

University of Nevada, Reno

**Resurvey of Historical Pika Records in California**

A thesis submitted in partial fulfillment of the  
requirements for the degree of Master of Science in  
Biology

By

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## ABSTRACT

Anthropogenic climate change is emerging as a growing threat to biodiversity conservation, but the degree to which species have been, and will be, affected remains an open question. The American pika has become a model organism for examining the effects of anthropogenic climate change on montane species conservation and has been evaluated for protection under the United States and California Endangered Species Acts. Climate envelope models predict that pikas will be forced to higher elevations by climate change, eventually being “pushed off” the tops of mountains by high temperatures. Chapter one examines current occupancy patterns at 19 historically occupied sites in the Northern Sierra Nevada. Chapter two examines current occupancy patterns at 67 precise historical pika record locations across California. Using logistic regression and an information theoretic approach, I modeled current pika occupancy as a function of environmental variables (habitat, climate, etc.). Chapter one, with its small sample size, did not find a significant climate or elevation effect. Chapter two found that pikas are especially sensitive to summer temperature and talus habitat abundance. Forecasting this relationship to the future the best-performing model predicts progressive site extirpations as summer temperatures continue to warm. Depending on the amount of climate change, the model predicts that by 2070, pikas will be extirpated from 63% to 94% of historical sites in California.

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## INTRODUCTION

In 2011 the American pika (*Ochotona princeps*) was advanced to candidacy for protection under California Endangered Species Act (CESA), making it the first species to be considered for CESA protection primarily due to threats from anthropogenic climate change. At that time, relatively little was known about the biogeographic trend of pika populations in California. The petition to list cited the Grinnell Yosemite Resurvey Project—which identified a single low elevation historical pika site as extirpated—as the primary evidence for upslope range contraction in California (Moritz et al., 2008). Outside of Yosemite National Park, multiple pika resurvey efforts had been initiated across California, but datasets remained segmented and largely unanalyzed. There was a clear need to synthesize these disparate resurvey efforts into one coherent analysis. Chapter one of this thesis, published in the *Wildlife Society Bulletin* (Stewart & Wright, 2012), represents an analysis of a regional subset of historical resurveys in California, while chapter two presents a synthesis of California-wide historical resurvey data.

Apart from longitudinal resurvey data in California, other lines of scientific evidence point to climate warming as a threat to pika persistence. Because the lower elevational limit for the pika is already relatively high with respect to other species, they may be especially vulnerable to local and regional extirpation (McDonald & Brown, 1992; Moritz et al., 2008). Physiological studies highlight the pika's sensitivity to hyperthermia and relatively low upper lethal temperature limit (MacArthur & Wang, 1973; Smith, 1974). Behavioral studies indicate strong limitations on pikas hours of foraging activity at low elevation sites (Hall, 1946; Severaid, 1955; Smith, 1974). On a



geological time scale, the paleontological record shows upslope range contraction in concert with climate warming since the last glacial maximum (Grayson, 2005). Perhaps most alarming, repeated resurveys in the Great Basin indicate accelerating upslope range retreat in tandem with accelerated climate warming during the first decade of the 21<sup>st</sup> century (Beever et al., 2011).

Chapter one (Stewart & Wright, 2012) presents results from resurvey of 19 historical pika locations in the northern Sierra Nevada Mountains of California. Using a standard one km radius site definition to score sites as occupied or extirpated we scored sites as occupied or extirpated. If pikas were not detected initially we searched all habitat within the search radius until either pikas were detected or we had completed an exhaustive search. We evaluated the predictive power of 13 environmental variables, derived via geographic information systems, in predicting the location of extirpation events.

Building on chapter one, chapter two presents results from resurvey of 67 historical pika sites across California. In this work, I aggregated data from six original resurvey teams, identified additional historical sites, coordinated resurveys, and paired historical records with incidental resurvey data. Again, I standardized the site definition as a one km search radius and scored sites as extirpated only if all habitat within that boundary was absent of pikas or current pika sign. To confirm apparent extirpations observed by the original resurvey team, I conducted exhaustive resurveys of all habitat within a one km radius site boundary. I evaluated the predictive power of 16 environmental variables in predicting the location of extirpation events in an information theoretic framework (Burnham & Anderson, 2002).

## CHAPTER 1

### 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.

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

## INTRODUCTION

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 & 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., 2007a, 2007b). 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).

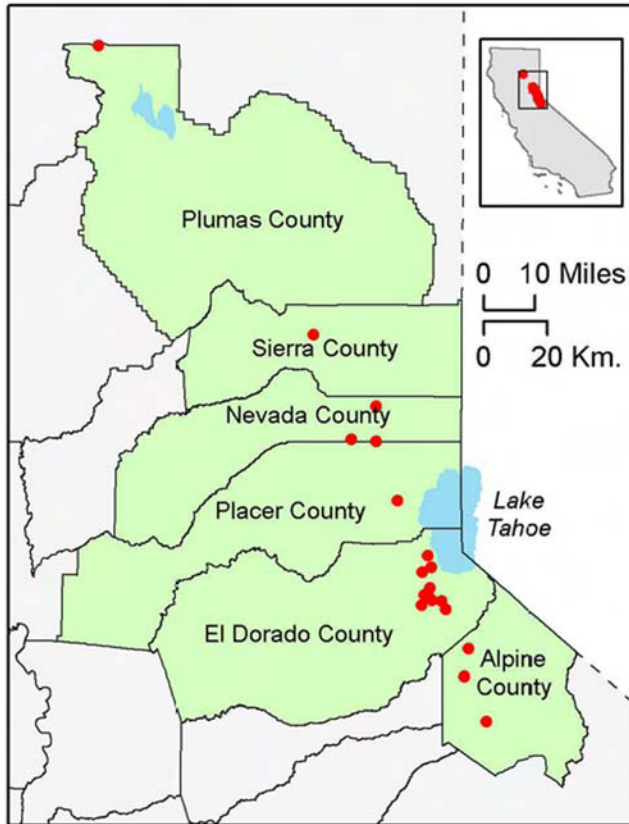
In the Sierra Nevada, average annual temperature has increased by 0.73 °C/100 year since the instrumental temperature record began in 1895 (CCT 1895–2010; Abatzoglou et al., 2009). This level of warming corresponds with approximately 120 m of upslope climate-envelope shift over the past century, at the 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 & Zwickel, 1972; Smith & Weston, 1990; Beever et al., 2011). Pikas are known to thermoregulate behaviorally during high summer temperatures by reducing the frequency and duration of foraging trips and thus spending more time in cool talus interstices (MacArthur & 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, 2010, 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 (Figure 1). We obtained historic American pika records 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](http://www.mvz.berkeley.edu)), and visits to natural history museums with offline pika records (University of California, Davis).



**Figure1.** 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.

## 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, 2010; 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 hand-held 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:  $\text{elevation (m)} = 14,087 - 56.6N - 82.9W$ , where  $N$  is latitude and  $W$  is west longitude.

## RESULTS

We located 19 geographically distinct and precise historic pika records within our study area (Figure 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.

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 misestimation 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.

**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.

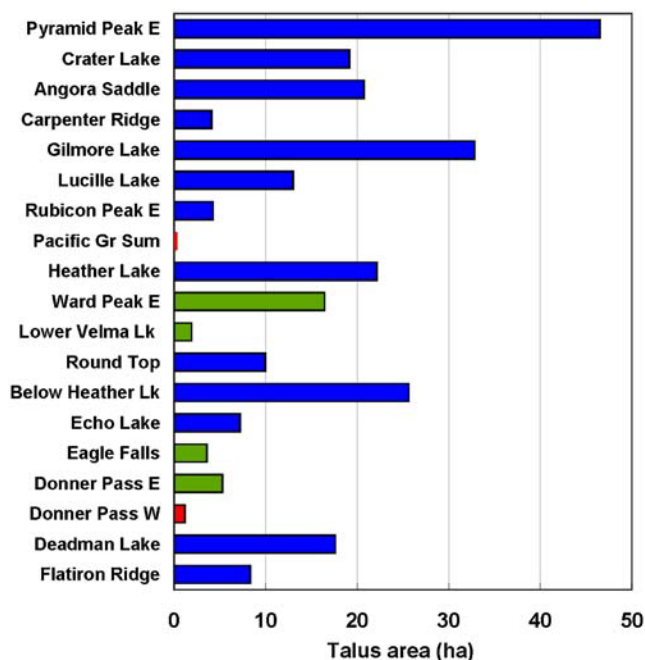
Historic Locality	Status	Elev	Effort	Detection	Lat	Long
Flatiron Ridge <sup>a</sup>	1	1678	15	A, GH, <b>PP</b>	40.4437	-121.365
Deadman Lake	1	1866	14	V, A, <b>PP</b>	39.6210	-120.552
Donner Pass W	0	2004	see text	None	39.3219	-120.410
Donner Pass E	1	2053	65	V, A, <b>PP</b>	39.3168	-120.318
Eagle Falls	1	2128	582	V, A	38.9543	-120.114
Echo Lake	1	2327	8	V, A, <b>PP</b>	38.835	-120.060
Below Heather Lk	1	2342	1	V, A, PP	38.8687	-120.121
Round Top	1	2349	3	V, A, GH, PP	38.6429	-119.993
Ward Peak E	1	2439	34	GH, <b>PP</b>	39.147	-120.239
Lower Velma Lk.	1	2419	45	A, <b>PP</b>	38.9406	-120.146
Heather Lake	1	2460	10	V, A, PP	38.8766	-120.138
Pacific Gr Sum	0	2477	see text	None	38.5159	-119.912
Rubicon Peak E	1	2496	20	A	38.9887	-120.127
Lucille Lake	1	2508	6	A	38.8607	-120.112
Gilmore Lake	1	2578	2	V, A, <b>PP</b>	38.8969	-120.118
Carpenter Ridge	1	2601	5	A, GH, <b>PP</b>	39.417	-120.318
Angora Saddle	1	2654	19	A, PP	38.858	-120.075
Crater Lake	1	2664	21	V, A, GH, <b>PP</b>	38.7229	-119.976
Pyramid Peak E	1	2705	1	V, A, PP	38.8462	-120.150

<sup>a</sup> Flatiron Ridge resurvey data courtesy J. Perrine and C. Massing, California Polytechnic State University, San Luis Obispo and Grinnell Resurvey Project

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, 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 =  $0.59$ ,  $P < 0.01$ ).



**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.

## 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 (Figure 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., 2008), 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, 2010). Finally, future research or monitoring should stratify pika surveys across talus-area and climate gradients so that potential climate effects can be teased apart from talus-area effects.

#### ACKNOWLEDGMENTS

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## CHAPTER 2

### Revisiting the past to foretell the future: summer temperature and habitat area predict pika extirpations in California

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#### ABSTRACT

**Aim** The American pika (*Ochotona princeps*) appears to have experienced climate-mediated up-slope range contraction in the Great Basin, but this result has not been previously generalized to another portion of the pika's range. Our goal was to determine the environmental constraints that most influence pika distribution within California, infer if these constraints imply that range contraction has also occurred in a California, and to advance methods for determining the degree to which pikas are threatened by climate change.

**Location** Historical pika record locations in California, USA, spanning four degrees of latitude and longitude, from Mount Shasta to the southern Sierra Nevada.

**Method** We identified 67 precise historical pika record locations and surveyed them

exhaustively, over multiple years, to determine whether pikas persist at those sites. We used an information theoretic approach to model current pika occupancy as a function of 16 environmental variables, tested our best-performing model as a predictor of historical occupancy, and used our model to predict future pika occupancy.

**Results** Pikas are currently extirpated from 10 of 67 (15%) historical sites in California. The best predictors of occupancy were average summer temperature and talus habitat area within a 1-km radius. A logistic model fit to this relationship correctly predicted current occupancy at 97% of sites and correctly hindcast past occupancy at 93% of sites. Depending on the future climate scenario, our model projects that by 2070, pikas will be extirpated from 63% to 94% of historical sites in California.

**Main conclusions** Our simple species distribution model for pikas performs remarkably well for both historical and current periods. Pika distribution appears to be governed primarily by behavioral restrictions mediated by summer temperature and by the configuration of talus habitat. Because summer temperature is projected to rise by more than annual temperature, pikas and other montane species may be subject to increased seasonal exposure to climate change.

**Keywords:** *Ochotona princeps*, climate change, extirpation, range shift, metapopulation, historical, pika, global warming.

## INTRODUCTION

Rapid anthropogenic climate change is projected to emerge as a leading threat to global biodiversity conservation in the 21<sup>st</sup> century (Thomas et al., 2004; Loarie et al.,

2008). The fingerprint of climate change is already apparent in natural communities in the form of range shifts, advanced phenology, and genetic changes (Parmesan, 2006). But predicting the fate of particular species in the face of climate change is complex, because species distributions are controlled by many biotic and abiotic factors. To make robust predictions about the fate of species in a warming world it is imperative that we identify the precise mechanisms that control distribution and abundance.

Mountain systems have inherent physical properties that both increase and decrease vulnerability of species to climate change. On one hand, because climate gradients are relatively steep in complex topographic environments, montane species may be able to track their climate envelope by dispersing relatively short distances upslope (Loarie et al., 2009), or by exploiting topographic heterogeneity such as by shifting slope aspects. On the other hand, geographic isolation and unique environmental adaptations may make montane species especially vulnerable to warming (La Sorte & Jetz, 2010). As climate change forces range contractions, species may effectively be “pushed off” the tops of mountains by warming climate (Thuiller et al., 2005). In Yosemite, resurveys of 28 small mammal species indicate that half of the species showed upslope range shifts (Moritz et al. 2008).

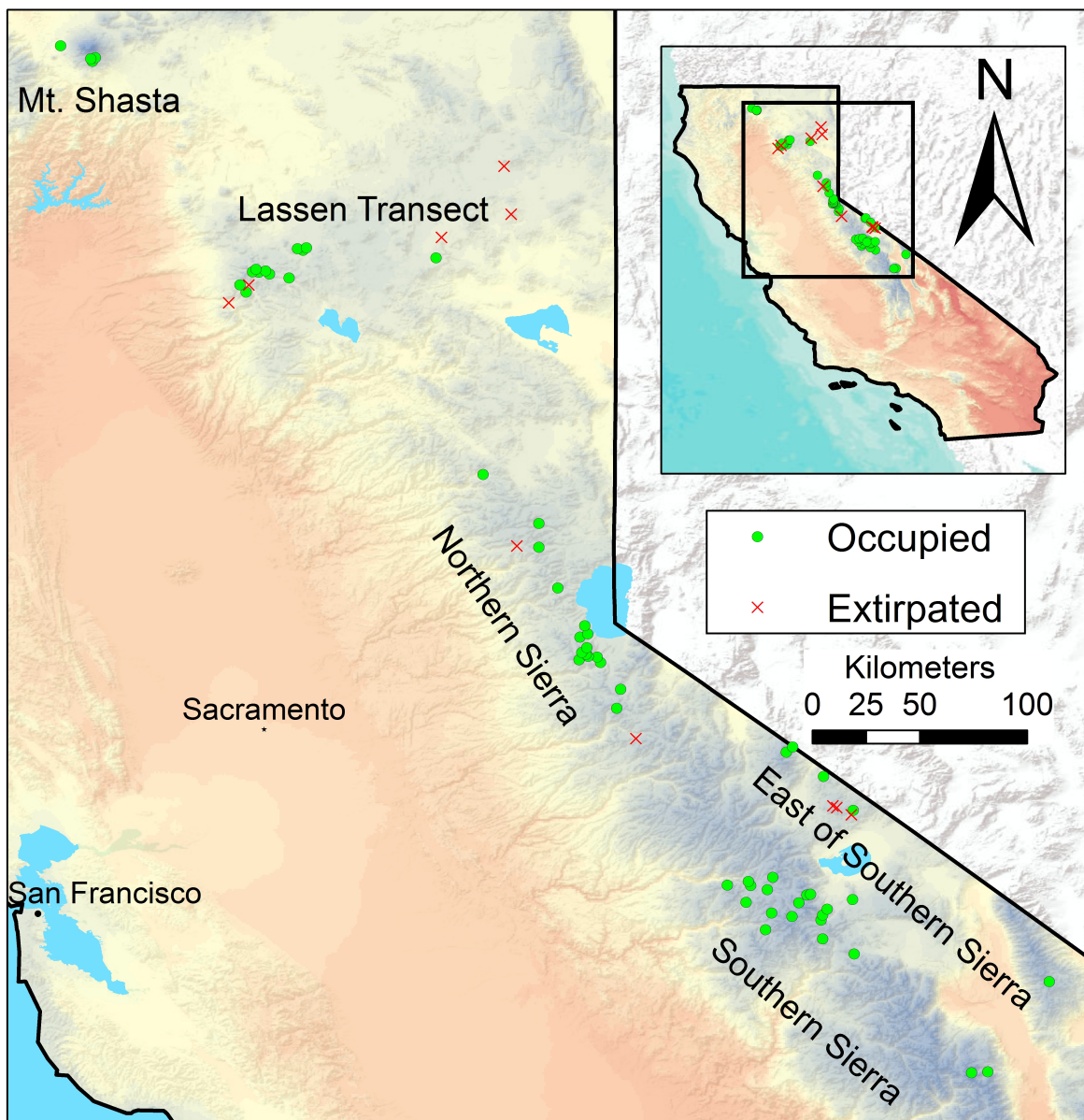
The American pika (*Ochotona princeps*) has emerged as a model organism for examining the effects of climate change on montane species. Pikas may be especially vulnerable to climate warming because their lower elevational limit is already relatively high with respect to other mammal species (McDonald & Brown 1992; Moritz et al. 2008). In the Great Basin, pikas appear to be experiencing accelerating upslope range contraction in concert with global warming (Beever et al. 2011). Because of this

vulnerability, the species has been petitioned for protection under the United States and California Endangered Species Acts (Wolf et al., 2007a, 2007b). Despite acknowledging that climate change is expected to cause continued range loss, both petitions were denied on the basis that presently available scientific evidence does not indicate pikas will experience range-wide extinction within the foreseeable future (United States Fish and Wildlife Service 2010, California Department of Fish and Wildlife 2013). In their responses, both agencies highlighted the need for more scientific information to determine the degree to which pikas are threatened by climate change.

Adaptations that allow pikas to survive in cold alpine climates appear to make them poorly suited to warmer temperatures. Low thermal conductance and high resting metabolic rate aid pikas in avoiding hypothermia during cold winters under the snow but make them vulnerable to hyperthermia in the summer (MacArthur & Wang, 1973; Smith, 1974). A key vulnerability is that their upper lethal body temperature is 3 °C above their resting body temperature (MacArthur & Wang, 1973; Smith & Weston, 1990). Thus, summer temperature may furnish a mechanism that restricts pika distribution. To avoid acute heat stress during high temperatures, pikas thermoregulate behaviorally by reducing their foraging activity, spending more time in the cool interstices of talus fields where they reside (Smith, 1974). In contrast to other montane species, pikas do not hibernate or accumulate fat stores. Instead, during the summer they cache vegetation in haypiles on which they subsist during the winter (Smith & Weston, 1990). Reduced foraging and caching capacity may result in reduced energy budgets, reproduction, and survival (Smith, 1974). This same mechanism of range limitation—reduced foraging as a result of behavioral thermoregulation to avoid high temperatures—has been proposed as a

common limitation for other montane mammals (Morelli et al., 2012) and animal species as a whole (Pörtner, 2002). Resurvey results in the Great Basin support summer temperature as a top predictor of pika extirpations, but this result has not previously been generalized to other portions of the pika's range (Beever et al., 2011; Erb et al., 2011; Stewart & Wright, 2012).

We use historical resurvey data from across California to assess potential causes of pika extirpation and to infer whether climate change has led to upslope range contraction in California. Two previous studies collected resurvey data on pikas within sub-regions of California, but both datasets suffered from small sample size and limited statistical power (Moritz et al. 2008; Stewart & Wright 2012). We fit a logistic model to current occupancy patterns, tested the model's ability to hindcast past occupancy, and used the model to forecast future pika distribution. This study advances previous projections of future pika distribution (Galbreath et al., 2009; Calkins et al., 2012) in three respects. First, in contrast to previous projections, which used "pseudo-absences" from random locations across the landscape, our model is parameterized with verified absence data. Second, our model tests and incorporates a non-climate environmental variable (i.e. habitat area) into projections of future pika distribution. Finally, we use future climate projections from the newest, IPCC 5, Generalized Circulation Models (GCMs) (Taylor et al., 2012). While this study focuses on the American pika, our methods and conclusions should be generalizable to other species, especially to saxicolous or burrowing animals and habitat specialists.



**Figure 1.** Location and current occupancy status of 67 historical pika sites in California. Background is colored by the intensity of average summer temperature.

## METHODS

### *Field Methods and Historical Data*

We identified 67 historically recorded pika locations across California from the 19<sup>th</sup> and 20<sup>th</sup> centuries, and resurveyed them to determine whether pikas have persisted at those sites. Our field methods were comparable to those of Stewart & Wright (2012) in



the northern Sierra Nevada, with minor modifications. We surveyed each site until we had either detected pikas, or until we had completed an exhaustive search of all pika habitat within a 1-km radius of the historic location. If pikas or current-year pika sign were detected at a site, the site was scored as occupied.

We aggregated data from six resurvey teams working in different regions of California (lead by coauthors of this study). We endeavored to include all reliable and spatially precise historical record locations that had been resurveyed prior to 2012. To obtain records, we queried biodiversity databases (GBIF, Arctos, MaNIS), read field notes, visited offline museums, contacted professional networks, and searched the literature. Records accompanied by a voucher specimen or observed by an experienced researcher (e.g. Joseph Grinnell, Annie Alexander) were considered reliable. Records were considered sufficiently precise only if all plausible interpretations of the historical description fit within a 1-km search radius.

The 67 records we resurveyed spanned the majority of the pika's geographic and elevational range in the state. Records extended over more than four degrees of latitude and longitude, from the slopes of Mount Shasta in the northwest to the John Muir Wilderness in the south, and to the White Mountains in the east (Figure 1). The records covered an elevational range from the lowest known pika population in California (1,380 m) to the high slopes of the southern Sierra (3,940 m). Spatial uncertainty associated with historical records ranged from 0 km (e.g. detailed field notes accompanied by historical photographs; Figure 2) to 1-km (e.g. museum skin with specimen tag specifying "east side of Pyramid Peak") with a median precision of 0.4 km. The original observation year for records ranged from 1897-2000 (median = 1927) and the interval between the historic

observation and our resurveys ranged from 12 to 109 years (median = 83). While 12 years may seem to be a relatively short interval for historical resurvey, our results indicate it is a sufficiently long period for sites to become extirpated



**Figure 2.** Historical photo retake from “4 miles southwest of McDonald Peak.” Note several distinct rocks are identifiable in both historical and modern photographs. Joseph Dixon’s field notes from 1924 read, “going on up the first foothill I came to a rock slide on a barren, warm, dry, south facing hillside at 5600 ft ... I had only been watching a few minutes when a cony poked his head out from behind the rocks and was auxed.” “Cony” was a commonly used epithet for pikas in the early 20<sup>th</sup>

century.

Resurveys were conducted during 2004-2012. We took several measures to increase our confidence in observed extirpations. Pikas' copious and persistent fecal pellets and frequent calls contribute to their high detectability. Previous studies indicate consistently high detection probability (> 90%) after 15-30 person-minutes (person-min) of search effort (Rodhouse et al., 2010; Beever et al., 2010; Erb et al., 2011; Jeffress et al., 2013). All sites where pikas were not initially detected during the first year were surveyed exhaustively in a subsequent year. Prior to exhaustive surveys, all potential habitat within the 1-km search radius was identified via aerial imagery. Depending on the amount of habitat, search effort at sites ranged from 5 to 56 person-hours searching talus (median = 11 person-hours) and 7 to 90 hours on site and within hearing distance of pika habitat (median = 24 person-hours). As a final measure, we listened for pika calls during the morning and evening hours when pikas are most active at hotter sites. In addition to pika sightings or calls, haypiles or pika scat were considered recent evidence if they contained green hues from un-decomposed chlorophyll. We also searched for and collected older, "relict" pika fecal pellets to confirm past occupancy. Pika fecal pellets tend to persist for a relatively long period of time after extirpation (at least 35 years) with gradual decline in size and change in color (Nichols, 2010).

#### *Analytical methods and predictor variables*

We modeled pika persistence as a function of 16 environmental variables—2 habitat, 2 elevation, and 12 climate variables—that we believe capture the most biologically significant processes for pikas (Table 1). These predictor variables were

combined into 58 biologically informed *a priori* combinations to test for predictive power. Each predictor variable was supported by a mechanistic hypothesis and/or by previously published literature. Twelve climate predictor variables were extracted from 270 m resolution grids, representing 30-year normal climate surfaces (Thorne et al., 2012; Flint & Flint, 2012). Climate variables included seasonal and annual temperature, precipitation, snowfall, snowpack depth, snowpack duration, climate water deficit, and actual evapotranspiration. Elevation was included as a high spatial-resolution proxy for coarser resolution climate variables. Absolute elevation was extracted from 10 m resolution digital elevation models. Corrected elevation was calculated as the difference between absolute elevations and latitude-longitude calculated minimum elevation for pikas (Hafner, 1993). Values for each climate and elevation variable were extracted for the most suitable location within our site boundary (e.g. minimum average temperature within 1-km radius site, maximum elevation, maximum average precipitation, etc.). For each site, talus habitat was hand-delineated into a GIS layer using the best available aerial imagery (ca. 3 person-hours spent on talus delineation per site) and total talus area and perimeter within the 1-km radius site boundary was calculated. Talus perimeter was included in addition to talus area because pikas may preferentially use edge habitat where there is greater access to forage (Moilanen et al., 1998; Jeffress et al., 2013). Two sites with anthropogenic pika habitat (ore dumps), where aerial talus mapping was not possible, were delineated on the ground.

**Table 1.** Variable abbreviations and definitions for 16 environmental variables included in this analysis.

<b>Variable Abbreviation</b>	<b>Definition</b>
<i>Habitat-area variables; derived from talus maps, hand-delineated using the best available year of local Google Earth aerial imagery and knowledge from on the ground surveys:</i>	
TalArea	Total talus area within the site boundary. Log transformed to reduce skew [km <sup>2</sup> ]
TalPerim	Total talus perimeter within the site boundary. Log transformed to reduce skew [km].
<i>Elevation variables; derived from 10 m grain digital elevation models. (Because elevation does not directly explain pika occupancy patterns, but instead serves as a proxy for climate, these elevation variables can be considered “phenomenological”):</i>	
Elev	Maximum elevation within the site boundary, derived from 10 m grain digital elevation models [m].
ElevCor	Latitude and longitude corrected elevation; calculated as the difference between Elev and predicted lower elevation limit for pikas [m] (Hafner 1993).
<i>Climate variables; calculated and downscaled to 270 m resolution from PRISM climate normals for 1971-2000 (Daly et al., 1994; Flint &amp; Flint, 2012). All climate variables represent the theoretically most suitable climate for pikas within the one km radius site boundary (e.g minimum temperature within the site boundary, minimum climate water deficit, maximum snow, maximum precipitation, maximum actual evapotranspiration, and maximum snowpack duration). Summer values are the average of June, July, and August. Winter values are the average of December, January, and February:</i>	
AnnT	Average annual temperature [°C].
SumT	Average summer temperature [°C].
AnnPpt	Average annual precipitation [mm].
SumPpt	Average summer precipitation [mm].
WinPpt	Average winter precipitation [mm].
AnnSnow	Average annual snowfall [mm].
AnnPck	Average annual depth of snowpack, averaged over 12 months [mm].
MnthsPck	Average number of months with at least 50 cm of insulating snowpack [months].
AnnCWD	Average annual climate water deficit; difference between potential evapotranspiration and actual evapotranspiration [mm].
SumCWD	Average summer (June, July, August) climate water deficit; difference between potential evapotranspiration and actual evapotranspiration [mm].
AnnAET	Average annual actual evapotranspiration [mm].
SumAET	Average summer actual evapotranspiration [mm].

We evaluated the performance of 58 biologically informed *a priori* models (Table 2) using logistic regression and multi-model inference techniques (Burnham & Anderson, 2002). To avoid over-fitting we restricted all models to a maximum of five events per

variable (Vittinghoff & McCulloch, 2007). With a total of 10 extirpations (“events”) in our data, this translated to no more than two predictor variables per model. Highly correlated variables ( $|r| > 0.7$ ) and variables that attempted to measure similar causal mechanisms were not included in the same model (e.g. temperature and elevation were not included in the same model).

**Table 2.** Variables combinations included in 58 *a priori* candidate models.

TalArea + AnnCWD	TalPerim + AnnCWD	AnnSnow + SumT	AnnCWD
TalArea + SumCWD	TalPerim + SumCWD	SumCWD + SumT	SumCWD
TalArea + AnnT	TalPerim + AnnT	SumT + AnnPpt	AnnT
TalArea + SumT	TalPerim + SumT	AnnPck + SumT	SumT
TalArea + AnnPck	TalPerim + AnnPck	SumCWD + AnnAET	AnnPck
TalArea + AnnPpt	TalPerim + AnnPpt	SumCWD + AnnPck	AnnPpt
TalArea + WinPpt	TalPerim + WinPpt	SumT + MnthsPck	WinPpt
TalArea + SumPpt	TalPerim + SumPpt	AnnPck + AnnPpt	SumPpt
TalArea + AnnSnow	TalPerim + AnnSnow	SumT + AnnAET	AnnSnow
TalArea + AnnAet	TalPerim + AnnAET	AnnPck + AnnAET	AnnAET
TalArea + SumAET	TalPerim + SumAET	AnnPck + AnnSnow	SumAET
TalArea + MnthsPck	TalPerim + MnthsPck	AnnSnow + AnnAET	MnthsPck
TalArea + Elev	TalPerim + Elev	MnthsPck + AnnAET	Elev
TalArea + ElevCor	TalPerim + ElevCor	AnnPpt + AnnAET	ElevCor
TalArea	TalPerim		

We projected pika occupancy at our sites for both historical and future climate conditions using the best-performing logistic model fit to current occupancy patterns. We assumed no change in the amount of talus habitat at our sites from the historical to future periods (1897-2070). Historical climate for a given time period was calculated using the delta method and a time series of statewide climate anomalies (Abatzoglou *et al.*, 2009; CCT 1895-2012). Downscaled CMIP5 future climate scenario surfaces (i.e. prepared for the IPCC’s 5<sup>th</sup> assessment report, (Taylor *et al.*, 2012) were obtained from the WorldClim

database (30 arc-second resolution, ~800 m grid cells, Hijmans *et al.*, 2005), and further downscaled to 270 m resolution to agree with current climate data. We projected pika distribution in 2070 using one low emission and one high emission RCP (RCP 4.5, “low,” and RCP 8.5, “high”) combined with a low sensitivity (GISS-E2-R), high sensitivity (MIROC-ESM) and ensemble mean GCM (mean of 17 GCMs), for a total of 6 future climate scenarios.

## RESULTS

### *Pattern of Apparent Extirpation in California*

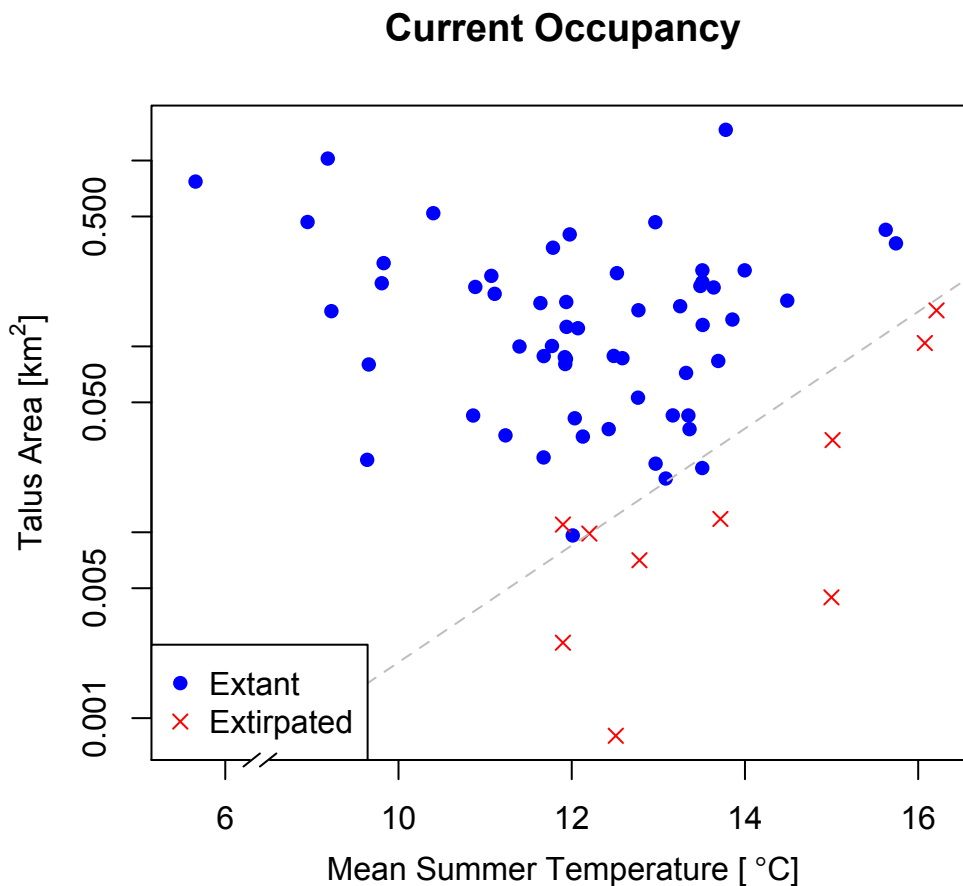
Overall, 57 sites were currently occupied by pikas (85%) and 10 sites were extirpated (15%). The average elevation of currently occupied sites (2,800 m) was 500 m higher than the average elevation of extirpated sites (2,300 m) ( $P < 0.05$ ). We found old pika feces, but no fresh sign, at all 10 extirpated sites, confirming previous site occupancy. Relatively easy detection (median = 13 person-min, range = 5-59 person-min,) of old pika feces at extirpated sites suggests that historical occupancy at these sites was robust, as opposed to transient or small populations. Of the 10 extirpated sites, five occurred in the Lassen Transect, two occurred in the northern Sierra, and three occurred in the Bodie Hills (Figure 1). For most occupied sites (81%) pika detection was easy, with pikas detected within 30 person-min (median = 5 person-min) and in the first talus field surveyed. Pika detection was more difficult at nine of the occupied sites (median = 65 person-min, range 34-582 person-min). Five occupied sites where pikas were not detected during the first resurvey were discovered to be occupied during exhaustive surveys conducted in a subsequent year.

**Table 3.** Information on top models ( $\Delta AIC_c \leq 10$ ) and variables included in top models.

Model	$\Delta AIC_c$	AUC	$R^2$	$w_i$	Predictor	$w_j$	$w_j/\text{model}$	Sign	CV
TalArea + <b>SumT</b>	0.00	0.99	0.86	0.95	<b>SumT</b>	0.960	0.107	-	0.487
TalArea + ElevCor	7.57	0.97	0.76	0.02	TalArea	0.990	0.066	+	0.538
TalPerim + <b>SumT</b>	9.30	0.97	0.73	0.01	ElevCor	0.022	0.007	+	0.416
TalArea + <b>AnnT</b>	9.46	0.96	0.73	0.01	<b>AnnT</b>	0.009	0.003	-	0.414
TalArea + Elev	9.75	0.97	0.72	0.01	Elev	0.007	0.002	+	0.416
Null Model	41.00	0.50	0.00	0.00	TalPerim	0.010	0.001	+	0.393

Left hand columns: models are listed in order of their difference from the best-performing model in Akaike's corrected information criterion ( $\Delta AIC_c$ ). Climate predictors appear in bold. Columns headings denote area under the receiver operating characteristic curve (AUC), Nagelkerke's max-scaled coefficient of determination ( $R^2$ ), and Akaike weights among all *a priori* models ( $w_i$ ). Right hand columns: column heading denote Akaike weights among all *a priori* models ( $w_j$ ), Akaike weights per model ( $w_j/\text{model}$ ), the sign of fitted variable coefficients (Sign), and the coefficient of variation across all fitted coefficient values (CV). Variables are listed in order of decreasing weight per *a priori* model. Coefficient signs (indicating a positive or negative relationship with occupancy) were consistent in all models and for all variables. Climate predictors appear in bold. Variable abbreviations are as follows: SumT = summer temperature, TalArea = talus area, ElevCor = corrected elevation, AnnT = annual temperature, Elev = elevation, TalPerim = talus perimeter; information on variable definitions can be found in Table 1.





**Figure 3.** Current status of pika occupancy at 67 historical pika record locations in California plotted against the best predictor variables, talus-area and summer temperature. The dashed grey line represents a 50% probability of occupancy as modeled by logistic regression.

The best-performing model (Talus Area + Mean Summer Temperature) received far greater support than the next best-performing model ( $\Delta\text{AIC}_c = 7.57$ ,  $\text{AUC} = 0.99$ ) and 95% of the Akaike weight for all *a priori* models (Table 3). Support for the best model was even more pronounced when models with climate-proxy variables (e.g. elevation) were excluded in order to extrapolate pika occupancy under past and future climate conditions ( $\Delta\text{AIC}_c = 9.30$ ,  $w_j = 0.98$ ). Given such a high level of support for the top-

performing model, model averaging reduced predictive power for both current and historic occupancy. The best model correctly classified current occupancy status at 97% of sites (65/67, Figure 3).

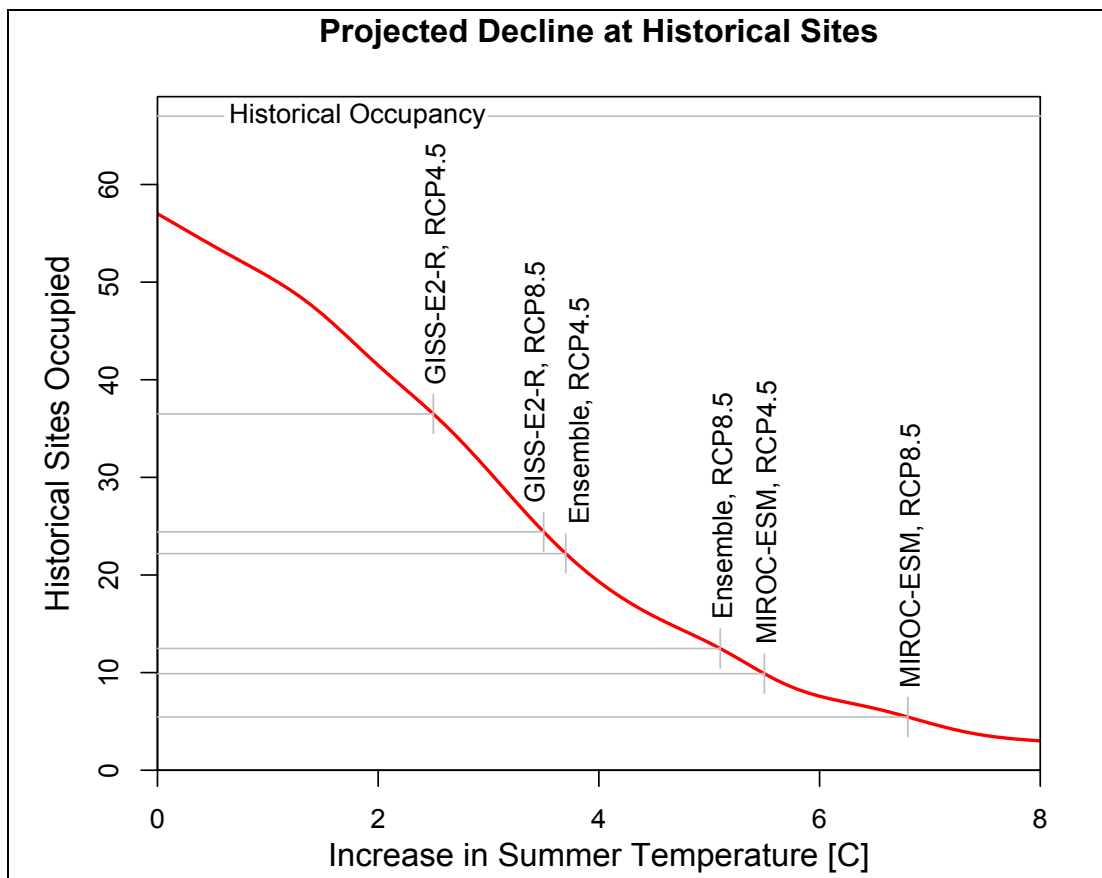
Another check on the model was hindcasting, to determine whether, given current occupancy, Talus Area, and Mean Summer Temperatures, the model could predict historically occupied sites. The best model correctly hindcast past occupancy, during the year of the original observation, at 93% of sites (62/67).

#### *Future of Pikas in California*

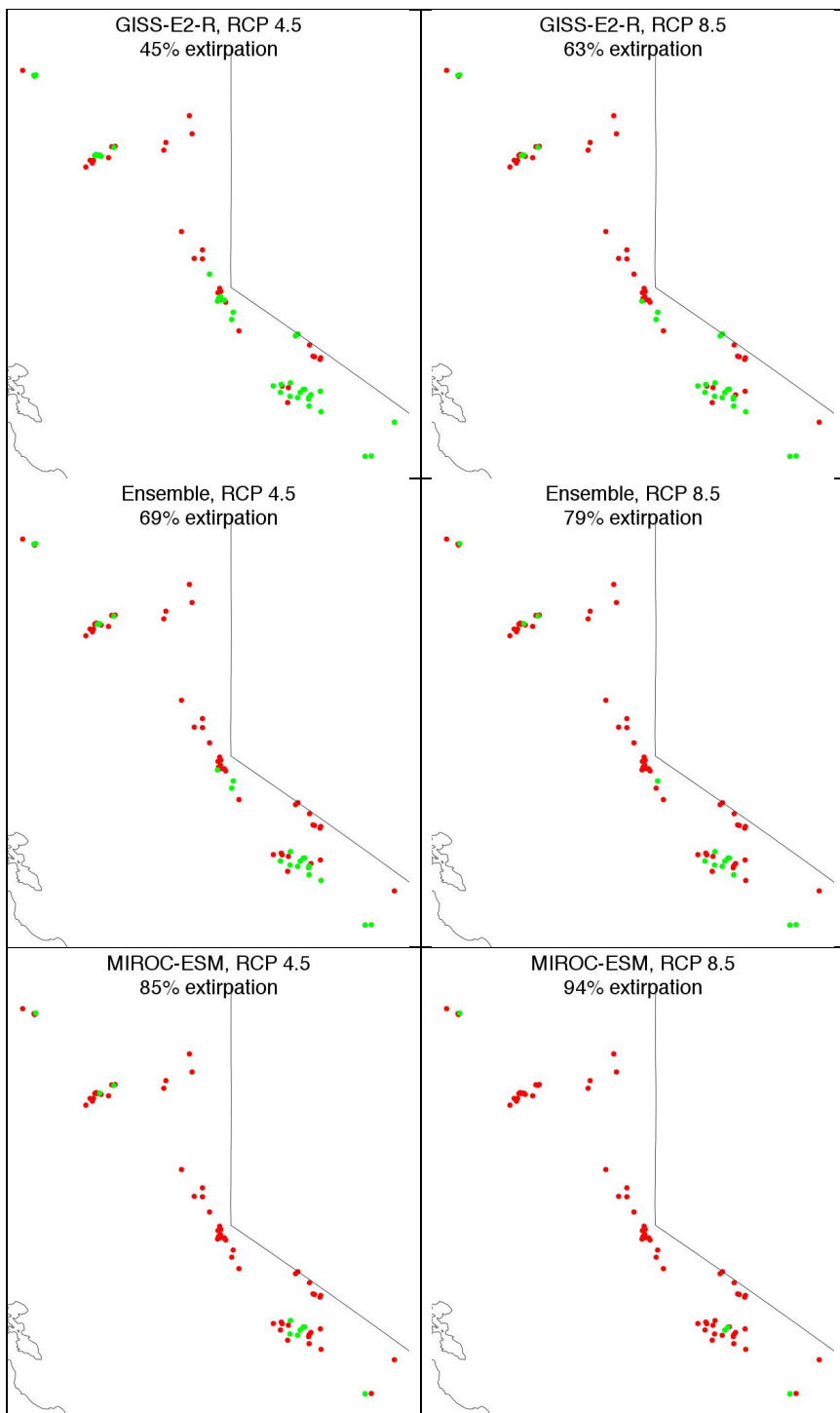
Projecting to the future, our best-performing model projected progressive site extirpations as summer temperatures warm. By 2070, overall extirpation at historical sites is projected to range from 45% to 94%, depending on the emissions pathway and the GCM used (Table 4, Figure 4, Figure 5). Under ensemble mean GCM climate scenarios the model projects 69% to 79% of sites will be extirpated for the low and high emissions scenarios respectively (RCP 4.5 and RCP 8.5). Extirpations at the historical localities are projected to be most pronounced in the northern Sierra (north of 38.5° latitude), the Lassen Transect, and the ranges east of the southern Sierra, where the model projects that by 2070, 56% to 100% of historical sites in these regions will be extirpated, depending on the future climate scenario. However, even for the worst-case future climate scenario considered (MIROC-ESM, RCP 8.5) some of our pika sites (at least 6% overall) are projected to persist through 2070 on the high peaks of the southern Sierra Nevada and Mt Shasta.

**Table 4.** Percent of sites regionally predicted to be extirpated by 2070 under six future climate scenarios.

California, Statewide	45%	63%	69%	79%	85%	94%
Northern California	56%	79%	79%	90%	92%	97%
Northern Sierra	56%	83%	83%	94%	100%	100%
Lassen Transect	65%	82%	82%	88%	88%	100%
Mount Shasta	25%	50%	50%	75%	75%	75%
Southern California	29%	39%	54%	64%	75%	89%
Southern Sierra	16%	21%	32%	47%	63%	84%
East of S. Sierra	56%	78%	100%	100%	100%	100%
	GISS E2-R RCP 4.5	GISS E2-R RCP 8.5	Ensemble RCP 4.5	Ensemble RCP 8.5	MIROC-ESM RCP 4.5	MIROC-ESM RCP 8.5



**Figure 4.** Projected decline in occupancy at historical sites under various degrees of summer warming as predicted by our best-performing model. Summer temperature increases, averaged across our 67 historical pika sites, for six climate change scenarios are given (vertical lines) along with corresponded predicted number of historical sites occupied assuming all sites experience a uniform increase in summer temperature (horizontal lines). See Table 4, or Figure 5 for site-specific projections without the simplifying assumption of uniform warming across all sites.



**Figure 5.** Predicted pika occupancy status mapped at historical sites for 2070 under six future climate scenarios. Green denotes occupied sites while red denotes extirpated sites. Climate change scenarios combine two representative concentration pathways with a low sensitivity GCM (GISS-E2-R), a high sensitivity GCM (MIROC-ESM), and the ensemble mean of 19 GCMs.

## DISCUSSION

Two variables, talus area and mean summer temperature, did a very good job separating sites where pikas are extant from sites where pikas have become extirpated since documented historical occupancy. Our best model, which incorporates these variables, strongly outperformed all other candidate models (Table 3), and correctly predicted current occupancy at 97% of sites (Figure 3). The model performed nearly as well in a test of transferability through time—correctly predicting past occupancy at 93% of sites. This level of performance through time is high relative to models applied to other species through historical time, including other montane small mammals (Morelli et al., 2012; Smith et al., 2013) and butterflies (Kharouba et al., 2009). Though the model has not yet been tested for geographic transferability, the same climate constraint—summer temperature—has also been identified as a primary limiting factor for pikas in the Great Basin, implying that geographic transferability may also be strong.

This study is the fourth published analysis of biogeographic data to indicate that mean summer temperature (Jun., Jul., Aug.) is the most important climate constraint on pika distribution. Two temporally distinct historical resurvey studies in the Great Basin indicated that mean summer temperature was the strongest limiting factor for pikas (Beever et al., 2010, 2011). Using MAXENT (Phillips & Dudik, 2008) and stepwise variable selection, mean summer temperature was selected from a candidate set of 19 bioclimatic variables as the best predictor of pika distribution across the contiguous United States (Calkins et al., 2012). Further, mean summer temperature is supported as a limiting factor by a mechanistic hypothesis of reduced forage ability as a result of

behavioral thermoregulation. This mechanism is supported by knowledge of the pika's natural history (Smith & Weston, 1990), behavioral observations of reduced activity during high ambient temperatures (MacArthur & Wang, 1974; Smith, 1974), and physiological studies indicating very limited ability to dissipate heat and avoid hyperthermia (MacArthur & Wang, 1973). Mean daily temperature should be a good measure of crepuscular conditions, governing pikas' ability to forage around dusk and dawn when daily maximum temperatures already restrict mid-day activity. Finally, temperature is supported as a limiting constraint by the paleontological record of upslope range retreat by pikas since the last glacial maximum (Grayson, 2005).

Talus area—the amount of habitat available to pikas locally—has been well accepted as a factor affecting population and metapopulation dynamics (Moilanen et al. 1998) and has been documented in other pika extirpation studies (Beever et al., 2003) including a subset of the California records (Stewart & Wright, 2012). Low talus area within our 1-km radius appears to be indicative of both small habitat islands and poor connectivity to other talus habitat. The precise mechanism behind this apparent relationship is not known, but reasonable hypotheses include: (a) larger populations are less vulnerable to stochastic extinction, (b) sites with more habitat have better connectivity with higher elevation habitat, and (c) sites with more habitat available are more likely to contain areas with more suitable meso-climate.

In this analysis, we used a conservative criteria—all talus within a 1-km radius absent of current year pika sign—to score sites as occupied or extirpated. We adopted this definition in order to differentiate patch-scale metapopulation fluctuations from landscape-level extirpations (which this study focuses on) and to accommodate inclusion

of records with moderately precise record descriptions. However, it is important to note that this definition does not address dynamics within sites. Four of our occupied sites appeared, anecdotally, to be functionally extirpated sink habitats, i.e., sites which may not currently sustain reproducing pika populations. At these sites, search effort necessary for first detection was high (median = 356 person-min searching talus), old pika feces were widespread, but evidence of current occupancy was scant ( $\leq 2$  individuals observed in any year). Two of these sites may have been very recently re-extirpated, as fresh pika sign was observed (green pellets and hay piles), but extensive late-summer surveys during morning and evening hours did not result in direct detection (sightings or hearing calls). At another site, one or two pikas were observed during two out of three years, but the same talus patch was never occupied two years in a row. At the fourth site, we observed evidence of only two pikas (one direct detection) and evidence of current occupancy had retreated upslope by ca. 300 m elevation. It seems that juvenile pikas are able to disperse to these sites from surrounding, higher elevation habitat, but that they are not able to re-establish functional populations. Though we treated these functionally extirpated sites as occupied in our analysis, our qualitative conclusions (i.e. talus area and summer temperature was the most informative model) are robust to treating these functionally extirpated sites as either occupied or extirpated. Using our best-performing model, the probability of occupancy at our "functionally extirpated" sites was significantly lower than at occupied sites ( $P < 0.05$ ) and significantly higher than at extirpated sites ( $P < 0.005$ ).

Our results, coupled with the documented ca. 1 °C increases in state-wide summer temperature over the past century (Abatzoglou et al., 2009; CCT, 1895-2012) strongly



suggest that the pikas have experienced climate-mediated range contraction in California over the past century. However, because historical absence data for pikas is limited, it is not possible to make definitive conclusions at this point. An alternative hypothesis is that all extirpations are purely the temporary result of normal metapopulation dynamics, and that the statistical relationship between temperature and pika extirpation (which has now been documented in both California and the Great Basin) is spurious. Under the “no climate effect hypothesis” we would expect that, in the intervening years, since the historical era, an equivalent number of historical sites would have been colonized as were extirpated. As we were only able to identify one site where pikas were observed to be historically absent (recorded by Joseph Grinnell; still not occupied by pikas) we are not able to make meaningful conclusions about a hypothetical rate of recolonization. However, given apparent difficulty re-establishing populations at our four “functionally extirpated” sites, the pika’s ability to recolonize marginally suitable extirpated areas may be limited.

#### *Future of Pikas in California*

Using future temperature projections for 2070, and our statistical model of extirpation in relation to summer temperature and habitat area, we projected extensive (63%) to dramatic (94%) extirpation among our sites (Table 4). We offer two important caveats to these projections. First, historical sites are not a random sample of the pika’s entire distribution throughout California, and thus our projections must not be interpreted as range-wide estimates of range contraction. A critical step in applying our model, or other models, to a broader scale is mapping talus distribution for an entire region.

Second, the performance and transferability of species distribution models is dependent on the models taking into account all important climate, and non-climate, environmental variables (Duncan et al., 2009). Our small number of events (10 extirpations) limits our statistical ability to estimate parameters for more than two predictor variables in our model (Vittinghoff & McCulloch, 2007). While it appears that talus habitat area and summer temperature are two of the most important limiting factors to pika distribution, other variables and variable interactions (e.g. hydrology) are undoubtedly also important (Beever et al., 2010; Erb et al., 2011; Jeffress et al., 2013).

That pikas' distribution is tied to mean summer temperature does not bode well for the future, especially because there is a near-consensus among climate models (16 of 17 models) that summer temperature will warm by more than mean annual temperatures in the Western U.S. (IPCC5; Taylor et al, 2012). This trend is also apparent in the historical instrumental record for California (CCT, 1895-2012). For sites in this study, summer temperature is projected to rise by 0.9 °C more on average than annual temperature (RCP 8.5, 2070). This may indicate that in the Western USA pikas, and other species that are primarily active in the summer (e.g. most montane species), may have higher seasonal exposure to climate change.

The finding that pika persistence is predicted by a combination of talus area and average summer temperature suggests that high talus area can compensate for the summer temperature effect (Figure 3). The implication here is that pika populations living in regions with more talus will be able to accommodate more summer heat without diminished site persistence. This relationship could be an important consideration for managers, as it implies that low-elevation extirpations could possibly be prevented by

supplementing talus habitat with anthropogenic talus-like material (e.g. riprap, ore dumps). Alternatively, if high talus area is beneficial due a correlation with presence of rock-ice features (Millar & Westfall, 2010), but not due to habitat-island-size or other factors, the relationship could inform managers of important refugia or dispersal corridors.

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## SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS

Chapter one (Stewart & Wright, 2012) presented results from resurvey of 19 historical pika locations in the northern Sierra Nevada Mountains of California. We determined that two of 19 historical locations had become extirpated since the historical era. We did not find a significant climate or elevation signal in our data. However we did find a significant habitat-area signal—sites with the least amount of pika habitat were most likely to be extirpated. This pattern was consistent with classic metapopulation dynamics, in which small and more isolated patches of habitat are more likely to be extirpated at any given point in time (Moilanen et al., 1998).

Chapter two examined occupancy status at 67 historical sites across California. Overall, we found that 10 of 67 sites were extirpated and that current occupancy was best predicted by a combination of habitat area and summer temperature—sites with low talus area and high summer temperature were most likely to be extirpated. These predictors of pika distribution were supported by previous biogeographic, behavioral, and physiological studies, but had not previously been demonstrated to limit pika distribution in California (MacArthur & Wang, 1973; Smith, 1974; Beever et al., 2011). Our model predicts that by 2070, pikas will be extirpated from 63% to 94% of our historical sites in California.

Resurveying historical records is the best method currently available for inferring changes in occupancy patterns from the historical era to the present. However, because historical pika surveys did not follow statistically rigorous sampling techniques, the conclusions we can draw are limited. For instance surveys were not randomly located and

sites where workers looked for pikas but did not find them were generally not recorded. These oversights have been corrected in some contemporary survey efforts (Jeffress et al., 2013; my work in Yosemite). Nonetheless, given the temperature limitations we detect in our analysis, and given observed increases in temperature over the past century, it is parsimonious to conclude that pikas have retreated upslope in California and will continue to lose ground to climate change as warming accelerates over the coming century.

The key question addressed in this thesis is to what degree are pikas threatened by climate change in California? This work represents a substantial advance beyond a previous assessment technique in answering this question (Galbreath et al., 2009; Calkins et al., 2012). However, additional work is necessary to refine models and to apply them across whole landscapes. Two critical steps are (1) collecting additional data on pika distribution patterns, and (2) developing automated techniques for mapping talus distribution—and other relevant environmental variables—across whole study regions. Additionally, mechanistic studies focusing on behavior and physiology may elucidate details of the processes that control pika distribution and abundance.

There are two key parameters necessary to judge how threatened a species is by climate change. First, how sensitive is the species to climate change, and second, by how much will the climate change in the species' range? This work attempts to place a value on the first parameter, the pika's sensitivity to climate change, and relies on a range of future temperature estimates prepared for the International Panel on Climate Change fifth assessment report (Taylor et al., 2012). The passage of time will be the ultimate arbiter of the accuracy of the predictions we make in this work. Finally, the amount that we warm

the planet's atmosphere depends partly on its sensitivity to green house gases, but also on the political choices our governments make about energy policy today and in the coming years.

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