	5.9
February maximum temperature (°C)	3.5	3.8		2.1	−0.2	1.0	3.2	−1.3	6.4
July maximum temperature (°C)	26.2	23.1		23.9	21.3	21.3	25.3	18.2	29.1
August maximum temperature (°C)	25.8	22.8		23.1	20.6	20.2	24.8	16.8	28.7
September maximum temperature (°C)	21.3	19.1		17.6	15.5	15.9	20.4	12.7	24.4
Annual minimum temperature (°C)	−0.7	−2.3		−1.7	−2.6	−3.2	**−1.1**	**−7.5**	**1.3**
December minimum temperature (°C)	−7.2	−8.7		−8.4	−10.9	−11.2	−7.8	−15.4	−5.6
January minimum temperature (°C)	−7.0	−8.8		−8.4	−10.9	−11.2	−7.7	−15.5	−5.7
February minimum temperature (°C)	−6.9	−9.0		−8.7	−10.8	−10.9	−7.6	−16.1	−5.0
July minimum temperature (°C)	8.3	7.1		8.3	8.7	7.5	8.1	3.3	11.1
August minimum temperature (°C)	7.9	6.2		7.6	7.9	6.8	7.6	2.6	10.6
September minimum temperature (°C)	4.2	2.9		3.9	3.7	2.9	3.9	−1.3	7.0

subregions except the NC. Summer Tmax was most highly correlated in the NC, SC, NE, and SE, but not in the SW or NW; summer Tmin was most highly correlated in the SW, NE, SC, and SE subregions, but not in the NW or NC. July dewpoint temperature added relatively high discrimination among ranges for all subregions except for the SW and NC.

Table 6. Correlations of elevation with climate variables in Great Basin subregions. Climate values derive from the PRISM climate model (1981–2010 normals; Daly, Neilson, and Phillips 1994).

	A. Extant				B. Extirpated[1]				C. Old				
	Northwest	Southwest	North Central	South Central	Northeast	Southeast	Northwest	Southwest	Northwest	Southwest	South Central	Northeast	Southeast
Annual precipitation (mm)	0.78	0.26	0.31	0.89	0.55	0.83	0.63	0.30	0.73	0.37	0.94	0.01	0.89
July precipitation (mm)	0.56	0.63	0.64	0.64	0.66	0.41	0.63	0.66	0.42	0.01	0.76	0.88	0.24
August precipitation (mm)	0.56	0.49	0.63	0.60	0.68	0.64	0.54	0.15	0.38	0.23	0.05	0.79	0.53
September precipitation (mm)	0.76	0.27	0.39	0.56	0.77	0.79	0.67	0.36	0.70	0.40	0.06	0.72	0.81
July dewpoint temperature (°C)	−0.80	−0.68	−0.29	−0.91	−0.69	−0.85	−0.77	−0.47	−0.81	−0.45	−0.97	−0.67	−0.93
Annual maximum temperature (°C)	−0.87	−0.93	−0.87	−0.92	−0.91	−0.96	−0.91	−0.93	−0.93	−0.88	−0.96	−0.78	−0.98
December maximum temperature (°C)	−0.81	−0.90	−0.80	−0.76	−0.85	−0.95	−0.79	−0.84	−0.81	−0.80	−0.86	−0.36	−0.98
January maximum temperature (°C)	−0.82	−0.92	−0.79	−0.86	−0.86	−0.94	−0.83	−0.86	−0.85	−0.82	−0.86	−0.56	−0.97
February maximum temperature (°C)	−0.82	−0.90	−0.76	−0.84	−0.85	−0.94	−0.87	−0.91	−0.86	−0.89	−0.91	−0.45	−0.96
July maximum temperature (°C)	−0.86	−0.90	−0.87	−0.94	−0.94	−0.96	−0.91	−0.94	−0.90	−0.88	−0.97	−0.88	−0.97
August maximum temperature (°C)	−0.87	−0.91	−0.89	−0.94	−0.95	−0.95	−0.92	−0.93	−0.91	−0.88	−0.97	−0.91	−0.94
September maximum temperature (°C)	−0.87	−0.93	−0.89	−0.87	−0.92	−0.96	−0.92	−0.94	−0.92	−0.89	−0.96	−0.84	−0.98
Annual minimum temperature (°C)	−0.63	−0.66	−0.76	−0.92	−0.69	−0.68	−0.40	−0.33	−0.48	−0.38	−0.95	−0.73	−0.80
December minimum temperature (°C)	−0.26	−0.49	−0.84	−0.91	−0.56	−0.54	−0.24	−0.04	−0.16	−0.14	−0.91	−0.66	−0.66
January minimum temperature (°C)	−0.38	−0.68	−0.75	−0.92	−0.58	−0.52	−0.01	−0.04	−0.31	−0.10	−0.91	−0.67	−0.71
February minimum temperature (°C)	−0.57	−0.51	−0.77	−0.90	−0.63	−0.65	−0.51	−0.32	−0.58	−0.38	−0.93	−0.72	−0.82
July minimum temperature (°C)	−0.64	−0.61	−0.59	−0.90	−0.67	−0.62	−0.30	−0.63	−0.33	−0.55	−0.97	−0.74	−0.68
August minimum temperature (°C)	−0.58	−0.49	−0.49	−0.91	−0.65	−0.66	−0.12	−0.19	−0.24	−0.25	−0.95	−0.70	−0.72
September minimum temperature (°C)	−0.31	−0.51	−0.70	−0.90	−0.68	−0.60	−0.06	−0.06	−0.09	−0.21	−0.94	−0.72	−0.57

Note.[1]NC subregion values not given, because the number of sites is small.

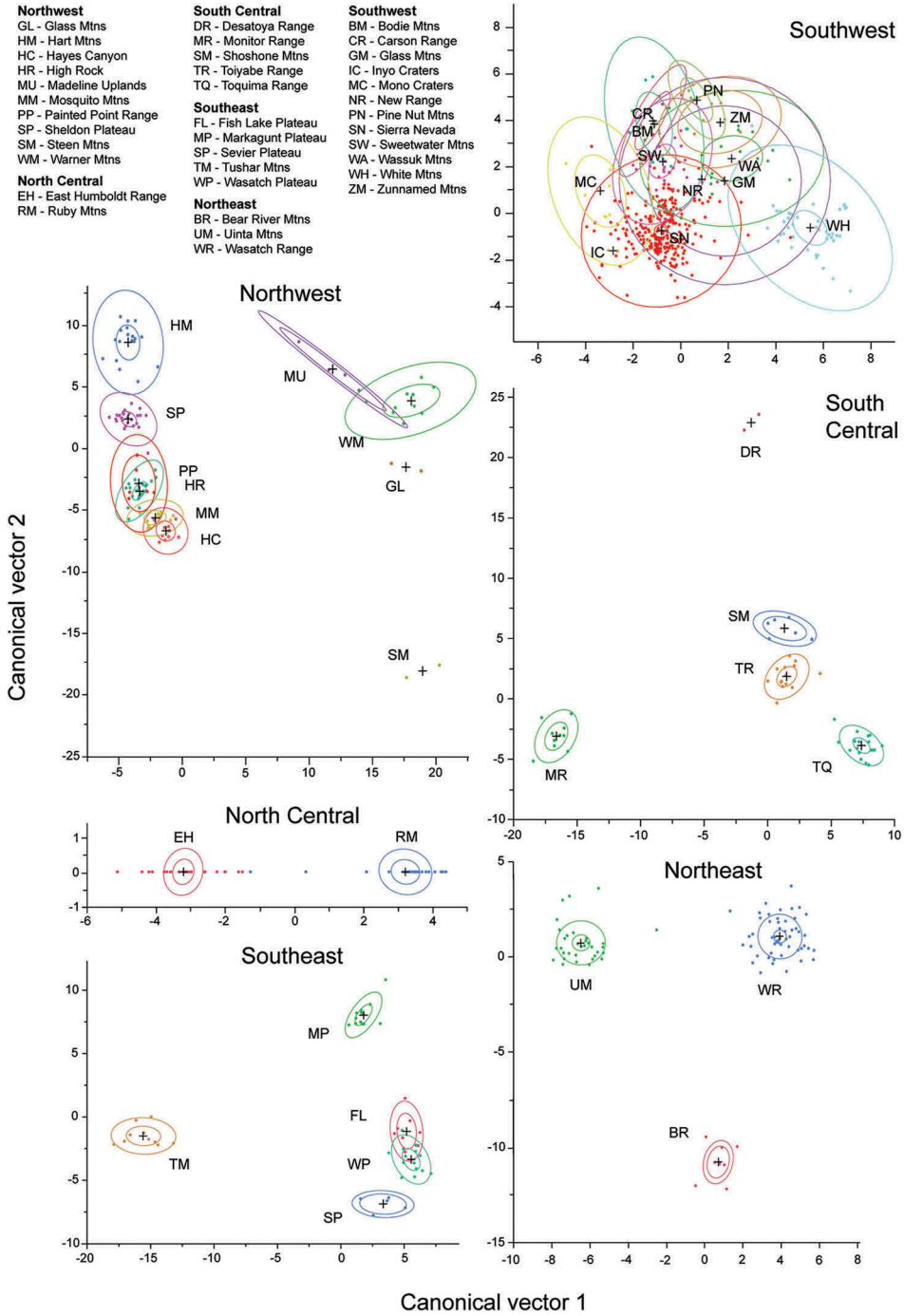

Figure 4. Discriminant analysis of extant American pika locations by mountain ranges within six subregions of the hydrographic Great Basin. Dots are pika sites as represented by PRISM tiles; many tiles overlap. Larger ellipsoids indicate 50 percent concentration of the points; smaller (inner) ellipsoids indicate 95 percent confidence intervals of the means; plus symbols indicate the center of concentrations.

Distribution and climate relationships of extirpated and old sites

To compare conditions of extant sites with relict locations, we compiled 89 individual pika records within the GB that were documented via resurveys of historic sites (based on the previous criteria) as extirpated and 774 records of old-sign-only sites (Table 1). These classes created 232 unique 50 m buffer clusters (i.e., that did not contain extant records). The remaining seventy buffer clusters contained extant records and records from one or both of the relict classes. Extirpated sites were distributed across eighteen mountain ranges in three subregions

Table 7. Mountain ranges within Great Basin subregions that contain extirpated pika sites.

Subregions	Mountain Ranges	State	Number of Pika Records	Elevation (m) Mean	Minimum	Maximum	Span
Northwest	Cascade Range	CA	2	1,812	1,615	2,009	394
	Fremont Mountains	OR	11	1,954	1,798	2,010	212
	Hart Mountains	OR	1	1,760	NA	NA	NA
	Idaho Canyon Range	NV	1	1,798	NA	NA	NA
	Madeline Uplands	CA	5	1,731	1,628	1,996	368
	Mosquito Mountains	NV	2	1,702	1,667	1,737	70
	Pine Forest Range	NV	1	2,560	NA	NA	NA
	Warner Mountains	CA/OR	3	2,113	1,811	2,326	515
Southwest	Bodie Mountains	CA	48	2,591	2,113	3,106	993
	Glass Mountains	CA	5	3,032	3,023	3,039	16
	Sierra Nevada	CA	1	2,769	NA	NA	NA
	Wassuk Mountains	NV	2	2,724	2,718	2,730	12
	White Mountains	CA/NV	1	2,704	NA	NA	NA
North Central	None						
South Central	Desatoya Range	NV	1	2,285	NA	NA	NA
	Monitor Range	NV	1	2,476	NA	NA	NA
	Shoshone Mountains	NV	1	2,886	NA	NA	NA
	Toiyabe Range	NV	1	2,160	NA	NA	NA
	White Pine Range	NV	2	2,727	2,701	2,754	53
Northeast	None						
Southeast	None						
18 Ranges			**89**	**2,420**	**1,615**	**3,106**	**1,491**

(Table 7; Appendix 4). The smallest number of records was in the SC (6) and the largest was in the SW (57), with the NW intermediate (26). Elevations of extirpated sites ranged from 1,615 m to 3,106 m (a span of 1,491 m; $\bar{x}$ = 2,420 m). Mean elevation in the NW subregion (1,929 m) was lower than in the remaining two subregions ($\bar{x}$ = 2,635 m), which were statistically nonsignificant differences ($p > 0.5$). The subset of

Table 8. Mountain ranges within Great Basin subregions that contain old pika sites.

Subregions	Mountain Ranges	State	Number of Pika Records	Elevation (m) Mean	Minimum	Maximum	Span
Northwest	Black Rock Range	NV	53	2,319	2,102	2,577	475
	Cascade Range	CA	1	1,859	NA	NA	NA
	Glass Mountains	OR	3	1,989	1,711	2,307	596
	Granite Range	NV	3	1,792	1,782	1,797	15
	Hart Mountains	OR	35	2,028	1,678	2,355	677
	Hays Canyon Range	NV	37	2,066	1,942	2,259	317
	High Rock	NV	175	1,889	1,771	2,081	310
	High Rock Canyon Hills	NV	1	1,746	NA	NA	NA
	Madeline Uplands	CA	8	1,745	1,628	1,924	296
	Massacre Rim	NV	9	1,871	1,830	1,941	111
	Mosquito Mountains	NV	149	1,883	1,714	2,009	295
	Painted Point Range	NV	19	1,855	1,770	1,933	163
	Pine Forest Range	NV	8	2,563	2,536	2,598	62
	Sheldon Plateau	NV	150	1,915	1,667	2,162	495
	Winter Ridge	OR	10	1,969	1,935	2,010	75
Southwest	Bodie Mountains	CA	50	2,584	2,113	2,847	734
	Carson Range	CA/NV	12	2,760	2,740	3,085	345
	Glass Mountains	CA	4	3,031	3,023	3,039	16
	Mono Craters	CA	1	2,012	NA	NA	NA
	Sierra Nevada	CA	4	2,500	2,104	2,768	664
	Sweetwater Mountains	CA	1	2,249	NA	NA	NA
	Wassuk Mountains	NV	4	2,586	2,135	2,760	625
North Central	none						
South Central	Monitor Range	NV	10	2,836	2,483	3,267	784
	Shoshone Mountains	NV	6	2,638	2,546	2,736	190
Northeast	Bear River Mountains	UT	4	2,619	2,463	2,726	263
	Uinta Mountains	UT	3	2,985	2,628	3,169	541
	Wasatch Range	UT	4	2,738	2,574	2,954	380
Southeast	Fish Lake Plateau	UT	3	3,242	3,048	3,435	387
	Markagunt Plateau	UT	4	2,943	2,656	3,372	716
	Sevier Plateau	UT	1	3,194	NA	NA	NA
	Tushar Mountains	UT	2	3,018	3,011	3,024	12
31 Ranges			**774**	**2,054**	**1,628**	**3,435**	**1,807**

extirpated records from published historic resurveys had a mean elevation of 2,196 m and range of 1,615–2,753 m. Aspects of extirpated pika sites were more northerly than extant sites (Table 3).

Old sites were distributed across thirty-one mountain ranges in five subregions (Table 8; Appendix 5). Most records were in the NW subregion (661), far fewer were in the SW (76), and only small numbers were located in the SC, NE, and SE subregions (16, 11, and 10, respectively). Elevations for the old records ranged from 1,628 to 3,435 m (a span of 1,807 m; $\bar{x}$ = 2,054 m). Mean elevation in the NW subregion (1,966 m) was lower than in the remaining four subregions. Of those, mean elevations in the SW, SC, and NE subregions did not differ significantly; mean elevation in the SE subregion ($\bar{x}$ = 3,099 m) was significantly higher than the other five ($p < 0.001$). Aspects of old pika sites were distributed in all octants with slight excess in the north, whereas south- and westward aspects were least represented (Table 3). Subregions showed significant heterogeneity ($p < 0.001$) in aspect. All octants were well represented in the NW and SW subregions, while the south and west octants were either lacking or of minor importance in the other three subregions.

By appending PRISM-derived climate data for relict sites to the extant-site dataset, we computed canonical scores for locations of the extirpated and old-sign sets and used discriminant analysis to compare these scores to the climate space for extant sites. The resulting analysis showed that the relict sites and extant sites lie largely within the same climate space, with some exceptions (Figures 2, 3). In the MANOVA, the order of differences was subregions ($p < 0.001$) > mountain range > pika status (extant, extirpated, old). Mean values for the extirpated and old-sign sites compared to the extant sites highlight the differences between these groups (Table 5). Overall, mean annual precipitation for the relict sites was lower than for the extant set. Comparing by subregions, however, the NW subregion had higher mean annual precipitation in the extirpated than in the extant sites, while old-sign site means were similar to those of extant sites. Considering summer precipitation, the extirpated and old sites had lower values than extant sites in the SW, SC, and SE subregions, but not in the NW and NE subregions, despite those two subregions being the driest and wettest of the six subregions.

Patterns of climate differences between relict and extant sites were complex, varied by subregion, and could not distinguish among the categories of occurrence. Annual temperature, Tmin and Tmax, and summer Tmax were higher for relict sites compared with extant sites in the SW and SC subregions, but not in the NW, NE, or SE subregions. Winter Tmins and Tmaxs were comparable between extirpated, old, and extant sites. In the SC and NE subregions, higher summer Tmins occurred at extirpated or old sites compared to extant sites, while in the NW and SW subregions, extant sites were warmer than either extirpated or old-sign sites (but never both), and there were no differences for the SE subregion among the three datasets.

Correlations between elevation and climate variables at relict sites in the NW and SW subregions were generally lower and had fewer significant values ($r < |0.6|$) than at extant sites, although they followed similar patterns to the extant group (Table 6). There were also differences in correlations between the sets of extirpated versus old-sign sites, especially in summer and winter Tmin: for the extirpated group, correlations were low and nonsignificant, and some were even positive, suggesting that Tmin may increase with elevation; for example, as a result of cold-air drainage effects. Annual, summer, and winter Tmin correlations with elevation, by contrast, for the old sites in the SC, NE, and SE subregions were all negative, and most were high and significant ($p < 0.05$). In summary, no obvious pattern emerged to distinguish extirpated and old-sign sites from extant sites; if anything, the low correlations between climate variables and elevation suggest great landscape complexity associated with these categories of occurrence.

Mountain ranges with no pika evidence

The island-like geography of mountain ranges in the GB, coupled with the large number of ranges, present biogeographic challenges for species dispersal (Brown 1971), resulting in both deterministic (climate, distance, source populations) and stochastically derived distributions for many GB mammal species. We compiled a list of mountain ranges that appear to have characteristic pika habitat and suitable bioclimatic zones, but where experienced surveyors have found no evidence of pika habitation, current or historic (Table 9). The list of 45 mountain ranges includes only areas where pikas have never been found in any part of the range. Surveys have not been comprehensive, however, and we encourage continued exploration of these and other mountain ranges with features capable of supporting pikas.

Discussion

Extant pika populations in the Great Basin and comparison with relict locations

The primary focus of our study was to clarify the current distribution of extant pika populations in the

Table 9. Great Basin mountain ranges where evidence for pika presence has not been detected during twentieth- and twenty-first-century surveys. High point elevations from D.A. Charlet (unpublished, Atlas of Nevada Mountains).

Mountain Range	County	State	Elevation Highest Point (m)	Most Recent Survey Date	Source
Anchorite Hills	Mineral	NV	2,905	2017	Millar, unpublished
Cherry Creek Range	White Pine	NV	3,215	1995	NDOW, Chris Ray
Clan Alpine	Churchill	NV	3,046	2017	Millar, unpublished
Copper Mountains	Elko	NV	3,021	2014	Millar, unpublished
Cortez Mountains	Eureka, Lander	NV	2,793	1993	NDOW, Chris Ray
Cowtrack Hills	Mono	CA	2,704	2012	Millar, unpublished
Deep Creek Range	Tooele, Juab	UT	3,684	2011	Millar, unpublished, UT Div of Wildlife, unpublished
DeLamar Mountains	Lincoln	NV	2,449	2010	Millar, unpublished
Desert Mountains	Lyon, Churchill	NV	2,046	1993	NDOW, Chris Ray
Duck Creek Range	White Pine	NV	3,160	2011	Millar, unpublished
Egan Range	White Pine, Lyon	NV	3,333	2014	Millar, unpublished
Excelsior Mountains	Mineral	NV	2,384	2015	Millar, unpublished
Fish Creek Mountains	Lander	NV	2,635	2017	Millar, unpublished
Garfield Hills	Mineral	NV	2,335	2017	Millar, unpublished
Gillis Range	Mineral	NV	2,404	1993	NDOW, Chris Ray
Humboldt Range	Pershing	NV	2,997	2000	NDOW, Chris Ray
Inyo Mountains	Inyo	CA	3,392	2012	Millar, unpublished
Jarbidge Mountains	Elko	NV	3,304	2016	Millar, unpublished
Last Chance Range	Nye	NV	2,645	2016	Millar, unpublished
Lone Mountain	Esmeralda	NV	2,776	1993	NDOW, Chris Ray
Marys River Range	Elko	NV	3,220	2014	Millar, unpublished
Oquirrh Mountains	Tooele, Utah	UT	2,763	2016	UT Division of Wildlife, unpublished
Pahroc Range, North and South	Lincoln	NV	2,423	2010	Millar, unpublished
Palmetto Mountains	Esmeralda	NV	2,830	2016	Millar, unpublished
Paradise Range	Nye	NV	2,638	2008	Millar, unpublished
Peqoup Mountains	Elko	NV	3,128	2014	NDOW, Mackenzie Jeffress
Pilot Range	Box Elder, Elko	UT, NV	3,267	2016	UT Division of Wildlife, unpublished
Quinn Canyon Range	Nye, Lincoln	NV	3,118	2014	Millar, unpublished
Raft River Range	Box Elder	UT	3,025	2016	UT Division of Wildlife, unpublished
Roberts Mountains	Eureka	NV	3,089	2017	NDOW, Mackenzie Jeffress; Millar, unpublished
Santa Rosa Range	Humboldt	NV	2,966	1993	NDOW, Chris Ray
Schell Creek Range	Lincoln, White Pine	NV	3,622	2014	NDOW, Mike Podborny
Seaman Range	Lincoln, Ney	NV	2,818	2010	Millar, unpublished
Sheep Range	Clark, Lincoln	NV	3,021	2010	Millar, unpublished
Silver Peak Range	Esmeralda	NV	2,880	2017	Millar, unpublished
Snake Mountains	Elko	NV	2,696	2017	Millar, unpublished
Snake Range, North and South	White Pine	NV	3,982	2016	Millar, unpublished
Sonoma Range	Humboldt	NV	2,864	1993	NDOW, Chris Ray
Spring Mountains	Clark, Nye	NV	3,621	1995	NDOW, Chris Ray
Stansbury Mountains	Tooele	UT	3,363	2016	UT Division of Wildlife, unpublished
Tobin Range	Pershing	NV	2,979	2017	Millar, unpublished
Tuscarora Mountains	Elko, Eureka	NV	2,678	1993	NDOW, Chris Ray
Volcanic Hills	Esmeralda	NV	2,255	1993	NDOW, Chris Ray
Wellsville Mountains	Cache	UT	2,857	2016	UT Division of Wildlife, unpublished
White Pine Range[a]	White Pine, Nye	NV	3,509	2015	Millar, unpublished; Jeffress, unpublished

Notes. [a]The occurrence of pikas, historic or modern, in the White Pine Range has been questioned; we include the records in Appendix 4 until further verification, but also include the Range here to encourage exploration.

hydrographic GB and to describe climatic conditions for this distribution of locations. Additionally, we compared conditions found at extant pika sites with those at relict sites to improve our understanding of environmental factors that may have been responsible for population declines. To the extent that our sites represent still-extant populations, we found that pikas are far more widely distributed across the GB than previously reported or assumed, and confirm prior observations (e.g., Jeffress et al. 2013; Ray, Beever, and Rodhouse 2016; Stewart and Wright 2012) that climate may represent only one of many factors influencing their current and recent distribution.

The broad GB distribution of extant pika populations extends across five degrees of latitude and ten degrees of longitude, represents three ecosystem provinces (Bailey 1980), encompasses six subregions of the GB, traverses forty mountain ranges, spans 2,378 m elevation, and comprises three of the five currently described subspecies (*O. p. princeps, O. p. schisticeps*, and *O. p. uinta*; Hafner and Smith 2010). The minimum elevation of extant populations (1,631 m) is approximately 900 m below the low range given for the southern portion of the species' distribution (Smith and Weston 1990); approximately 200 m lower than the minimum elevations from prior distribution studies of extant central and western GB sites (Millar and Westfall 2010; Millar, Westfall, and Delany 2013); and slightly below the minimum elevation of extant sites in a study of pikas of the northern GB (1,648 m; Collins and Bauman 2012). Our samples also extend the reported

maximum elevation of extant GB sites by 122 m, from 3,887 m (Millar and Westfall 2010) to 4,009 m.

Extant sites are distributed across all aspects, with a slight excess of north-facing slopes. This broad representation was surprising. Given the thermal sensitivity of pikas, we expected cooler, north-facing aspects to be more strongly represented, especially in relatively warm environments. Apparently adequate physical environments exist across the GB on many aspects and with sufficient local microclimatic conditions to support pika populations. Perhaps equally unexpected is the large proportion of relict sites that occurred on cool, northern aspects.

How does the distribution of previously published historic resurvey sites (e.g., Beever, Brussard, and Berger 2003; Beever et al. 2011, 2016; Stewart et al. 2015; Wilkening et al. 2011) compare to our newly compiled set? Resurvey sites were neither chosen nor intended to represent the distribution of pikas in the GB, and the set of historic sites is slightly biased toward lower elevations and a narrower distribution of sites than in our study. Our data include fifteen more mountain ranges than are included in the historic resurveys, and significantly extend the elevational range of occupied pika sites to 1.5 times greater than historic resurvey sites (including extensions into higher montane elevations). Overall, the mean elevation of the resurvey sites was 119 m lower than the mean for our compiled extant set. Historic resurvey sites might represent lower elevations as a result of limited access during historic periods, when travel into high and remote mountain areas was more restricted than at present. Whatever the reason, interpretations from resurvey studies are best understood in the context of their relative environments, which do not necessarily represent those of pikas across the GB.

The broad geographic distribution of pika sites across the GB also demonstrates a larger range of climate values for locations of extant pika sites than previously reported. Our basin-wide perspective highlights wide subregional climate differences among pika locations. Differences in mean annual precipitation among subregions, for instance, were greater than 760 mm, from a low in the NW subregion to a high in the NE subregion. Mean summer precipitation varied greatly across the GB. Pika sites in the NW and SW subregions have arid summers (~7% of annual precipitation), while sites in the NE and SE subregions experience proportionately more precipitation in summer (~20% of annual). Temperature ranges also exhibited strong variation among subregions, with more than 6°C difference in mean maximum summer temperature among the extremes (NW and SW subregions). These ranges of values underscore the breadth of climatic environments that extant pika sites represent in the GB.

Multivariate climate analyses within subregions further revealed that extant pika site locations are climatically more heterogeneous than previously thought. Climatic distinctions among mountain ranges were large, even among adjacent ranges, within all subregions except the SW. The complex climatic overlap of mountain ranges in that subregion was unexpected, given the rain-shadow effect of the Sierra Nevada and cumulative effects eastward that would be assumed to accentuate differentiation. Low sample numbers in some ranges, however, likely lowered our ability to accurately discriminate distinctions.

A climate envelope for extant GB pika sites, if such can be considered from the range of average and extreme values of extant sites derived from PRISM (Figure 3, Table 5), could be described as follows: annual precipitation, 259–1,787 mm; summer precipitation, 7–83 mm; annual Tmin, −9.1–1.1°C; summer Tmin, −0.1–10.5°C; winter Tmin, −17.1–4.9°C; annual Tmax, 2.7–16.6°C; summer Tmax, 11.4–29.9°C; winter Tmax, −5.2–6.7°C; and July dewpoint temperatures, −6.3–4.2°C. These values generally conform with estimates from other studies that used PRISM or similar climate models, with notable exceptions. Annual precipitation in the GB fell mostly within the species-wide requirement of more than 300 mm (Hafner 1994). Several sites, however, had less precipitation, as was also found in the wide-ranging study of Jeffress et al. (2013; low range = 231 mm, Craters of the Moon National Monument, ID). The GB sites had slightly higher maximum values of annual precipitation than previously reported—for example, 1,407 mm in the southern Rocky Mountains (Erb, Ray, and Guralnick 2011)—but considerably less than the 3,084 mm estimated in the survey by Jeffress et al. (2013). This result is unsurprising given the semiaridity of the GB region relative to other pika environments of the West.

Temperatures for extant GB sites were mostly within the range of, or warmer than, temperatures reported for pika sites outside the GB. Our July maximum temperatures (13.3–30.6°C) closely match those of Jeffress et al. (2013; 13.5–29.8°C), while our December minimum temperatures (−16.8°C to −4.8°C) were warmer (−19.3°C to −4.1°C). Summer mean temperatures in the GB were similar to the means and ranges of Jeffress et al. (2013). They had wider ranges and thus lower mean values than low-elevation, high-latitude sites in British Columbia (Henry, Henry, and Russello 2012), and much lower temperatures and wider ranges of temperature (but with similar warm extremes), as reported at the well-studied, low-elevation Bodie site in California (Smith and Nagy 2015). Notably, summer maximum temperatures in the GB were warmer than reported elsewhere, with an upper mean value of 28.2°C; 5–6°C warmer than those reported by Smith and Nagy

(2015) for the Bodie site. Compared to mean annual temperatures for a subset of pika sites in the western GB (1.5–6.9°C; Millar and Westfall 2010), the current basin-wide set had a broader range of values (−2.4–8.5°C).

The newly compiled list of relict sites reveals a large number of extirpated and putatively extirpated (old) sites. Several caveats need to be mentioned: first is the unverified status of many of the records scored by surveyors as old. Often these sites were intermingled with and within the dispersal distance of extant sites; potentially some of these sites are transiently vacant patches that might be recolonized. In other situations, rapid surveys might have missed signs of occurrence (i.e., false absence), as has been noted before (Jeffress, Van Gunst, and Millar 2017; Millar, Westfall, and Delany 2013; Smith, Nagy, and Millar 2016). Further, we have found that detection was consistently much lower at lower elevation and/or marginal habitat, even where pikas were present and abundant, making the rapid-survey issue even more problematic (Smith, Nagy, and Millar 2016). Finally, old sign has only recently been recorded as a survey variable, and there were differences in survey effort by subregions. Those factors likely contribute to variability in the numbers of sites reported as old and bias our summary analyses.

Importantly, most of the old-site records are the result of single-survey visits without repeat surveys, such as have been conducted by Beever and colleagues (2011, 2016) and Stewart and colleagues (Stewart et al. 2015; Stewart and Wright 2012); thus, extirpation cannot be accurately documented. For instance, on repeat visits to several putatively extirpated sites in the western GB, we have documented subsequent occurrence (Millar, Westfall, and Delany 2013). We urge more widespread use of repeat surveys and long-term monitoring for old sites as well as extant sites in the future, as well as studies to assess site-specific survival and reproduction. Additionally, radiocarbon dating methods can be used to clarify the age of old sites (e.g., Millar et al. 2014a; Stewart, Wright, and Heckman 2017).

Our findings suggest that although local climate appears to have a role in defining extirpated locations, it does not adequately explain the current state. Relict sites tend to be in lower, warmer, and drier parts of the climate envelope of extant GB pika location, as prior studies have shown (Beever, Brussard, and Berger 2003; Beever et al. 2010; Stewart et al. 2015; Wilkening et al. 2011). Our climate profiles for relict sites were mostly within the envelope of the extant sites, and although there are sets of climate variables that distinguish them, there is considerable overlap between the extant and relict climate spaces. Similar results have been found in northwest Nevada (Jeffress, Van Gunst, and Millar 2017). Further, in some cases extant sites were warmer, drier, or occurred at lower elevations than extirpated sites, even in the same subregion or mountain range. Local differences among microsites; microclimatic processes; quality of forage; size, quality and connectivity of taluses; and dispersal, among other factors, may emerge as important predictive factors as well (Castillo et al. 2016; Stewart and Wright 2012). Untangling these influences from regional climatic constraints is a key area for future research.

Climate analyses in the current study relied on PRISM data, which are modeled as standard surface-air temperature (1.5 m above ground surface; Daly, Neilson, and Phillips 1994). Millar, Westfall, and Delany (2014b, 2016) documented that although surface-air temperatures correlate with talus surface temperatures, they correlate poorly with the thermal conditions within talus and should not be used to represent the conditions that pikas routinely encounter within talus. With our climate analyses and discussion, we do not mean to imply that these values are those encountered by pikas in all habitat components. Rather, our analyses of surface-air temperatures allow comparison with prior studies that used similar modeled climate values, and afford clarification of the range of local-to-regional temperatures and environments associated with pika locations. Where extreme high values would seem to be unfavorable given the thermal physiology of pikas (as in sites with warm summers or cold, dry winters), we suspect that thermal conditions are mitigated by microclimates associated with talus landforms. Rocky landforms have thermal regimes shown to be decoupled from surface air, which results in cooler temperatures with low variance during warm summer days and warmer temperatures under snow in cold winters (Hall et al. 2016; Millar, Westfall, and Delany 2014b, 2016; Otto, Wilson, and Beever 2015; Rodhouse, Hovland, and Jeffress 2017; Smith, Nagy, and Millar 2016; Wilkening, Ray, and Varner 2015). These landforms also support vegetation in their forefields on which pikas depend for summer forage and winter caching (Millar et al. 2015). In this way, talus environments can provide refuge from unfavorable daily and seasonal weather (Rodhouse, Hovland, and Jeffress 2017), and, over longer times, internal temperatures lag changes in free air (Gentili et al. 2015; Millar, Westfall, and Delany 2014b), providing potential climate refugia into the future (Morelli et al. 2016).

Implications for the status of pikas in the Great Basin

The addition of a large number of extant pika sites, spanning the northern three-quarters of the GB, changes our understanding both of the current status of pikas and their

susceptibility to risk from a changing climate. Prior efforts to assess the vulnerability of pikas to climate have relied on projections from models (e.g., Calkins et al. 2012; Galbreath, Hafner, and Zamudio 2009; Stewart et al. 2015), statistical analyses of extirpated versus extant conditions, or assessments of populations along bioclimatic gradients (e.g., Beever et al. 2010, 2011; Erb, Ray, and Guralnick 2011; Jeffress et al. 2013). Models suffer compound uncertainties (Stephenson, Millar, and Cole 2010) that are especially significant for a small mammal such as the pika. These include general uncertainties, as in estimating future greenhouse gas emissions, regional downscaling processes, and ecological interactions, as well as difficulties in scaling because of the highly restricted and decoupled habitat components used by pikas (Millar, Westfall, and Delany 2016). In some studies, only a small number of sites was available from which broad implications were projected. Combined, these can create cumulative errors with misleading end results. For instance, MaxEnt models that attempted to map current distributions of pikas generated distributions far from where pikas have been known to exist (e.g., Calkins et al. 2012). Statistical models increasingly include factors that pertain to specific ecological requirements of pikas, although much remains unknown, such as the conditions and constraints of the dispersal environment, the importance of talus area and quality, and intertalus isolation distance. Conclusions from such studies, including those we make here, increasingly highlight the role of dependence on context, as has been described previously for pikas (Jeffress et al. 2013; Jeffress, Van Gunst, and Millar 2017).

Our description of a wide geographic distribution, encompassing a broad climate envelope within and across subregions, adds new dimensions to understanding the tolerances of pikas in the ecoregion. The results underscore that pikas are not rare in the GB, and, given the geographic breadth of locations, are likely better able to tolerate climate variability than previously understood. In addition, the diversity of environments suggests lower exposure to the impacts of climate change than previously reported. Although pikas are commonly described as an alpine (the zone above tree line) species, we now understand that this characterization is incomplete. Prior studies of low-elevation and marginal pika sites, as well as our current survey, demonstrate that pikas are found in the GB in environments not described as alpine (Beever et al. 2008; Jeffress, Van Gunst, and Millar 2017; Millar and Westfall 2010; Millar, Westfall, and Delany 2013; Smith 1974; Smith, Nagy, and Millar 2016). Nonalpine sites outside the region also have been documented (e.g., Henry, Henry, and Russello 2012; Jeffress et al. 2013; Manning and Hagar 2011; Ray, Beever, and Rodhouse 2016; Shinderman 2015; Simpson 2009). Pikas in the GB are better described as wide-ranging across montane zones, albeit highly dependent on specific landforms that lie within the species' climate envelope. Occupied sites extend from sage-steppe shrublands and woodland communities, through montane forests, wet and dry montane meadows and shrublands, and subalpine forest zones, to diverse alpine communities.

Recognizing the wide range of pikas in the GB neither denies extirpation rates that have been documented nor ignores the possibility of continuing declines. In fact, our analyses document a large number and widespread occurrences of apparently recent population extirpations across the GB, which anticipate further changes in the range of environments supportive of American pikas. There is a need for further exploration at intensive scales in many portions of currently little surveyed parts of the GB to provide more consistent assessment of the regional distribution of the species. Even with the current levels of survey, however, the broad range of pikas, and the capacity of the species to persist across diverse bioclimatic environments and through significant Holocene climate variations (Hafner 1993; Hafner and Sullivan 1995), suggest that a core of stable populations exists across the GB. At the margins of these core areas, on interior as well as exterior edges (Ray, Beever, and Rodhouse 2016; Stewart, Wright, and Heckman 2017), population fluxes have occurred in the past, are occurring at present, and are expected to occur in the future. While these fluctuations may not portend bioregional extirpation of the species or losses of populations from subregions or major mountain ranges, they do point to the need for greater exploration of nonclimate factors, as well as continuing research on the relationship of climate to pika persistence. Finally, it must be stressed that the Great Basin composes only a small portion of the species-wide distribution of pikas, is a region where pikas are least represented, and is where the species has faced prehistoric climate challenges (Grayson 2005). Our findings of the wide distribution and persistence of pikas even in this marginal ecoregion suggest that at the species level, pikas may have greater resilience to environmental change than has been assumed.

Acknowledgments

We thank Don Grayson (University of Washington) and Chrissy Howell (U.S. Forest Service) for critical reviews of the draft manuscript, Harriet Smith for editorial review, and Rob Klinger (USGS) and one anonymous reviewer for constructive comments on the submitted

manuscript. We thank Jessica Castillo Vardaro (Princeton University) for sharing details on her pika records, and all surveyors and agencies who contributed pika observations to our databases, particularly Brad Bauman, Mark Enders, Christy Klinger, and Rory Lamp (all NDOW); Brian Maxfield, Anthony Wright, Keith Day, Adam Brewerton, and Theresa Pope (all UDWR); and Eric Rickart (Natural History Museum of Utah).

References

Bailey, R. G. 1980. *Ecoregions of the United States*. Miscellaneous Publication No. 1391. Washington, DC: USDA Forest Service.

Beever, E. A., P. F. Brussard, and J. Berger. 2003. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. *Journal of Mammalogy* 84:37–54.

Beever, E. A., J. D. Perrine, T. Rickman, M. Flores, J. P. Clark, C. Waters, S. S. Weber, B. Yardley, D. Thoma, T. Chesley-Preston, et al. 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* 97:1495–511.

Beever, E. A., C. Ray, P. W. Mote, and J. L. Wilkening. 2010. Testing alternative models of climate-mediated extirpations. *Ecological Applications* 20:164–78.

Beever, E. A., C. Ray, J. L. Wilkening, P. F. Brussard, and P. W. Mote. 2011. Contemporary climate change alters the pace and drivers of extinction. *Global Change Biology* 17:2054–70.

Beever, E. A., J. L. Wilkening, D. E. McIvor, S. S. Weber, and P. F. Brussard. 2008. American pikas (*Ochotona princeps*) in northwestern Nevada: A newly discovered population at a low-elevation site. *Western North American Naturalist* 68:8–14.

Brown, J. H. 1971. Mammals on mountaintops: Nonequilibrium insular biogeography. *The American Naturalist* 105:467–78.

Calkins, M. T., E. A. Beever, K. G. Boykin, J. K. Frey, and M. C. Anderson. 2012. Not-so-splendid isolation: Modeling climate-mediated range collapse of a montane mammal *Ochotona princeps* across numerous ecoregions. *Ecography* 35:780–91.

Castillo, J. A., C. W. Clinton, M. R. Jeffress, C. Ray, T. J. Rodhouse, and D. Schwalm. 2016. Replicated landscape genetic and network analyses reveal wide variation in functional connectivity for American pikas. *Ecological Applications* 26:1660–76.

Collins, G. H., and B. T. Bauman. 2012. Distribution of low-elevation American pika populations in the northern Great Basin. *Journal of Fish and Wildlife Management* 3:311–18.

Daly, C. R., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology* 33:140–58.

Erb, L. P., C. Ray, and R. Guralnick. 2011. On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*). *Ecology* 92:1730–35.

ESRI. 2015. *ArcGIS 10.3.1 for Desktop*. Redlands, CA: Environmental Systems Research Institute.

Galbreath, K. E., D. J. Hafner, and K. R. Zamudio. 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* 63:2848–63.

Gentili, R., C. Baroni, M. Caccianiga, S. Srmiraglio, A. Ghiani, and S. Citerios. 2015. Potential warm-stage microrefugia for alpine plants: Feedback between geomorphological and biological processes. *Ecological Complexity* 21:87–99.

Grayson, D. 2005. A brief history of Great Basin pikas. *Journal of Biogeography* 32:2103–11.

Hafner, D. J. 1993. North American pika (*Ochotona princeps*) as a late Quaternary biogeographic indicator species. *Quaternary Research* 39:373–80.

Hafner, D. J. 1994. Pikas and permafrost: Post-Wisconsin historical zoogeography of *Ochotona* in the southern Rocky Mountains, USA. *Arctic and Alpine Research* 26:375–82.

Hafner, D. J., and A. T. Smith. 2010. Revision of the subspecies of American pika, *Ochotona princeps* (Lagomorpha: Ochotonidae). *Journal of Mammalogy* 91:401–17.

Hafner, D. J., and R. M. Sullivan. 1995. Historical and ecological biogeography of Nearctic pikas (Lagomorpha: Ochotonidae). *Journal of Mammalogy* 76:302–21.

Hall, L. E., A. D. Chalfoun, E. A. Beever, and A. E. Loosen. 2016. Microrefuges and the occurrence of thermal specialists: Implications for wildlife persistence amidst changing temperatures. *Climate Change Responses* 3:8.

Henry, P., A. Henry, and M. A. Russello. 2012. Variation in habitat characteristics of American pikas along an elevation gradient at their northern margin. *Northwest Science* 86:346–50.

Jeffress, M. R., T. J. Rodhouse, C. Ray, S. Wolff, and C. W. Epps. 2013. The idiosyncrasies of place: Geographic variation in the climate-distribution relationships of the American pika. *Ecological Applications* 23:864–78.

Jeffress, M. R., K. J. Van Gunst, and C. I. Millar. 2017. A surprising discovery of American pika sites in the northwest Great Basin. *Western North American Naturalist* 77:252–68.

Manning, T., and J. C. Hagar. 2011. Use of nonalpine anthropogenic habitats by American pikas (*Ochotona princeps*) in western Oregon. *Western North American Naturalist* 71:106–12.

Massing, C. P., 2012: *American pika (*Ochotona princeps*): Persistence and activity patterns in a changing climate*. M.S. thesis, Department of Biological Sciences, California Polytechnic University, San Luis Obispo, California.

Millar, C. I., K. Heckman, C. Swanston, K. Schmidt, R. D. Westfall, and D. L. Delany. 2014a. Radiocarbon dating of American pika fecal pellets provides insights into population extirpations and climate refugia. *Ecological Applications* 24:1748–68.

Millar, C. I., and R. D. Westfall. 2010. Distribution and climatic relationships of the American pika (*Ochotona princeps*) in the Sierra Nevada and western Great Basin, U.S.A.: Periglacial landforms as refugia in warming climates. *Arctic, Antarctic, and Alpine Research* 42:76–88.

Millar, C. I., R. D. Westfall, and D. L. Delany. 2013. New records of marginal locations for American pika (*Ochotona*

princeps) in the western Great Basin. *Western North American Naturalist* 73:457–76.

Millar, C. I., R. D. Westfall, and D. L. Delany. 2014b. Thermal regimes and snowpack relations of periglacial talus slopes, Sierra Nevada, California, USA. *Arctic, Antarctic, and Alpine Research* 46:191–212.

Millar, C. I., R. D. Westfall, and D. L. Delany. 2016. Thermal components of American pika habitat: How does a small lagomorph encounter climate? *Arctic, Antarctic, and Alpine Research* 48:327–43.

Millar, C. I., R. D. Westfall, A. Evenden, J. G. Holmquist, J. Schmidt-Gengenbach, R. S. Franklin, J. Nachlinger, and D. L. Delany. 2015. Potential climatic refugia in semi-arid, temperate mountains: Plant and arthropod assemblages associated with rock glaciers, talus slopes, and their forefield wetlands, Sierra Nevada, California, USA. *Quaternary International* 387:106–21.

Morelli, T. L., C. Daly, S. A. Dobrowski, D. M. Dulen, J. L. Ebersole, S. T. Jackson, J. D. Lundquist, C. I. Millar, S. P. Maher, W. B. Monahan, et al. 2016. Managing climate change refugia for climate adaptation. *PLoS One* 8:e0159909.

Otto, H. W., J. A. Wilson, and E. A. Beever. 2015. Facing a changing world: Thermal physiology of American pikas (*Ochotona princeps*). *Western North American Naturalist* 75:429–45.

Ray, C., E. A. Beever, and T. J. Rodhouse. 2016. Distribution of a climate-sensitive species at an interior range margin. *Ecosphere* 7:e01379.

Rodhouse, T. J., M. Hovland, and M. R. Jeffress. 2017. Variation in subsurface thermal characteristics of microrefuges used by range core and peripheral populations of the American pika (*Ochotona princeps*). *Ecology and Evolution* 7:1514–26.

SAS Institute. 2015. *JMP® 12.2*. Cary, NC: SAS Institute Inc.

Shinderman, M. 2015. American pika in a low-elevation lava landscape: Expanding the known distribution of a temperature-sensitive species. *Ecology and Evolution* 5:3666–76.

Simpson, W. G. 2009. American pikas inhabit low-elevation sites outside the species' previously described bioclimatic envelope. *Western North American Naturalist* 69:243–50.

Smith, A. T. 1974. The distribution and dispersal of pikas: Influences of behavior and climate. *Ecology* 55:1368–76.

Smith, A. T., and M. E. Gilpin. 1997. Spatially correlated dynamics in a pika metapopulation. In *Metapopulation dynamics: Ecology, genetics and evolution*, ed. I. A. Hanski and M. E. Gilpin, 407–28. San Diego, CA: Academic Press.

Smith, A. T., and J. D. Nagy. 2015. Population resilience in an American pika (*Ochotona princeps*) metapopulation. *Journal of Mammalogy* 96:394–404.

Smith, A. T., J. D. Nagy, and C. I. Millar. 2016. Behavioral ecology of American pikas (*Ochotona princeps*) at Mono Craters, California: Living on the edge. *Western North American Naturalist* 76:459–84.

Smith, A. T., and M. L. Weston. 1990. *Ochotona princeps. Mammalian Species* 352:1–8.

Stephenson, N. L., C. I. Millar, and D. N. Cole. 2010. Shifting environmental foundations: The unprecedented and unpredictable future. In *Beyond naturalness: Rethinking park and wilderness stewardship in an era of rapid change*, ed. D. N. Cole and L. Yung, 50–66. Washington, DC: Island Press.

Stewart, J. A. E., J. D. Perrine, L. B. Nichols, J. H. Thorne, C. I. Millar, K. E. Goehring, C. P. Massing, D. H. Wright, and B. Riddle. 2015. Revisiting the past to foretell the future: Summer temperature and habitat area predict pika extirpations in California. *Journal of Biogeography* 42:880–90.

Stewart, J. A. E., and D. H. Wright. 2012. Assessing persistence of the American pika at historic localities in California's northern Sierra Nevada. *Wildlife Society Bulletin* 36:759–64.

Stewart, J. A. E., D. H. Wright, and K. A. Heckman. 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.

Wilkening, J. L., C. Ray, E. A. Beever, and P. F. Brussard. 2011. Modeling contemporary range retraction in Great Basin pikas (*Ochotona princeps*) using data on microclimate and microhabitat. *Quaternary International* 235:77–88.

Wilkening, J. L., C. Ray, and J. Varner. 2015. Relating subsurface ice features to physiological stress in a climate sensitive mammal, the American pika (*Ochotona princeps*). *PloS ONE* 10:e0119327.