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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

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Abstract

We used a rapid assessment to survey American pika (*Ochotona princeps*) populations and documented 420 pika site occurrences in southwestern U.S.A. These included 329 sites from the Sierra Nevada (SN), California; 67 from six southwestern Great Basin (swGB) ranges, California and Nevada; 16 from three central Great Basin ranges, Nevada; and 8 from the central Oregon Cascades. Of these, 67% were currently occupied, 27% modern (indirectly scored active), and 6% old. Sites were grouped into 148 demes, 88 regions, and 11 mountain ranges. Current elevations ranged from 1645 m (1827 m excluding Oregon) to 3887 m, extending the lower elevational range of the species at the study latitude. Sites were distributed on all slope aspects with a preference for north to easterly aspects, and without preference for substrate. Rock-ice-feature (RIF) till, notably rock-glacier and boulder-stream landforms, accounted for 83% of the sites. Climatic relationships from the PRISM model for the SN and swGB sites showed wide tolerance, with average precipitation 910 mm, average minimum temperature −3.9 °C, and average maximum temperature 8.7 °C. Average minimum temperatures for old sites were not significantly different from recent sites, whereas average maximum temperatures were significantly higher in old sites. Unusual features of RIF landforms make them important refugia for pikas as climates warm. In contrast to studies that document species vulnerability elsewhere, pikas in the SN and swGB appear to be thriving and tolerating a wide range of thermal environments.

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Introduction

American pikas (*Ochotona princeps* Richardson, Family Ochotonidae) are small, diurnal, and generalist herbivores that inhabit patchily distributed, rocky slopes of western North American mountains (Smith and Weston, 1990). A relative of rabbits and hares (Order Lagomorpha), pikas tolerate cold-climate environments through a combination of physiological and behavioral adaptations that includes dense pelage, high basal metabolism, high core body temperature, discriminate forage choice, food stockpiling, and habitat selection (Smith and Weston, 1990). While these and other characteristics enable pikas to exploit cold habitats and high elevations, many of the same features render them sensitive to even mildly warm conditions. This vulnerability has been shown under experimental conditions (Smith, 1974), documented in late Quaternary paleoclimatic transitions (Grayson, 2005), and as a response to contemporary anthropogenic climate warming (Beever et al., 2003). Physiological sensitivity to warming, coupled with the geometry of decreasing area at increasing elevation on mountain peaks, has raised concern for the future persistence of pikas in the face of climate change. The species has been petitioned under California state and federal laws for endangered species listing (Wolf et al., 2007a, 2007b), elevating the urgency to monitor current distribution and improve understanding of climatic relations and biogeography. Pikas may also serve as early-warning indicators for climate-change effects in mountain environments generally, and thus understanding their current and historic ranges and habitat needs has broad implications.

Of the 36 pika subspecies described in North America, four occur in our primary study region of California (CA) and adjacent regions of Nevada (NV), including the Yosemite pika (*O. p. muiri*) from the central Sierra Nevada, CA and adjacent NV ranges; Mt. Whitney pika (*O. p. albata*) from the southern Sierra Nevada; White Mountain pika (*O. p. sheltoni*) from the White Mountains, CA and NV; and *O. p. tutelata* from the central NV mountains (Hall, 1946). The historic elevations for these subspecies range from 2140 m to over 3900 m, with most records from the central Sierra Nevada and Great Basin above ~2500 m (Grinnell and Storer, 1924; Hall, 1946), and records in the southern Sierra Nevada above ~3050 m (Grinnell, 1912). The highest published elevation in our region is 3960 m (Howell, 1924). Our observations of pika in Oregon are classed in a fifth subspecies, *O. p. fumosa* (Hall, 1946). A phylogenetic analysis based on allozyme diversity described four evolutionary lineages in the species (Hafner and Sullivan, 1995); our CA and NV sites are in one lineage, and the Oregon sites are in a second.

Grinnell (1917) made an early observation in the Sierra Nevada of a relationship between elevational distribution and temperature limitations of pikas, that is, that the species is limited to high elevations because temperatures are cool. This association subsequently was corroborated in our region by Smith (1974) and Hafner (1994). Resurvey studies in two major regions of pikas' species range, the western Sierra Nevada and Great Basin,

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recorded extirpation of historic low-elevation pika populations. In Yosemite National Park, Moritz and colleagues resampled early 20th-century small mammal transects conducted by Grinnell (Grinnell and Storer, 1924). Their analyses document 20th-century contraction upward of pikas' lower range at one site in Yosemite Park (Moritz et al., 2008). Similarly, in a resurvey of 25 historic populations in the Great Basin ranges, Beever et al. (2003) found that seven sites had been abandoned. Their analysis of associated factors concluded elevation to be a primary correlate with extirpation, and that low elevations and warm habitats were most at risk. Results from continuing resurvey and extensive direct (temperature logger) and indirect (modeling) climate inference give evidence of a far more massive and climate-dependent collapse of pika populations in the Great Basin than had been previously suspected (Erik Beever and Chris Ray, unpublished and personal communications, 2008).

STUDY GOALS

Our goals were to improve understanding of the current status, distribution, and habitat use of the American pika in mountains of eastern California and western Nevada, and to assess climatic relationships of occupied and unoccupied habitat. In so doing we sought to develop a rapid assessment method for pika occurrence that would reliably document recent use of a site; be readily learned and applied by minimally trained observers with no or little equipment; require little time for survey; apply under diverse weather, seasons, times of day, and across regions of the species' range; and enable compilation of a database that includes associated environmental and geographic statistics. Using this method our first objective was to survey pikas in the eastern California and western Nevada and to build a database of occurrence and non-detection sites covering a wide range of elevations and environments. A second objective was to use the database to assess geomorphic affinities of pika habitat, analyze climatic relationships of sites, and evaluate refugium environments for pikas under warming climates.

Methods

STUDY AREA AND FIELD METHODS

The study region was central-eastern Sierra Nevada (SN), CA, and adjacent Great Basin (GB) ranges, CA and NV (Fig. 1). In the SN, our study extended at the north from the West Fork Carson River southward to Big Pine Creek, with focused survey in the region between Robinson Canyon (Cyn; Bridgeport area) and Duck Pass (south of Mammoth Lakes [Lks] area). We considered mountain ranges that occur east of the Sierra Nevada crest and west of the Walker Lane (Unruh et al., 2003) as a GB subregion of ecologic, geologic, and climatic integrity; here we call this region the southwestern GB (swGB). Ranges that we explored in this area were the White Mountains, Monitor Pass Range, Glass Mountain Range, Bodie Mountains, Sweetwater Mountains, and the Wassuk Range. We made minor forays into the central Oregon Cascades and central NV mountains (Shoshone, Toiyabe, and Toquima Ranges).

During 2007 through early 2009 we searched for evidence of pikas in montane environments that have been described previously as pika habitat. These included diverse talus and fractured boulder slopes having rock fragments with diameters ranging from 10 cm to 200 cm, and where boulder fields were situated adjacent to vegetation suitable for forage. For each site we ranked the geomorphic setting using 10 categories. When sites

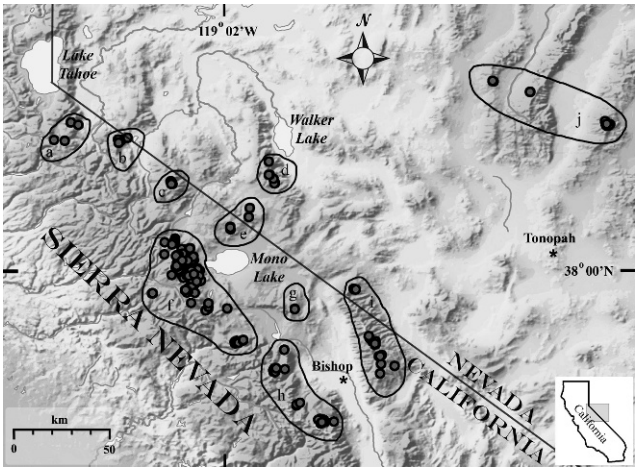


FIGURE 1. Map of study region showing distribution of pika sites recorded in the Sierra Nevada, six southwestern Great Basin ranges, and three central Great Basin ranges, California and Nevada. Sites in Oregon are not shown. Mountain regions with pika samples include: Sierra Nevada (north, *a*; central, *f*; and southern, *h*); southwestern Great Basin ranges including Monitor Pass range (b), Sweetwater Mtns. (c), Wassuk Range (d), Bodie Mtns. (e), Glass Mtn. Range (g), and White/Inyo Mtns. (i); and central Great Basin ranges (j), including, from west to east, Shoshone, Toiyabe, and Toquima Ranges.

were on till of rock-ice features (RIFs), we used the classification of Millar and Westfall (2008). RIFs are glacial- and/or periglacial-derived landforms primarily occurring in high, semi-arid temperate mountain ranges and arctic landscapes. Most relevant to pika habitat were three RIF types (rock glaciers, boulder streams, and solifluction slopes), briefly described as follows. Rock glaciers comprise complexly lobed, elongate landforms of highly sorted rock debris and having distinctly oversteepened fronts (Millar and Westfall, 2008). They are situated in distinct contexts, either in cirques, in which case they flow down-valley, or along ridge slopes, in which case they flow perpendicular to the valley axis. Rock glaciers can be active, in that they contain persistent ice, move as a discrete body, and have ongoing freeze-thaw processes influencing their morphology and movement. Conversely, relictual or inactive features contain no or little persistent ice and are characterized by remnant till. Related RIF boulder streams are small to large talus landforms characterized by highly sorted, shattered, angular rocks of consistent clast size, lacking oversteepened fronts but having characteristic sharp boundaries with adjacent turf, occurring on steep ridge and cirque slopes, and dominantly influenced by freeze-thaw processes. Solifluction fields derive from saturated slopes moving over frozen rock or permafrost substrate to form extensive fields of terraced slopes; terraces are characterized by steep rocky risers and flatter, vegetated treads. The remaining categories in which we searched were non-RIF rocky environments including eroding bedrock slopes, rockslides and talus cones, till of glacial moraines, tors and inselbergs, and a miscellaneous category that included Holocene lava flows and cinder cones, cliff crevices, and caves. We also classified anthropogenic pika settings.

Within these environmental settings, we searched during the snow-free seasons using no set criteria for weather, time-of-day, slope aspect, or substrate. We surveyed montane environments above ~1640 m. At each site, we surveyed up to 30 minutes, after which time we scored the site as non-detection if pika evidence as described below was not present. We recorded latitude, longitude, elevation, slope aspect by azimuth degree (subsequently binned

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into eight 45° groups centered on cardinal and diagonal azimuths), substrate to major geologic type, site age, and presence of other mammal signs.

Our basic unit was a *site occurrence*, defined by the presence of >25 pika fecal pellets within a single area <1.0 m^2. Pika pellets are round, hard, 2–3 mm diameter, and not confused with sign of other mammals. Sites were vouchered by pellet collections, which are archived at the USDA Forest Service Pacific Southwest Research Station (Albany, California); all sites were photographed. Exceptional sites where pika were seen or heard but pellets not collected were also recorded. Site age (occupancy) was recorded in three categories: *current*, if sightings, vocalizations, or fresh (green) vegetation in haypiles occurred—these sites we considered to be definitively identified as actively occupied; *modern*, if none of the above signs were present but fecal pellets were fresh (hard, brown or green, non-decomposing), urine sign was fresh (yellow-white, smeary, often with fresh fecal pellets encased), and haypiles had only brown vegetation—these sites we considered indirectly identified as active; *old*, if pellets were white and decomposing, urine sign was chalky white and flaking, and no other sign was present—these sites we considered unoccupied.

Site occurrences were recorded only where they were more than 50 m apart, which exceeds the largest nearest-neighbor distance and home-range diameter for pikas (Smith and Weston, 1990; Beever, et al., 2008). Sites were grouped geographically into hierarchic categories as follows: *demes*, groups of sites separated from other groups by more than 3 km, which exceeds the average maximum dispersal distance of 2 km cited for adult pikas (Smith and Weston, 1990); *regions*, groups of demes separated by significant but relatively short (5–15 km) isolation barriers (i.e., unfavorable pika environment such as snow, ice, non-rocky ground), mostly demes within an obvious canyon system or plateau region; and *mountain ranges*, distinct ranges separated by long-distance (>15 km) isolation barriers.

CLIMATIC RELATIONSHIPS

We evaluated climatic conditions of pika occurrence and non-detection sites with the PRISM climate model (Daly et al., 1994), using 30 arc-sec data and extracting means for annual, January, and July minimum temperatures; annual, January, and July maximum temperatures; and annual, January, and July precipitation, for the published period of record, 1971–2000. We used downscaling methods described in Millar et al. (2006) and Hamman and Wang (2005) to adjust resolution to 16 ha grids. In a previous study of the same general region and for the same time interval we tested accuracy by comparing PRISM estimates to nearby long-term observational weather-station records and found high correlations between station observations and model estimates, especially in temperature variables (Millar et al., 2006). In the analyses we have performed, sites that are close together have the potential to be repeat samples of a PRISM cell, but autocorrelation is not a factor. Given repeats, we might underestimate climatic variance, but because our database is widely distributed spatially and involves many PRISM cells, underestimating spatial variance should not be a problem either.

We summarized climatic data and correlations with elevation for the overall data set by site age, and by SN versus southwestern GB groups and by occurrence versus non-detection sites. Correlations, discriminant analysis, and tests of significance (*t*-tests, Pearsons, likelihood, and analysis of variance [ANOVA]) were performed in JMP (SAS Institute Inc., 2004).

In addition to estimations from the PRISM model, we present data from RIF locations in the Sierra Nevada where we installed temperature dataloggers (Thermochron iButton, Maxim Integrated Products, Sunnyvale, CA). Although we originally deployed these instruments for reasons other than to monitor pika habitat, 13 of them were serendipitously located at pika sites. The instruments were set for 4-h intervals, inserted within white PVC tubes to avoid direct solar radiation, and placed either in ambient air in a rock-sheltered location at the RIF surfaces, or within RIF rock matrices ~1 m below the surface of the RIF. We extracted data for the warm season, defined as 15 June–15 September. These instruments recorded one to two seasons during the years 2006 to 2008, which varied by location.

Results

GEOGRAPHIC, ELEVATIONAL, AND GEOMORPHIC DISTRIBUTION

Pika Occurrence Sites

In total, we recorded 420 pika site occurrences, distributed into 148 demes, 88 regions, and 11 mountain ranges (Table 1; Fig. 1). These include 329 sites in the SN (6 north of Robinson Cyn, 294 in the central SN, and 29 south of Duck Pass); 67 sites in the southwestern GB (including all ranges in which we searched); 16 sites in the central GB; and 8 sites in the Oregon Cascades. The lower numbers in the GB and Oregon relative to the SN reflect the significantly less time we spent in these areas as well as differences in non-detection.

Ages of pika sites varied by region (Table 1). Overall, 94% of the total were classed as recent, combining *current* (67%) and *modern* (27%), and 6% were *old* sites. The relative number of *old* sites increased from the SN eastward into the GB ranges: 2% in the SN, 17% in the southwestern GB ranges, and 50% in the central GB ranges. Of the 8 sites in Oregon, all were recent.

Considering the CA and NV locations, pika site elevations ranged from 1827 m to 3887 m, with an average of 3038 m (Table 1). Oregon sites ranged from 1645 m to 2323 m. Sites averaged non-significantly higher for SN (3052 m) than GB (3041 m southwestern GB; 2992 m central GB) sites, with a narrower elevation range of the Great Basin sites. The latter may be related to the difference in our sampling and exploration efforts among the regions as well as the smaller area at high-elevation in the GB ranges compared to SN.

Pika sites were distributed on all slope aspects (Fig. 2), with slight preference to eastern, northeastern, and western orientations; below 2800 m, by contrast, pika sites were skewed to northern and southern aspects. Of the 420 pika sites, 6 were anthropogenic settings, including mine tailings, stone walls, rockwork dam, and historic foundations. At the remaining sites, pikas used a variety of substrates: 135 sites were dark metamorphic, 63 light metamorphic, 151 granitic, 42 dark volcanic, 13 light volcanic, 9 carbonate, and 7 sedimentary in origin. Among the total, 88 sites were in areas of at least moderate human visitation; 28 of these were within 1 m of heavily used recreational foot- and pack trails.

Excluding the anthropogenic sites, 83% of the pika sites overall occurred in RIF landforms, both old and active (Table 1). The most common was the *boulder stream* category, which accounted for 66% of all pika sites, with nearly equal proportions in the SN and GB. Cirque rock glaciers (RGC), old and active, were the second most common, composing 12% of all locations. Pika sites occurring in RGC landforms, as well as the remaining

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TABLE 1

Distribution, age, and geomorphic setting of pika occurrence and pika non-detection sites (within 30-minute search period) in the Sierra Nevada, Great Basin, and central Oregon Cascades. Rock-ice features include cirque rock glaciers, RGC; valley rock glaciers, RGV; boulder streams, BSC; solifluction slopes, MWA; see text for further description.

Mountain region		Age (%)			Elev (m)			Geomorphic Setting										
	Number							Rock-	Ice	Features		Glacial	Insel-	Rock-slide/	Eroding	Lava	Other		Anthro-
Range	of sites	Current	Modern	Old	Average	Minimum	Maximum	*RGC*	*RGV*	*BSC*	*MWA*	moraine	berg/tor	Talus cone	bedrock	flow	Cliff	Cave	pogenic
I. PIKA OCCURRENCE SITES (letters refer to Fig. 1)																			
Sierra Nevada (*a*, *f*, *h*)	329	77	21	2	3052	1827	3768	51	15	226	2	3	3	5	19	0	1	0	4
Southwest Great Basin	67	35	48	17	3041	2113	3887	0	0	39	0	0	8	2	13	3	0	0	2
Bodie Mtns (e)	*16*				*2632*	*2113*	*3395*			*12*					*2*				*2*
Glass Mtns (g)	*5*				*2751*	*2533*	*3031*			*2*						*3*			
Monitor Pass (b)	*6*				*2577*	*2470*	*2689*			*5*			*1*						
Sweetwater Mtns (c)	*8*				*3029*	*2310*	*3348*			*6*					*2*				
Wassuk Range (d)	*6*				*2865*	*2539*	*3153*			*2*			*2*		*2*				
White Mtns (i)	*26*				*3381*	*2442*	*3887*			*12*			*5*	*2*	*7*				
Central Great Basin	16	6	44	50	2992	2637	3493	0	3	12	0	0	1	0	0	0	0	0	0
Shoshone (j)	*6*				*2827*	*2760*	*2868*			*6*									
Toiyabe (j)	*3*				*2648*	*2637*	*2655*			*3*									
Toquima (j)	*7*				*3280*	*3011*	*3492*		*3*	*3*			*1*						
Oregon Cascades	8	50	50	0	1974	1645	2310	0	0	0	0	0	0	1	0	5	1	1	0
All occurrence sites	**420**	**67**	**27**	**6**	**3017**	**1645**	**3887**	**51**	**18**	**277**	**2**	**3**	**12**	**8**	**32**	**8**	**2**	**1**	**6**
II. PIKA NON-DETECTION SITES																			
Sierra Nevada	45				2885	1827	3822	2	1	8	3	5	0	13	13	0	0	0	0
Southwest Great Basin	39				2128	1637	2775	0	0	14	0	0	0	3	16	2	2		2
Bodie Mtns (e)	*13*				*2217*	*1721*	*2848*			*6*					*5*		*1*		*1*
Glass Mtns (g)	*8*				*2209*	*1999*	*1783*							*1*	*4*	*2*			*1*
Monitor Pass (b)	*3*				*1912*	*1943*	*2214*			*2*					*1*				
Sweetwater Mtns (c)	*7*				*2011*	*1637*	*2278*							*2*	*5*				
Wassuk Range (d)	*4*				*2335*	*2075*	*2775*			*3*							*1*		
White Mtns (i)	*4*				*2086*	*1818*	*2736*			*3*					*1*				
Central Great Basin	13				2493	2035	3533	0	0	6	0	0	0	0	5	0	2	0	0
Shoshone (j)	*3*				*2415*	*2153*	*2709*								*2*		*1*		
Toiyabe (j)	*7*				*2282*	*2035*	*2679*			*5*					*1*		*1*		
Toquima (j)	*3*				*2782*	*2327*	*3533*			*1*					*2*				
Oregon Cascades	0							0	0	0	0	0	0	0	0	0	0	0	0
All non-detection sites	**97**				**2520**	**1637**	**3822**	**2**	**1**	**28**	**3**	**5**	**0**	**16**	**34**	**2**	**4**	**0**	**2**

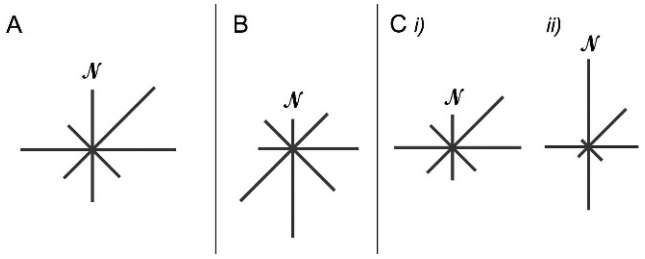


FIGURE 2. Slope aspects of pika occurrence and non-detection sites in the Sierra Nevada and southwestern Great Basin ranges. Azimuths were binned into eight 45° groups; arm lengths indicate the number of sites in that aspect group. Figures are scaled by sample size for each group, with center of diagram being zero. Figures A and Ci are scaled −65 to +65; Figs B, Cii, and Ciii are scaled −20 to +20. (A) All pika occurrence sites ($n = 396$; longest arm, NE = 65). (B) Non-detection sites ($n = 92$; longest arm, S = 19). (C) Sites grouped by elevation ranges: (i) pika sites >2800 m ($n = 303$; longest arm NE = 63), (ii) pika sites ≤2800 m ($n = 93$; longest arm N = 30).

RIF category, occurred only in the SN with the exception of three sites in the Toquima Mtns. In the GB, more pika sites (30%) were in non-RIF eroding bedrock slopes than in the SN (9%). Unusual sites included 2 cliff faces, 8 Holocene lava flows, and 1 large cave. In the Oregon Cascades, we searched only in the region of the North Sister Mountain and McKenzie Pass, both of which are areas dominated by extensive lava fields and cinder cones; all eight Oregon pika sites were in these non-RIF, volcanic contexts.

We recorded pika sites within the context of diverse vegetation associations, ranging from lower-elevation *Artemesia* and *Chrysothamnus* shrubland, *Pinus monophylla* woodland, *P. jeffreyi* forest, *Salix* riparian and wetland communities, through mid-montane forests types with *P. contorta*, *Abies concolor*, *A. magnifica*, or *Populus tremuloides* dominant, subalpine forest types including *Tsuga heterophylla*, *Pinus contorta*, *P. albicaulis*, *P. flexilis*, and *P. longaeva*, to many above-treeline alpine meadow, tundra, and fell-field communities. Although many sites adjoined dense grass, herb-, and forb-dominated vegetation patches, we commonly encountered sites where pika-inhabited taluses adjoined dry forest or woody shrublands with little to no plant understory. We also commonly encountered pika sites in the midst of expansive talus environments that were distant (up to 3 km) from obvious patches of vegetation. We encountered heavily used, active pika sites on very small tors and rocky spurs isolated from each other by ≥2 km. In these situations, the intervening environments were non-rocky and supported vegetation not usually considered pika habitat, for instance, alpine meadows or sagebrush-shrub communities.

We found sign of several other mammal species intermixed with pika pellets in our sites. Most common was scat of yellow-bellied marmot (*Marmota flaviventris*), frequent at mid- to upper elevation pika sites in all regions. Less common, and without obvious elevation association, were feces of rabbit (*Lepus*, *Sylvilagus* spp.), mule deer (*Odocoileus hemionus*), very small (<3 mm) rodent/shrew feces of diverse types, and, in four instances, domestic horse (*Equus caballus*). Woodrat (*Neotoma* spp.) sign occurred in only six sites, all below 2580 m.

Pika Non-detection Sites

We recorded 97 sites in otherwise optimal-appearing habitat where no pikas were detected after 30 minutes of searching (Table 1). Relative to the total sites in a region (occurrence plus non-detection), these were distributed disproportionately among the regions, with 12% of SN sites non-detected, 37% of southwestern Great Basin sites non-detected, and 45% of central GB sites non-detected. We recorded no non-detection sites in Oregon. The average elevation of non-detection sites compared to pika occurrence sites in CA and NV was 518 m lower, although the elevation ranges were similar between occurrence and non-detection sites (Table 1). Slope aspects of non-detection sites were significantly ($p < 0.01$) different from those for occurrence sites, with southern aspects dominating (Fig. 2b). Non-detection sites were far less common on RIF landforms than occurrence sites (35% vs. 83%, respectively), and far more common on rockslides, eroding bedrock, and glacial moraines (56% vs. 14%, respectively; Table 1). The range of substrates on which non-detection sites occurred was similar to occurrence sites.

CLIMATIC RELATIONSHIPS

Pika Occurrence Sites

As intersected with the PRISM climate grids, the 396 pika sites from the SN and southwestern GB occupy a wide range of climatic conditions. Average annual precipitation for these sites ranged from 279 to 1610 mm with an overall mean of 910 mm (Fig. 3). The sites classed as *old* were significantly drier than recent sites (*current* and *modern* classes combined) in annual and January precipitation ($p < 0.0001$), but were not significantly different in July precipitation. At the latitude of our sites, most precipitation falls in winter, as evidenced by the high average precipitation in January (166 mm for recent sites) compared to July (19 mm). The distribution of precipitation values in both January and July deviated from normal by more values in the tails, with the summer distribution bimodal. Considering regional contrasts, southwestern GB pika sites were significantly drier than SN sites (Table 2). In both annual and January precipitation means, southwestern GB sites averaged in the lowest 25% quartile for January precipitation. By contrast, GB sites averaged slightly higher July precipitation values than SN sites.

Temperature values of the pika sites were also modeled with PRISM (Figs. 4, 5). Minimum temperatures for the 396 SN and southwestern GB sites overall averaged −3.9 °C and maximum temperatures averaged 8.7 °C. January minimum temperatures for all sites averaged −10.8 °C and July minimum temperatures for all sites averaged 5.3 °C. January maximum temperatures averaged 1.0 °C, and July maximum temperatures averaged 19.0 °C. Average minimum temperatures for the *old* compared to recent sites were not significantly different for annual, January, or July values, although in each case the actual values of means for the *old* sites were lower (colder) than for the current sites. In contrast, *old* sites exhibited significantly higher (warmer) maximum temperatures than current sites for annual ($p < 0.01$), January ($p < 0.01$), and July ($p < 0.01$) means. Distributions of annual and the two monthly minimum temperatures and also the July maximum temperature distribution were truncated or skewed, with fewer values in the warm range than in normal distribution.

Comparing regions, southwestern GB sites had small but significantly lower mean minimum temperature and non-significantly higher mean maximum temperature than SN sites overall (Table 2). Southwestern GB pika sites were colder than SN in minimum temperature for both January and July, whereas GB sites were warmer than SN in maximum temperature for both seasons. In general these sites reflect the more continental climate and the effect of the summer monsoon in the GB—

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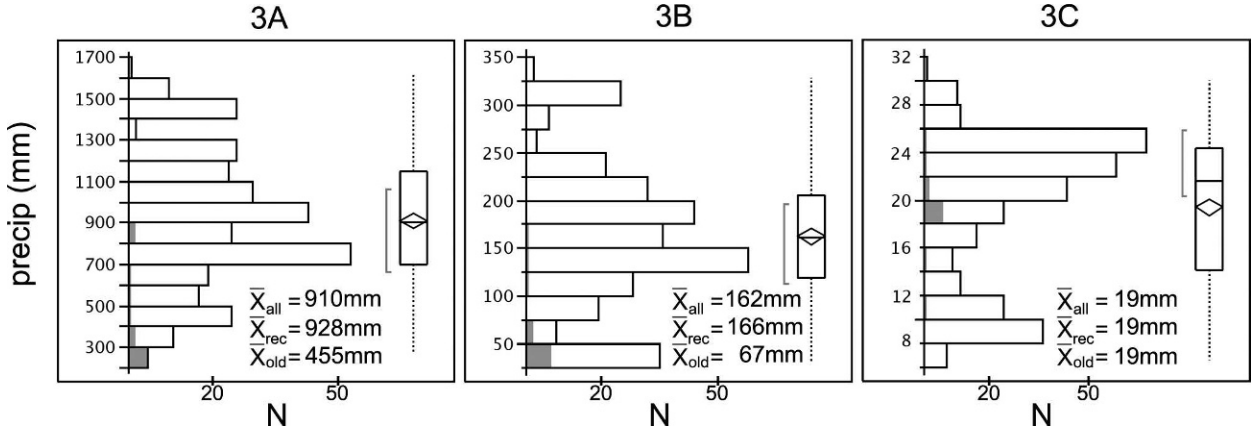


FIGURE 3. Precipitation (mm) estimated from the PRISM climate model (Daly et al., 1994) and adjusted for elevation, for 343 pika sites from the Sierra Nevada and southwest Great Basin ranges. Means are given for all sites, for recently used sites (rec; including *current* plus *modern*), and for old sites. The last are indicated by dark shading. (A) Average annual precipitation. (B) Average January precipitation. (C) Average July precipitation. Dark shading indicates the 13 old sites and no shading indicates the 330 current sites. Box plots show overall mean (horizontal center of diamond), 95% confidence interval of the mean (upper and lower points of diamond), 25% and 75% quartiles (box boundaries), 50% density of values (bracket), and range of data (dotted line).

colder in winter, warmer in summer, overall drier but with relatively more of the annual precipitation during summer than in the SN.

Correlations between elevation and climate values of pika sites (SN and southwestern GB) indicate distinct and contrasting patterns (Figs. 6, 7). Higher elevation sites had generally greater January and July precipitation, although the correlation was weak ($r = 0.30$ and 0.20, respectively). Minimum temperatures of pika sites had weak negative correlations with elevation ($r = -0.58$ and -0.39 for January and July, respectively). By contrast, maximum temperature and elevation of pika sites were strongly negatively correlated: $r = -0.95$ for average annual maximum temperature, $r = -0.87$ for January maximum temperature, and $r = -0.97$ for July maximum temperature. These contrasting trends are echoed also in low correlations of minimum and maximum temperatures: the average annual correlation (r) was 0.37 and the correlation of July minimum and maximum temperatures was 0.22 (not graphed).

Warm-season air temperatures (15 June through 15 September) recorded by temperature dataloggers in till of rock glaciers and boulder streams at 13 pika sites averaged 10.0 °C (Table 3). The mean site elevation for these instruments was 3191 m and sites ranged from 2829 m to 3466 m. Sensors placed in sheltered locations near the RIF rock surfaces were significantly warmer ($p < 0.01$) than those located more than 1 m below the surface in rock matrices (means 11.5 °C and 7.7 °C, respectively). This difference is not readily explained by the lower elevation of locations of the surface-air versus subsurface sensors (mean 88 m lower), as a standard lapse rate differential (−0.65 °C/100m increase in elevation) would account for ~0.6 °C whereas the observed difference was 3.8 °C. The high extreme temperatures ranged from 13 °C to 26 °C, the latter being the upper limit of the instruments. This limit was met in three circumstances; in every case it occurred on fewer than two days. The lower range varied from 6 °C to −6 °C, the latter being the low range limit of the units; this limit was reached on only one day for the single unit that recorded this minimum temperature.

Pika Non-detection Sites

Considering the SN and southwestern GB, climatic values estimated for the non-detection sites were significantly different ($p < 0.0001$) from those of pika occurrence sites in discriminant analysis, and significantly different by ANOVA for all climate variables ($p < 0.0001$) except July precipitation, where the differences were non-significant ($p = 0.069$). Relative to occurrence sites, non-detection sites were drier by 270 mm (annual) and 57 mm (January); warmer in minimum temperature by 1.6 °C (annual), 1.2 °C (January), and 1.7 °C (July); and warmer in maximum temperature by 4.0 °C (annual), 2.6 °C (January), and 4.8 °C (July).

Discussion

GEOGRAPHIC AND ELEVATIONAL DISTRIBUTION OF PIKA SITES

Using a rapid-assessment method, we located and described 420 American pika site occurrences over the course of two field seasons in the Sierra Nevada (CA), southwestern Great Basin (CA

TABLE 2

Summary of climatic data from PRISM climate model (Daly et al., 1994). Sierra Nevada vs. southwestern Great Basin pika sites. Significance differences: *** $p < 0.001$; * $p < 0.05$; ns, non significant.

Group	*N*	Mean ann ppt (mm)	Mean Jan ppt (mm)	Mean July ppt (mm)	Mean ann T_{min} (°C)	Mean Jan T_{min} (°C)	Mean July T_{min} (°C)	Mean ann T_{max} (°C)	Mean Jan T_{max} (°C)	Mean July T_{max} (°C)
Significance		***	***	*	*	ns	ns	ns	ns	ns
Sierra	329	1001	184	19	−3.7	−10.6	5.6	8.7	1.1	18.9
swGB	67	487	60	21	−4.9	−11.7	4.2	8.8	0.5	19.7

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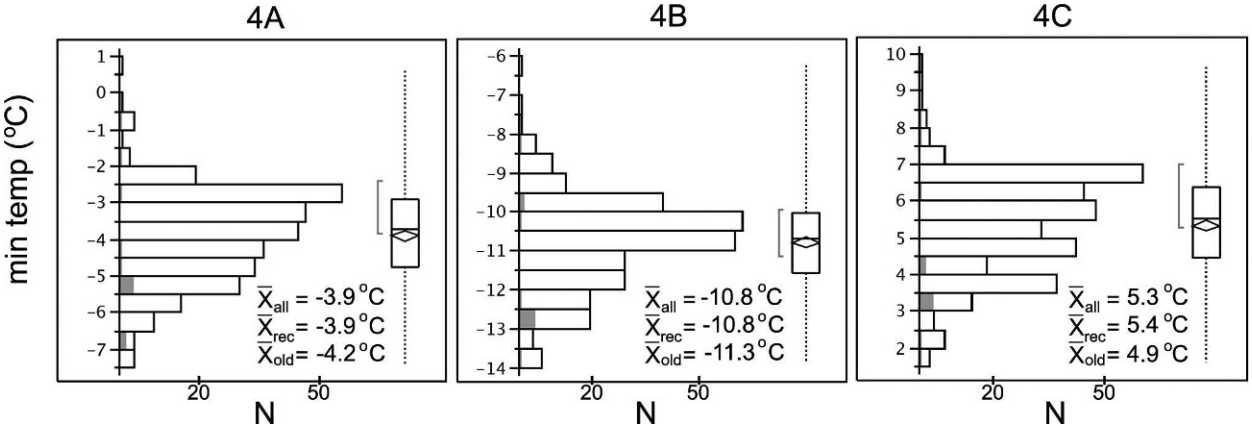


FIGURE 4. Minimum temperatures (°C) estimated from the PRISM climate model (Daly et al., 1994) and adjusted for elevation, for 343 pika sites from the Sierra Nevada and southwest Great Basin ranges. Means are given for all sites, for recently used sites (rec; including *current* plus *modern*), and for old sites. The last are indicated by dark shading. (A) Average minimum temperature. (B) Average January minimum temperature. (C) Average July minimum temperature. Shading for 13 old and 330 recent sites, and box plot format as in Figure 3.

and NV), and central Great Basin (NV), extending over 2060 m elevation, two degrees latitude (39°0.47′N to 37°7.38′N), and three degrees longitude (119°59.06′W to 116°54.69′W), and in a small area in the central Oregon Cascades. While this represents only a portion of the species' range, the survey greatly increases the geographic extent and number of pika sites previously documented in CA and NV; expands information on slope aspects, substrate lithologies, and location of known sites to new mountain ranges; and refines understanding of habitat preference and climatic associations. Whereas concern exists for diminishing range of pikas relative to early surveys, the distribution and extent in our study, pertinent to four subspecies and the Pacific southwest lineage of pikas, resemble the diversity of range conditions described in early 20th-century pika records (e.g., Grinnell and Storer, 1924). A similar situation occurred for another lagomorph of concern, pygmy rabbit (*Brachylagus idahoensis*), where a rapid assessment method revealed much wider distribution than had been implied from historic population databases or resurvey efforts (Himes and Drohan, 2007).

Within these regions, however, and notwithstanding the relatively small number (16) of central Great Basin sites, the trend of increasing *old* sites eastward from the Sierra Nevada was strong, from only 2% in the SN to 50% in the central Great Basin. One interpretation of this finding is that variability in population status exists across the species' range, and specifically that population viability may be lower in the central Great Basin relative to Sierra Nevada, a situation previously implicated (Beever et al., 2003; Grayson, 2005). Lack of association of elevation with age of sites contrasted with other studies, which have found extirpated sites to be at lowest elevations (Beever et al., 2003; Beever et al., 2008); our old sites occurred at low to high elevations (2113–3551 m). An alternate explanation to the increased number of *old* sites may be that local populations are simply more influenced by stronger metapopulation perturbations in the isolated ranges of the central Great Basin, which does not necessarily indicate lower viability, rather longer periods of time between extirpation and recolonization.

The abundance of low elevation occupied sites in our study is noteworthy. Our lowest elevation extends the lower elevational range published for either current or historic condition. For instance, Smith (1974) indicated Bodie, CA (2553 m) locations to be at the low limit of the species' elevational range, and Smith and

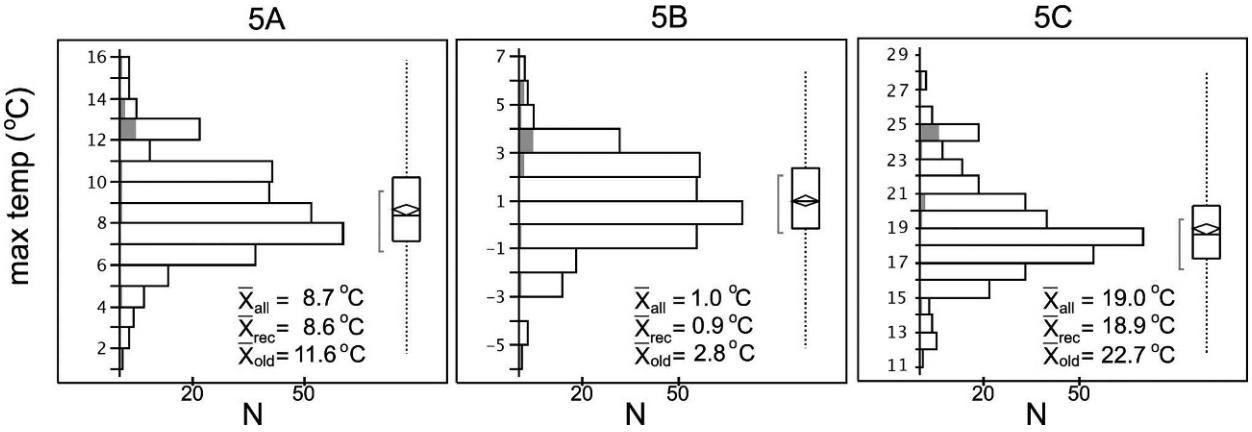


FIGURE 5. Maximum temperatures (°C) estimated from the PRISM climate model (Daly et al., 1994) and adjusted for elevation, for 343 pika sites from the Sierra Nevada and southwest Great Basin ranges. Means are given for all sites, for recently used sites (rec; including *current* plus *modern*), and for old sites. The last are indicated by dark shading. (A) Average maximum temperature. (B) Average January maximum temperature. (C) Average July maximum temperature. Shading for 13 old and 330 recent sites, and box plot format as in Figure 3.

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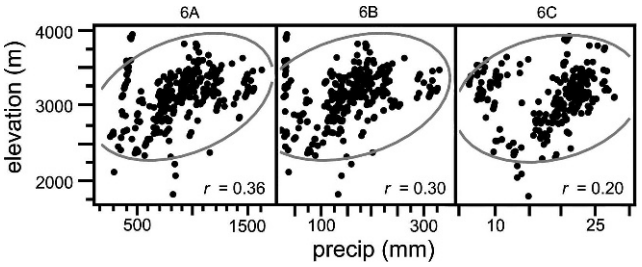


FIGURE 6. Scatterplot of correlations between elevation and precipitation for 339 pika sites from the Sierra Nevada and southwest Great Basin ranges . All pika sites combined. (A) Average annual precipitation. (B) Average January precipitation. (C) Average July precipitation. Correlation values (*r*) are given for each graph. Ellipsoids indicate 95% concentration of values.

Weston (1990) describe sites below 2500 m as unusual for our latitude. In our database, however, 14% of our sites were at or below the elevation of Bodie, and 10% were below 2500 m. Hall (1946) considered populations at 2590 m on Mt. Rose to be marginal, and Howell (1924) indicated the southern Sierra Nevada low-elevation range to be 2590 m. Our lowest site, at 1827 m, is below the historic lowest elevation of 2350 m recorded for the subspecies by Grinnell and Storer (1924) in Yosemite National Park; below the low elevation range limit for the White Mountains populations given by Howell (1924) as 2440 m; and below the lowest elevation described for the southern Sierra Nevada populations of 2134 m (Sumner and Dixon, 1953). In resurveys of Grinnell's historic transects, Moritz et al. (2008) documented an upward contraction in Yosemite Park of pikas' lower elevational range by 153 m, rendering the current lower species elevation in the Grinnell transect locations to 2530 m, which is 603 m higher than our lowest active site.

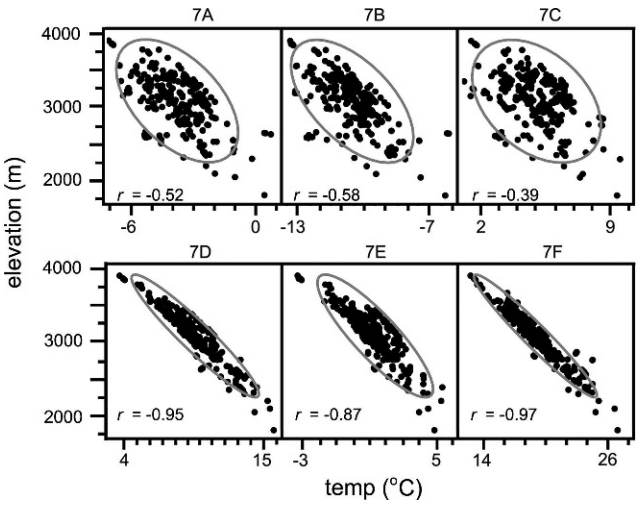


FIGURE 7. Scatterplot of correlations between elevation and temperature for 339 pika sites from the Sierra Nevada and southwest Great Basin ranges. All pika sites combined. (A) Average annual minimum temperature. (B) Average January minimum temperature. (C) Average July minimum temperature. (D). Average annual maximum temperature. (E) Average January maximum temperature. (F) Average July maximum temperature. Correlation values (*r*) are given for each graph. Ellipsoids indicate 95% concentration of values.

TABLE 3

Summary of observed air temperatures from 13 mini-dataloggers (iButtons). (A) Sensors placed on sheltered surface of rock-ice features (RIF). (B) Sensors placed in rock matrices (more than 1 m below the RIF surface) in the Sierra Nevada. Temperatures are summarized for 15 June to 15 September; years were 2006–2008. RIF types: cirque rock glacier (RGC) and scree boulder streams (BSC) (Millar and Westfall, 2008).

Site	Elevation (m)	RIF type	Mean temp (°C)	Temp range[1] (°C) low	Temp range[1] (°C) high	Year(s) of record
A. RIF Surface						
Karolyn Cyn	2829	RGC	16.7	6.0	26.0	2007
Tenaya Pk	2911	RGC	10.5	0.1	21.0	2007–2008
Oneida Lk	2926	RGC	13.8	1.0	26.0	2006–2007
Barney Lk	3071	RGC	11.6	−0.6	26.0	2007
Deer Lk	3313	RGC	9.7	−0.5	23.0	2007
Helen Lk	3353	BSC	8.5	−5.0	23.0	2006–2007
Kuna Crest	3423	RGC	10.4	3.0	17.0	2007
Excelsior Pk	3433	RGC	10.9	4.0	18.0	2007–2008
B. Rock Matrix Below RIF Surface						
Oneida Lk	3033	RGC	14.4	0.5	20.0	2006–2007
Gibbs Cyn	3113	RGV	8.1	0.0	15.8	2007–2008
Gibbs Cirque	3179	RGC	7.5	0.0	25.6	2007–2008
Excelsior Pk	3435	RGC	7.4	−0.8	15.0	2007–2008
Kuna Crest	3466	RGC	0.9	−0.9	13.0	2008
OVERALL AVERAGE	3191		10.0	0.5	20.7	2006–2008
RIF surface average	3157		11.5	1.0	22.5	2006–2009
Rock matrix average	3245		7.7	−0.2	17.9	2006–2010

[1] iButton instrumental minimum and maximum ranges are −5.0 °C and 26.0 °C, respectively. These values were reached during no more than 1–2 days for the relevant instrument during its period of record.

The upper elevation range of our sites (3887 m) is higher than the historic elevation range for the SN subspecies (3700 m; Grinnell and Storer 1924), and only 73 m below the upper range given for the southern SN and White Mountains subspecies (3960 m) by Howell (1924). Recognizing that we spent little effort searching above 3800 m, our survey was biased to elevations below that elevation.

CLIMATIC RELATIONSHIPS

Climatic dependence of pikas and vulnerability of pika habitat to global warming have been escalating concerns documented by recent research (Grayson, 2005; Beever et al., 2003, 2008; Moritz et al., 2008) and conservation assessments (Wolf et al., 2007a, 2007b). Pikas' thermal tolerance range has been considered to be quite narrow, restricting the species to cool, moist microhabitats with short summers (<20 days yr^{-1} with maximum temperatures >35 °C), long winters (>180 days yr^{-1} with maximum temperatures <0 °C), short frost-free period (<90 days yr^{-1}), high mean annual precipitation (>300 mm) (Hafner, 1994), and low maximum temperature extremes. Smith (1974) calculated mean maximum temperature for June through September in CA at a low-elevation pika population (Bodie, ~2500 m) as 22.8 °C and at a high elevation population (near Tioga Pass, ~3200 m) as 14.5 °C. At the high elevation site, no summer days exceeded 25 °C, while 43 days exceeded this value for the warm months at the low-elevation

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site. Beever et al. (2008) observed warm season (15 June to 31 September) temperatures at extant pika populations distributed through the Great Basin to average 16.8 °C to 5.1 °C. Vulnerability to temperature has been tested experimentally on caged pikas, which died soon after ambient (shade) temperatures reached 25.5–29.4 °C (Smith 1974).

These climatic values compare reasonably with our estimates from the PRISM model, although our large number of sites yielded a wider climate envelope for our region. The multi-modal distribution of precipitation values suggests pikas can tolerate a range of dry to wet conditions. Our average annual precipitation for 67 southwestern Great Basin sites (487 mm) was lower than the average for 18 extant GB sites (589 mm) of Beever et al. (2008) and similar to the value they calculated for seven extirpated interior GB sites (474 mm). Our upper annual precipitation range (1611 mm) was greater than most other estimates. The Great Basin sites in our study defined a much drier climatic envelope than our Sierran sites, the latter of which more closely resembles diversity cited for the entire species' range.

Temperature averages and ranges calculated from the PRISM model for our database indicated a relatively wide thermal tolerance for the species compared to published estimates. Annual (2.4 °C), January (−4.9 °C), and July (12.2 °C) average temperatures for the Sierran and southwestern Great Basin sites were much warmer and had wider ranges than those estimated previously for our region (Smith, 1974; Beever et al., 2008). The truncated and skewed nature of several temperature variables suggests a recent disequilibrium in pikas' range wherein sites at warmer values have been recently abandoned and a new, normally distributed range of occupation sites has not been achieved. Whereas the pattern of these distributions aligns with other studies that indicate loss of pika sites where warm-season temperatures are high (Beever et al., 2003), the similar pattern in winter minimum temperatures is less clearly interpreted.

In addition to estimates of surface temperature from the PRISM model, we can compare our datalogger temperature records to Beever et al.'s (2008) results. At a low-elevation population slightly north of our study region in NV, Beever et al. estimated mean mid-June to late-September temperatures within rock matrices to be 17.3 °C, and compared these to values ranging from 16.8 °C to 5.1 °C for their other Great Basin locations. Our mean mid-June to mid-September within rock-matrix temperature of 7.7 °C in the Sierra Nevada was near the low range of Beever et al.'s estimate, likely representing the higher elevation locations of our sensors. Our low mean within rock-matrix temperature (0.9 °C) was colder than Beever et al.'s low value, but our high mean (14.4 °C), was also colder than other estimates. We interpret these findings to suggest that pikas in our region tolerate a wider range of temperatures and precipitation than previously interpreted.

GEOMORPHIC RELATIONSHIPS

Pika sites occurred on a range of rocky landform classes but had clear dominance on certain categories. Whereas pika habitat is classically described as *talus* or *rockslides* (Smith and Weston, 1990), the strong association in our study to RIF till, especially the boulder stream category (Millar and Westfall, 2008), refines preferred pika habitat within broad hillslope categories. We found rockslides and talus cones infrequently associated with pika sites in our region, likely due to the high proportion of fine sediments, inconsistency, and wide range of rock size, lack of open matrices, and frequent absence of adjacent forage opportunities. By corollary, a high proportion of non-detection sites occurred in eroded bedrock talus; these environments also had poorly sorted clasts with abundant fine sediments and shallow inter-rock matrices. Till of rock glacier and boulder stream landforms is generated via glacial and/or periglacial processes, characterized by repeat freeze-thaw and frozen-ground action. These autonomous processes, occurring during historic cold periods and/or persisting at present, create environments with features that appear to be highly favorable to pikas' persistence, at least in the subspecies and lineages of our region. These are elaborated as follows:

Rock and Rock-Matrix Conditions

The unique freeze-thaw action and clast-sorting processes of RIFs contribute to development of expansive areas of rock fields characterized by even-sized and loosely arranged rock clasts within relatively stable rock fields. Given the lithology of Sierra Nevada and Great Basin ranges (granitic, volcanic, and metamorphic, with little sedimentary), clast sizes that occur in these features are routinely in a range preferred by pikas, that is, 0.2–1.0 m diameter (Tyser, 1980). The sorting processes of these landforms remove soil and fine sediments, leading to deep accumulation (often many meters) of rock clasts and open matrices ideal for pikas to move, hide, eat, shelter, and den within, and from which to perch and survey. These landforms afford ample opportunity for pikas to move easily within rock openings in winter under dense snowpacks, a situation that has not been investigated. Climatic conditions of the arid Southwest (SN and GB) during historic cold periods were such as to favor extensive development of RIFs across mountain slope and even low hilly areas (Millar and Westfall, 2008). The result of this is the existence, especially in the Sierra Nevada and less so in the Great Basin ranges, of abundant RIF terrain, capable of supporting one to many pika territories with relatively short distances between RIF environments. Thus, continuity for dispersal is relatively high, kin territories can be supported in single landforms, and mating potentials remain adequate within close distance.

Topographic-Climatic Conditions and Intra-RIF Microclimates

The topographic contexts of rock-glacier and boulder-stream landforms are such that climatic conditions tend to be cooler than means expected for their elevations (Millar and Westfall, 2008). This results not only from northerly aspects of these RIFs but also from local topographic contexts that favor cold micro-sites and foster RIF development. These include steep rocky slopes; narrow and deep canyons; cirque head locations; slopes below cliffs, rock chutes, and avalanche tracks; and contexts where solar insolation is reduced and cold-air drainage, cold-air pooling, and inversions are common (Lundquist and Cayan, 2007; Daly et al., 2007, 2009). These conditions result in cooler summer temperatures favored by pikas and could contribute to local depression of pikas' elevation limit.

Amplifying the climatic effect of cool topographic contexts are the distinctively cold microclimates created by intra-RIF air circulation (Juliussen and Humlum, 2008). These unique processes are of considerable interest in current periglacial research yet remain virtually unknown outside that research community. Because these are not obvious characteristics and because delineating refugial sites for pikas has high conservation

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priority (S. Wolf, Center for Biological Diversity, personal communication), we explain climatic processes here to interpret important habitat features of RIFs for pikas. RIFs generate unique microclimatic conditions within the rock landform in both summer and winter that depart from expected surface air temperatures for their elevation, topographic context, or season. During the warm season, within-rock matrix air temperatures are significantly lower than adjacent bedrock or soil, a condition known as negative thermal anomaly (Juliussen and Humlum, 2008). These anomalies have been recorded as large as 4–7 °C within boulder-stream talus relative to adjacent mineral soil (Harris and Pedersen, 1998) and up to 2 °C colder than adjacent morainal till and bedrock (Juliussen and Humlum, 2008). Cold air is often felt as a persistent breeze as it circulates out the base of RIF landforms (Suwada et al., 2003; Delaloye and Lambiel, 2005). These unique circulation processes are known to create conditions cold and persistent enough to depress local permafrost elevations at temperate latitudes by as much as 1000 m and to occur in locations where the mean annual air temperature is as high as +5 °C (Delaloye and Lambiel, 2005). Several hypotheses have been advanced to explain these intra-talus negative thermal anomalies (Ohata et al., 1994; von Wakonigg, 1996; Harris and Pedersen, 1998; Juliussen and Humlum, 2008). Our temperature datalogger records corroborate this effect, recording warm season temperatures within rock matrices to average 3.8 °C colder than sensors in rock shelters on the RIF surface.

During the cold season, an opposite thermal anomaly can develop within open RIF block fields such that within-rock matrix winter temperatures are warmer than ambient surface air (Keller and Gubler, 1993; Bernhard et al., 1998; Suwada et al., 2003; Delaloye and Lambiel, 2005). This occurs more commonly in the upper elevations within the rocky matrix of the landforms, in that internally heated air is ventilated upslope within the talus and exhaled through snow windows (Delaloye and Lambiel, 2005) or snow funnels (Suwada et al., 2003) created by the warm air. Temperatures of ventilated air have been recorded in the Japan Alps at the top of RIF blocky fields that are as much as 11.7 °C warmer than air near the base of the landform over an elevational difference of only 100 m (Suwada et al., 2003).

This pattern of RIF within-rock matrix environments being cooler than expected for elevation mean summer temperatures, and warmer than expected for winter temperatures creates highly favorable thermal conditions for pikas. This may be a primary reason explaining the importance of RIFs as important habitat. Beever found a similar functional correlation in Great Basin habitat wherein recently extirpated pika sites had both colder minimum winter temperatures and warmer maximum summer temperatures relative to actively occupied sites, implying that extant sites might be less thermally variable (Erik Beever, U.S. Geological Survey, personal communication, 2008). The contrasting pattern of correlations between temperature and elevation in our data might also be a function of the association of pika habitat with RIFs and the unusual climatic conditions these landforms have relative to elevation. Very low correlation of elevation with minimum temperatures could be a result of pika association with RIF environments, which would confound and depress temperatures relative to those expected for the elevation. Hafner (1994) found that temperature limits pika distribution more than elevation, a conclusion that also points to local environments such as RIFs creating appropriate microsite conditions.

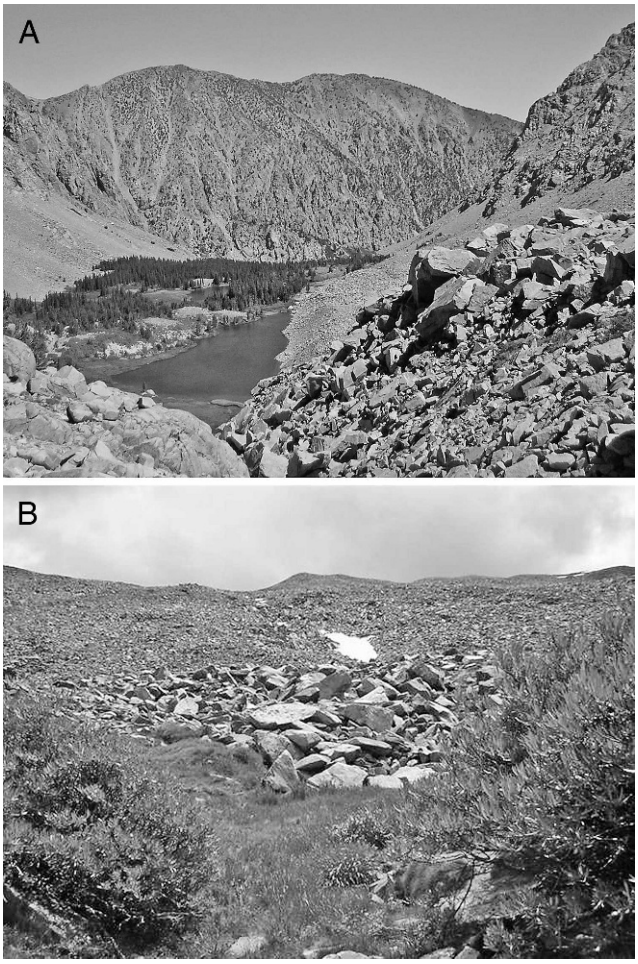


FIGURE 8. Rock glaciers and related rock-ice features in the Sierra Nevada are typically situated in cold locations, including northward-facing cirques and valleys, and in topographic locations that favor cold-air drainage. Embedded ice and high groundwater tables provide sources for persistent water even during the dry season, which support wetlands at their bases. Together the rock features and their adjacent wetland vegetation associations create optimum pika habitat. (A) Wetlands and lake at the base of rock glaciers in Lake Canyon, Mono Basin. (B) Willow-sedge association at the base of boulder streams in the upper Tuolumne River drainage, Yosemite National Park.

Wetland Vegetation Communities

A final component of RIF environments conducive to pika habitat is the occurrence of dense, wetland forb, shrub, and herbaceous vegetation patches directly adjacent to RIF fronts and sides (Fig. 8; Millar and Westfall, 2008). The juxtaposition of active RIFs with wetland vegetation likely develops as a result of cool air exhalation downslope within the rock body and out the base of the RIF during the warm season, combined with persistent seepage of water out the base of the RIF. Our studies reveal that dense wetland vegetation areas occur directly below nearly all active boulder-stream and rock glacier RIFs we have surveyed (Millar and Westfall, 2008), that these wetlands average more than twice the surface area of the RIFs, and that shrub and herbaceous plant species diversity is high relative to adjacent alpine and subalpine habitats in these environments (Millar and Westfall, unpublished surveys, 2006–2008). Such close proximity of diverse and abundant forage seems likely an important co-factor in

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making RIFs favored pika habitat (Huntly et al., 1986; Roach et al., 2001).

RAPID ASSESSMENT METHOD FOR SURVEYING PIKAS

We developed a rapid method to assess pika presence and used this effectively in several portions of the species range (see http://www.fs.fed.us/psw/programs/snrc/staff/millar/ for sample survey form and instructions). We offer this as a method for opportunistic use by minimally trained observers. It can be used during any time of the day, throughout the field season as access and snowcover permit; it requires little time or equipment to undertake; and it applies across the geographic range of the species. This approach complements and should not replace intensive transect- and plot assessments or repeat surveys of historic populations. The latter are essential for basic species understanding but are limited in geographic coverage due to the effort required.

A potential limitation of our rapid method is that age of occupancy is only certain if pikas are actually observed or heard or if cut green vegetation is present (scored as "*current*" in our approach, and used with the same interpretation by Beever et al., 2003). The other signs indicating occupancy (scored as "*modern*") are reliable but as they are indirect, we noted them separately. While some observers have noted that pellets remain intact for several years, our observations do not corroborate this. Even in dry and/or low-elevation environments of the western Great Basin we find that heavy rains or one winter season washes away all pellets except those concentrated in old haypile caches. Similar reliance and interpretation of pellets and other indirect signs in our method underlie the logic of the intensive pika monitoring protocol developed for British Columbia (Ministry of Environment, Lands, and Parks, 1998) and for a related Great Basin lagomorph, pygmy rabbit (Ulmschneider, 2004). Variable decomposition time of pellets is likely in different regions of pikas' range, and assigning actual age estimates to this criterion will depend on local tests for persistence of marked pellets, which we are currently undertaking.

A limitation of any rapid survey is false negative results (type II error), that is, scoring a site non-detection when in fact it is occupied. In that we determined occurrence sites within 5–10 minutes with only one observer, searches at other sites beyond that time and up to one hour yielded no evidence. While these sites could well still have pikas present, detection would depend on repeat visits or intensive assessments. We reconcile this problem by suggesting that in rapid surveys non-detection scores be clearly indicated as pertaining to a specified time interval, 30 minutes in our example. Such sites can thus be highlighted for re-visit with intensive survey methods.

Conclusions

We developed and propose for wide use a simple and rapid survey method to assess pika presence. With it, we located and described 420 American pika site occurrences in the Sierra Nevada, Great Basin, and central Oregon. These represent 11 mountain ranges and extend across a broad range of isolated regions, canyons within regions, and local demes. Our survey vastly increases the geographic extent and number of pika sites previously documented from our region, refines habitat preferences for pikas in the subspecies and lineages of our region, and expands knowledge of the species' climatic envelope in eastern CA and western NV. The pika sites occurred on all slope aspects with minor preference for northeast and eastern orientations, and on a diverse range of representative substrate lithologies including granitic, metamorphic, and volcanic. Considering the SN and southwestern GB sites (396 sites) combined, 98% and 83% of these sites respectively were evaluated as recently occupied, that is, most likely current year. The pattern of increasing *old* sites eastward from the Sierra Nevada was strong, from only 2% in the SN to 50% in the central Great Basin. This finding suggests variability across the species range even within our region, and either lower viability of pikas in the GB or dispersal-limited metapopulation dynamics there. How such variability is influenced by differences in environment and topography, climate, and/or evolutionary relationships within the species is not clear.

Excluding the eight Oregon sites, the elevational range of CA and NV sites was very broad, covering 2060 m elevation, and extending from a low of 1827 m to a high of 3887 m. We did not find an association of elevation with age of sites; old sites occurred at low to high elevations. This number, diversity of sites, occupancy, and elevational range suggest greater distribution in the SN and GB than has been found in other studies in our region. Our large number of sites also yielded a wider climate envelope than has been described for our region, suggesting a wide thermal tolerance for pikas there. Average minimum temperatures for the old sites were not significantly different from the recent sites, whereas average maximum temperatures were significantly higher in old relative to recent sites.

The strong association of pika sites with rock-ice feature (RIF) till, and especially the boulder stream category of RIFs (Millar and Westfall, 2008), refines the preferred pika habitat within various hillslope categories that have been defined previously as pika habitat. We found rockslides and moraines little used by pikas, and ascribed the preference for RIF environments to their conditions of rock-clast and rock-matrix, topographic-climatic (cold-air pooling) and intra-RIF microclimates, and associated wetlands with dense herbaceous vegetation of high pika forage value. With global warming, non-RIF habitats in high likelihood will become warmer and increasingly marginal for pikas, whereas RIF environments are highly likely to remain buffered against temperature change and lag in response to warming due to the insulation of the rocky carapace (Pelto, 2000; Brenning, 2005; Millar and Westfall, 2008). As such, RIF environments are likely to become increasingly important refugial habitat for pikas in the future, and an effort to map and delineate such areas would be a valuable conservation exercise.

In conclusion, our rapid survey results suggest that the pika populations in the Sierra Nevada and southwestern Great Basin are thriving, persist in a wide range of thermal environments, and show little evidence of extirpation or decline. Central Great Basin populations, from our relatively smaller number of sites, appear more subject to the perturbations of metapopulation dynamics. Distribution data such as ours are important as baseline surveys that can be used in future remeasurements and further interpretation of pika ecology and population status. Conclusions from our study should be considered representative of conditions in the southwest portion of the species' range only.

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