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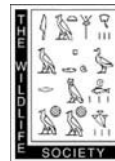
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Original Article

Assessing Persistence of the American Pika at Historic Localities in California's Northern Sierra Nevada

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ABSTRACT The American pika (*Ochotona princeps*) appears to have experienced a substantial upslope range contraction in the Great Basin in response to climate warming. In California, models predict range contraction, but whether the species' lower elevational limit has already shifted remains unclear. We located and determined current occupancy at 19 historic pika localities in the northern Sierra Nevada of California, USA, in 2009–2012. We found that 17 localities were currently occupied by pikas at or near the original record location, while at 2 localities pikas appeared extirpated. No strong climate signal was detected in our data; however, the distribution of historic points does not allow us to rule out upslope range contraction in our region. Talus area was closely correlated with pika persistence, consistent with the application of metapopulation theory to pikas. © 2012 The Wildlife Society.

KEY WORDS climate change, elevation range, extirpation, global warming, metapopulation, montane, *Ochotona princeps*, talus.

The American pika (*Ochotona princeps*) is a small, herbivorous lagomorph that appears to be relatively common at high-elevation talus in the Sierra Nevada of California, USA (Millar and Westfall 2010; J. Stewart, D. Wright, personal observation). The species has been proposed for federal and California state endangered species listing primarily because of its projected vulnerability to climate warming (Wolf et al. 2007). Correlative climate envelope models project that under future climate scenarios the species' range will contract upslope considerably, with the potential for extirpation especially strong in northern California (Galbreath et al. 2009, Calkins et al. 2012). Pika response to climate effects has been reported in the Great Basin of the United States, as measured by extirpations at warmer and lower elevation historic localities and upslope retreat of some surviving populations (Hafner 1993; Beever et al. 2003, 2010, 2011; Grayson 2005; Wilkening et al. 2011).

In California, the literature published to date is not conclusive on whether pikas have retreated from low-elevation habitat during the past century. Longitudinal data on pika persistence in California are sparse, but the few documented extirpations at historic locations have occurred in relatively low-elevation habitat. In Yosemite National Park, pikas appeared extirpated from two aggregated historic locations

in the vicinity of Glen Aulin and McGee Lake at approximately 2,400 m during surveys conducted in 2003, 2006, and 2008 (Moritz 2007, Moritz et al. 2008). These two areas were the lowest elevation of nine pika re-survey localities in the study, and pikas were detected at all other localities. Extirpation of historic record locations has also been documented in and around Bodie State Historic Park at approximately 2,600 m (Moilanen et al. 1998).

In the Sierra Nevada, average annual temperature has increased by $0.73 \pm 0.28^\circ \text{C}/100$ year since the instrumental temperature record began in 1895 (CCT 1895–2010; Abatzoglou et al. 2009). This level of warming corresponds with approximately 120 m of upslope climate-envelope shift over the past century, at the standard adiabatic lapse rate (ISO International Standard 2533–1975). However, lapse rates vary (Minder et al. 2010) and rugged topography, cold air drainages, latitudinal gradients, and geologic features lead to a complex relationship between climate and elevation (Dobrowski et al. 2009). Further, average annual temperature may not be the proximal or strongest climate variable to which pikas respond (Beever et al. 2010, Wilkening et al. 2011).

A mechanistic biological hypothesis consistent with some empirical findings is that chronic high summer temperatures cause a decline in foraging time during the growing season and a reduction in available nutrition during harsh winters when pikas depend on vegetation cached during summer months (Millar and Zwickel 1972, Smith and Weston 1990, Beever et al. 2011). Pikas are known to thermoregulate behaviorally during high summer temperatures by reducing

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the frequency and duration of foraging trips and thus spending more time in cool talus interstices (MacArthur and Wang 1973, Smith 1974). Variables determined to correlate with pika persistence at historic sites include August maximum temperature, grazing intensity, talus area, latitude-adjusted maximum elevation within 3 km, number of days below -10° C, mean annual precipitation, presence of water under the talus, and distance from roads (Beever et al. 2003, 2011; Erb et al. 2011; Wilkening et al. 2011).

The goal of our study was to increase the sample size of historic site re-surveys in California, focusing first on our local, less studied area, so that we may better determine whether the species' response to warming in the state is similar or in contrast to upslope retreat in the Great Basin. In keeping with previously published research we also sought to examine multiple competing hypotheses to explain extirpation patterns, such as 1) localities at lower elevations or with warmer temperatures are more likely to be extirpated; 2) localities with lower annual precipitation are more likely to be extirpated; 3) localities with less available talus are more likely to be extirpated; and 4) localities closer to roads are more likely to be extirpated.

STUDY AREA

Our study region, the northern Sierra Nevada, extended from Alpine County to Plumas County, California, USA (Fig. 1). We obtained historic American pika records

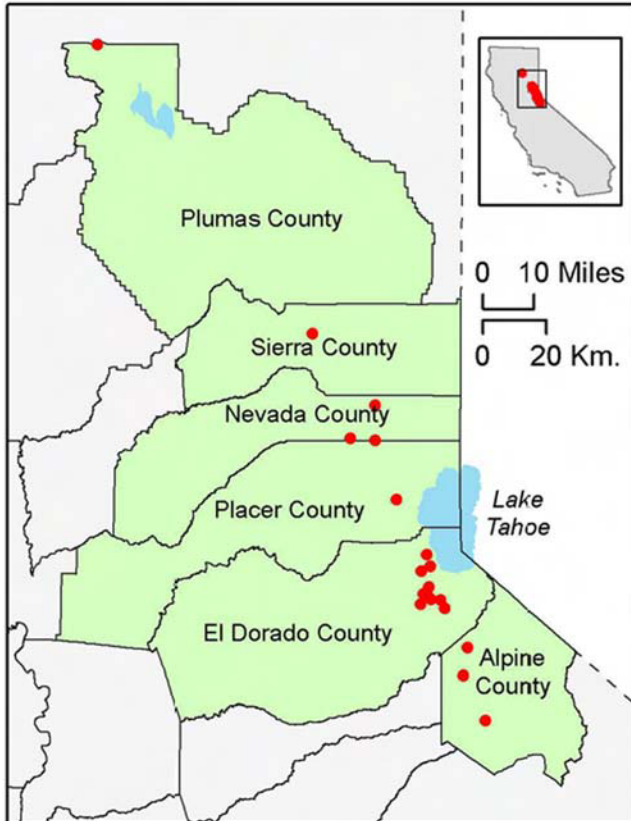


Figure 1. Location of 19 historic pika (*Ochotona princeps*) records and extent of our study region in the northern Sierra Nevada, California, USA, during 2009–2012. Ten records are clustered in the southwest Tahoe Basin.

primarily through online database searches (California Natural Diversity Database: <http://www.dfg.ca.gov/biogeodata/cnddb/>, Arctos: <http://arctos.database.museum/home.cfm>, Mammal Networked Information System: <http://manisnet.org/>, and Global Biodiversity Information Facility: <http://www.gbif.org/>). Additional historic records were found by review of historic field notes (e.g., www.mvz.berkeley.edu), and visits to natural history museums with offline pika records (University of California, Davis).

METHODS

We selected records for inclusion in this study based on reliability, age, and spatial precision. Skins or field notes prepared by an experienced observer (e.g., Joseph Grinnell, Annie Alexander) constituted reliable records. We considered pika records after 1983 as possibly too recent and did not include them in this study. We aggregated records occurring within 1 km of each other into a single historic locality and excluded records with information too vague to locate them within a 1-km radius (e.g., one historic record specified only “Mount Tallac”).

We sought to identify the exact talus where the record originated using all available information, including archival field notes, specimen tags, aerial imagery, historic and modern topographic maps, and on-the-ground interpretation. To account for variable spatial precision of historic records (e.g., detailed field notes vs. “east side Pyramid Peak”), we established a 1-km search radius around our centroid of each historic locality. We set the centroid as the center of the minimum encompassing circle for all talus patches plausibly fitting the historic description. We used National Agricultural Imagery Program (NAIP) 2009 aerial imagery, Google Earth (Google, Inc., Mountain View, CA), and other available snow-free imagery to visually identify talus within this search radius prior to fieldwork.

We visited and surveyed the resulting historic record localities for pikas, using a protocol modified from Beever et al. (2003). Working outward from the center, we surveyed talus patches successively until we determined that the historic locality was currently occupied. For apparently extirpated localities we searched every talus patch within the 1-km search radius. After arriving at a talus patch, we listened silently for pika vocalizations for 5 minutes, we then began actively searching for ≥ 30 person-minutes or until the entire patch was searched. We walked transects across the talus looking for current pika sign. We used hand mirrors and flashlights to search talus cavities for pika sign. Previous studies suggest that 30 person-minutes of search effort are sufficient to determine pika occupancy with approximately 90% detection probability (Beever et al. 2010, Rodhouse et al. 2010). At this rate, if a series of occupied talus patches within a locality is each searched for 30 person-minutes, then in theory, a 99% chance of detection is reached after 2 patches, and a 99.9% chance is reached after 3 patches, though in practice all patches may not be occupied.

We considered seeing or hearing a pika or observing current pika sign to be confirmation of current occupancy, and recorded time to our first detection of occupancy. Pika sign

was distinctive, not readily confused with sign from other animals (Elbroch 2003). Haypiles were considered current when they contained fresh or dried green vegetation. Unlike Beever et al. (2003), we accepted fresh-appearing pika fecal pellets as current sign when they were perched: adherent or stacked above the angle of repose. Fresh pika pellets tend to have a greenish-gold hue, especially inside the pellet when crushed, and often adhere to other pellets or to the sides of rocks. Fecal pellets remain detectable when calls and sightings are less frequent (e.g., during midday or warm conditions), so although we recorded time of survey, we did not constrain survey hours or temperature.

We observed and collected older, “relict,” fecal pellets to document past occupancy. Pika fecal pellets do not decompose readily and can remain observable in the field for many years, with changes in color, size, and texture (Nichols 2011; though presumably pellets in our less-arid study area may degrade more rapidly than those Nichols studied at Bodie, CA). Pika observations were geo-referenced using a handheld Global Positioning System unit. These locations will be archived in the California Department of Fish and Game, California Natural Diversity Database (<http://www.dfg.ca.gov/biogeodata/>).

We tested 13 variables for correlation with pika persistence using univariate logistic regressions. We calculated both binomial and multinomial logistic regressions—binomial using occupied/apparently extirpated status ($n = 17$ occupied, 2 apparently not), and multinomial using three ease-of-detection categories: easy (≤ 30 person-min), difficult (30–582 person-min), and no detection (> 500 person-min, all talus visited; $n = 13$ easy, 4 difficult, 2 no detection). To correct our experiment-wise significance level to account for 13 variables tested, we used a Dunn–Bonferroni-corrected critical $\alpha = 0.05/13$, or 0.00385 (Dunn 1961). Climate values for

the years 1984–2009 were extracted from 4-km PRISM (Parameter-elevation Regressions on Independent Slopes Model) grid cells encompassing our locality centroids (Daly et al. 1994), and we included 7 climate variables among the 13 tested: annual maximum temperature, annual precipitation, summer maximum temperature (Jun, Jul, Aug), winter minimum temperature (Dec, Jan, Feb), recent annual precipitation (2007–2009), recent summer maximum temperature (2007–2009), and recent winter minimum temperature (Dec 2006–Feb 2009). Talus area within the 1-km search radius was delineated using aerial imagery as described above. Road distance was calculated from centroids to the nearest road (U.S. Department of Transportation, 2002 Bureau of Transportation Statistics: includes primarily paved roads and some unpaved major roads; does not include most National Forest unpaved roads). Mid-range elevation for a site was calculated from all current pika observation points within our search radius. For apparently extirpated localities the mid-range of all survey points was used. We defined Hafner-equivalent elevation as the difference between the mid-range elevation and the predicted lower elevation limit of pikas across western North America as derived from Hafner’s (1993) equation: elevation (m) = 14,087 – 56.6N – 82.9W, where N is latitude and W is west longitude.

RESULTS

We located 19 geographically distinct and precise historic pika records within our study area (Fig. 1). The records dated from 1892 to 1982. One of these localities was about to be re-surveyed by other researchers prior to our fieldwork. We surveyed the remaining 18 localities (63 distinct talus patches) during the summers of 2009–2011 with some follow-up in 2012.

Table 1. Historic pika (*Ochotona princeps*) localities and re-survey results in the northern Sierra Nevada, California, USA, from 2009 to 2012. Status: 1 = extant; 0 = apparently extirpated. Elevation (Elev.), in meters, is the mid-range of current pika observations for extant localities or of all survey locations for extirpated localities. Effort to first detection is given in person-minutes. Detection types are abbreviated V: visual, A: auditory, GH: green haypile, or PP: fresh perched pellets. Coordinates of site centroids given in NAD83.

Historic locality	Status	Elev.	Effort	Detection	Latitude	Longitude
Flatiron Ridge ^a	1	1,678	15	A, GH, PP ^b	40.4437	–121.365
Deadman Lake	1	1,866	14	V, A, PP ^b	39.6210	–120.552
Donner Pass W	0	2,004	See text	None	39.3219	–120.410
Donner Pass E	1	2,053	65	V, A, PP ^b	39.3168	–120.318
Eagle Falls	1	2,128	582	V, A, PP ^b	38.9543	–120.114
Echo Lake	1	2,327	8	V, A, PP ^b	38.835	–120.060
Below Heather Lk	1	2,342	1	V, A, ^b PP	38.8687	–120.121
Round Top	1	2,349	3	V, ^b A, ^b GH, PP	38.6429	–119.993
Ward Peak E	1	2,439	34	GH, PP ^b	39.147	–120.239
Lower Velma Lk	1	2,419	45	A, PP ^b	38.9406	–120.146
Heather Lake	1	2,460	10	V, ^b A, ^b PP	38.8766	–120.138
Pacific Grade Summit	0	2,477	See text	None	38.5159	–119.912
Rubicon Peak E	1	2,496	20	A ^b	38.9887	–120.127
Lucille Lake	1	2,508	6	A ^b	38.8607	–120.112
Gilmore Lake	1	2,578	2	V, A, PP ^b	38.8969	–120.118
Carpenter Ridge	1	2,601	5	A, GH, PP ^b	39.417	–120.318
Angora Saddle	1	2,654	19	A, ^b PP	38.858	–120.075
Crater Lake	1	2,664	21	V, A, GH, PP ^b	38.7229	–119.976
Pyramid Peak E	1	2,705	1	V, A, ^b PP	38.8462	–120.150

^a Flatiron Ridge re-survey data courtesy J. Perrine and C. Massing, California Polytechnic State University, San Luis Obispo and Grinnell Resurvey Project.

^b First detection.

We determined 17 of 19 historic localities in our region to be currently occupied, while two localities appeared extirpated (Table 1). Pikas were seen or heard at 16 localities; one locality was determined to be occupied via sign only (green haypile and perched pellets). Haypiles were observed at 7 localities, of which 5 localities had haypiles with green vegetation.

Fresh perched pellets were observed at 15 of 17 occupied localities visited; and all localities (1 km radius) with such pellet detection were accompanied by additional evidence of current pika occupancy. Within specific talus patches, however, on 2 occasions we found fresh perched pellets without additional evidence of current occupancy.

For most occupied localities ($n = 13$), detection was easy—pikas or current pika sign were observed in the first talus patch surveyed and effort to first detection was low (median = 8 person-min, range = 1–21). Detection was difficult at four localities—we found evidence of current pika occupancy only after more than one talus patch was surveyed and with greater effort to first detection (median = 55 person-min, range = 34–582).

Apparent extirpations occurred at Pacific Grade Summit and Donner Pass West localities. In order to survey both sites exhaustively, including every talus in the search radius, we visited both extirpated localities for extended periods and during field seasons of 2 years. At Pacific Grade Summit, survey effort was about 9 person-hours within talus or 28 person-hours when time spent navigating between talus patches was included. Pika calls can be heard at a distance; therefore, time on the ground in the vicinity of suitable habitat is relevant even if it was not dedicated visual search time. West of Donner Pass, survey effort was about 9 person-hours within talus, or 26 person-hours total.

Detailed field notes that allowed us to determine the historic location with relative precision accompanied both apparently extirpated historic records. At Pacific Grade Summit in 1943, A. H. Miller heard and saw pikas in a small talus “within a few hundred yards” of Mosquito Lakes. His notes reference a small talus “no more than 50 ft across and no more than 20 ft up and down.” All talus patches in our search radius were similarly small, with the largest talus approximately 20 m × 20 m. We searched 8 distinct talus and granite outcrops at this site and found relict pika pellets at 6 distinct locations, including 1 anthropogenic talus below an old road grade. At the second apparently extirpated site, in 1934, W. B. Davis collected pikas in anthropogenic habitat, “four miles west of Donner Summit on the talus of the railroad tracks.” In order to buffer for possible distance mis-estimation in the historic field notes, we modified our search boundary to between 3.2 km (2 mi) and 9.7 km (6 mi) west of Donner Summit and within 244 m of the railroad. This search boundary is equivalent in area to a 1-km-radius circle and does not exclude any talus that would have otherwise been included. We searched 14 distinct talus patches, all consisting of railroad riprap, and found relict pika pellets 6.4 km (4.0 mi) west of Donner Summit.

Given our small sample size of 19 historic sites, 2 apparent extirpations, and 4 seemingly marginal sites (difficult to detect pikas) from which to identify an environmental signal,

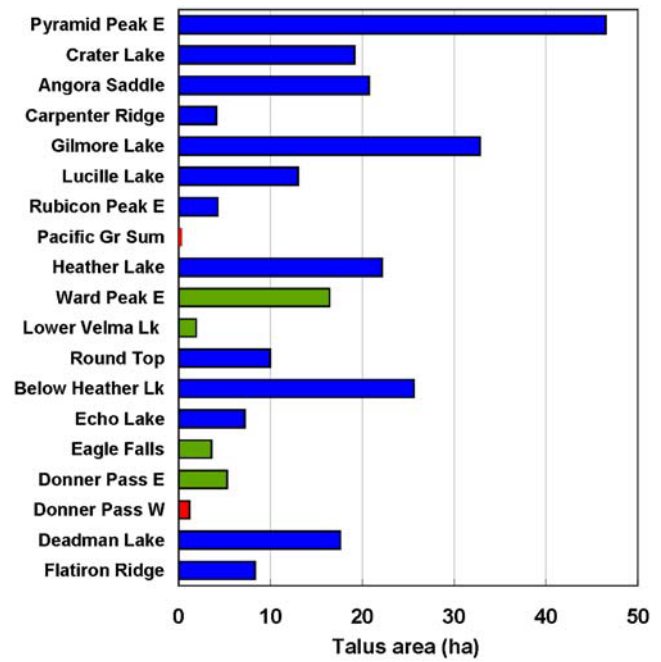


Figure 2. Amount of talus delineated within 1 km of historic pika (*Ochotona princeps*) record centroid in the northern Sierra Nevada, California, USA. Sites are ordered by elevation (see Table 1). The two extirpated localities, shown with red bars, rank lowest in amount of talus. Sites where pika were found but were difficult to detect (>30 person-min) are shown in green.

and a large number of candidate variables, we offer our statistical analyses with caution. Of the 13 variables we analyzed, talus area was the strongest correlate of pika persistence, with the two apparently extirpated localities ranking lowest in talus area and difficult-to-detect sites averaging intermediate (Fig. 2). Both the binomial logistic regression and multinomial logistic regression of 3 ease-of-detection categories versus talus area met our Dunn–Bonferroni-corrected test of significance ($P < 0.00385$, $R^2 = 1.00$ and 0.53, respectively).

No other variables in logistic regression achieved Dunn–Bonferroni-corrected significance or appeared informative. Distance to road showed a positive correlation with occupancy (i.e., sites farther from roads more likely occupied, $P < 0.05$), but this was confounded by a positive correlation between distance-to-road and talus area (Spearman rank correlation = 0.59, $P < 0.01$).

DISCUSSION

Our results suggest that, within their core elevation range in the northern Sierra Nevada, pika populations largely have persisted over the past century. High occupancy of talus was suggested by our quick detections of pika in the first talus searched at 76% of occupied localities. Persistence at historic localities in our study was demonstrated by 89% present occupancy at or near the historic site. This high rate of historic site occupancy, with only two extirpations, also resulted in low power to detect potential causes of extirpation.

Within our circumscribed data set, talus area was perfectly correlated with persistence (Fig. 2). This result is consistent with the application of metapopulation theory to pikas: small, isolated patches of habitat appeared most likely to become locally extinct. An effect of talus area also has been reported from the Great Basin by Beever et al. (2011). We expect occupancy to be especially sensitive to patch size where conditions are already marginal for the species, such as close to the lower elevation limit of the pika—whatever the cause(s) of that limit.

We did not detect a strong thermal or elevation signal in our data; however, we had limited power to reject the null hypothesis of no climate effect. Millar and Westfall (2010) showed that historic sampling in the southern Sierra Nevada was not sufficient to reveal the pika's lower elevation distributional limit for those latitudes. The same is likely true in our region, where historic samples were fewer and most records were from elevations above 2,200 m. Because the historic record in our region may not adequately capture the pika's hypothesized "hot-zone" (i.e., dynamic locations with local populations prone to extirpation, and perhaps re-colonization, near the lower elevational limit, not necessarily due to thermal effects) with these data, we cannot yet say with confidence whether pikas have undergone an upslope range contraction in the northern Sierra Nevada. Based on our study, we speculate that the pika's hot-zone in our study area is primarily below 2,200 m elevation. Note, however, that topography and air flow strongly influence microclimate in rugged areas, so that "out of zone" pikas may readily occur on cool slopes, in precipitation pockets or cold air drainages. This latter observation seems to imply that the pika's lower limit is due to adverse physio-ecological responses to warm temperatures, but another hypothesis is that suitable talus habitat is generated and maintained by freeze-thaw conditions, and thus is sparse at low elevations (Hafner 1994).

Because we used a spatially extensive re-survey method, we may have classified some localities as occupied even if the precise original record location no longer supports pikas. This could obscure extirpations occurring in microclimates and at a scale smaller than our 1-km search radius. Some of our search areas encompassed talus of variable aspects and ranging over hundreds of meters of elevation. We chose a 1-km search radius to accommodate inclusion of historic records that could not be precisely tied to a specific talus patch, and to detect substantial distribution shifts as opposed to metapopulation fluctuations. However, the fact that most re-surveys found extant pika at the first talus patch searched (13 of 19 localities) suggests that extirpations within core pika areas were relatively rare, short-lived, or occurred on a small spatial scale.

Millar and Westfall (2010) provided some evidence that pikas in the Sierra Nevada may have experienced upslope range retraction as a result of warming temperatures. Among 396 pika surveys (329 Sierra, 67 southwest Great Basin), "old," apparently extirpated sites exhibited significantly higher maximum temperature than did "current" pika-occupied sites (annual, Jan, and Jul mean temperatures). However, inclusion of southwestern Great Basin sites in

the analysis inhibits conclusions specific to California or the Sierra Nevada. Further, differential use of direct and indirect detection methods in identifying current versus old sites adds a complicating factor in the apparent upslope retreat detected in their data. Millar and Westfall's (2010) "current" detection category included visual, aural, and green haypile detection only. In contrast, their "old" detection category consisted only of relict fecal pellet detection. Because pikas are less likely to be detected by sight or sound when temperatures are warmer (Smith 1974, Hersey et al., 2009), and we have found that green haypiles are often absent from the surface of occupied talus in the northern Sierra Nevada, the statistical relationship between temperature and "old" or "current" sites could be skewed by reduced aural and visual detection at warmer sites (i.e., false absences). As in our study, the data are consistent with either upslope range-shift or with greater metapopulation turnover at lower elevations, but more data are needed to draw strong conclusions.

If pika range has not contracted upslope in the northern Sierra Nevada or has contracted less than in the Great Basin, there are several plausible explanatory hypotheses. First, temperature increase in the Sierra Nevada has been relatively slight in comparison with the wider regional trend (Cordero et al. 2011). This fact would suggest a lower magnitude range contraction in our study area. Second, the Sierra Nevada generally experiences higher precipitation than the Great Basin (Leung et al. 2003), especially west of the crest. Differing precipitation patterns may moderate pikas' ecological responses to temperature. In particular, insulating snow cover in winter, vegetative productivity, and vegetation water content (Beever et al. 2010, Erb et al. 2011) have been suggested as important factors for persistence of pikas. Third, Millar and Westfall (2010) suggested that rock-ice features in the Sierra Nevada buffer talus from warming ambient air temperatures. Rock-ice features are known in the high, southern Sierra Nevada but are less well-documented in the hydrographic Great Basin or within our study area north of Alpine County, California (Péwé 1983). This is a topic greatly in need of expert investigation. Finally, initial observations suggest that suitable talus is less abundant at lower than at higher elevations in the northern Sierra Nevada. Low talus availability and habitat isolation may affect the lower elevation limit of pikas in our region.

MANAGEMENT IMPLICATIONS

With most pika habitat in the northern Sierra Nevada within public ownership, and a lack of statistical evidence of impacts to pikas or their habitat from human activities there (such as road building or timber harvest), finding management options for pika populations may require novel approaches. From our general observations of pika habitats in the northern Sierra Nevada, it is not obvious to us whether grazing and human recreational use affect pikas there; these uses may need dedicated study. To determine the effects of climate change on pikas in California, monitoring for biogeographic trends and studies that demonstrate mechanisms of extirpation will be necessary. In addition to the historic record,

we believe future work should examine relict pika pellets to assess past occupancy (Nichols 2011). Finally, future research or monitoring should stratify pika surveys across talus-abundance and climate gradients so that potential climate effects can be teased apart from talus-area effects.

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