

Within-talus temperatures are not limiting for pikas in the northern Sierra Nevada, California, USA

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The American pika (*Ochotona princeps*) is a temperature-sensitive lagomorph reported to be in decline in warmer sites in California, Nevada and portions of Utah. Talus is used for denning and retreat habitat by the species. Climate envelope modeling and climate projections suggest the species' distribution will retract in coming decades—but other studies suggest pikas may be resilient in the face of warming by taking advantage of talus as a thermal refuge from warming air temperatures. We investigated the thermal environment of mid to low elevation talus habitats in the northern Sierra Nevada between 2010 and 2012 using automated temperature loggers placed generally 0.5 to 1 m below the talus surface. We found temperatures within talus are rarely challenging to pikas—even in taluses well below the inhabited elevational range of pikas. Occurrence of temperature extremes within talus was only weakly correlated with elevation, and exhibited substantial variation between talus patches. Temperatures deeper in talus than we were able to probe but that pikas can likely reach are certain to be even more stable and less physiologically challenging. Despite buffered temperatures in the subsurface talus environment, we observed multiple instances of pika-accessible, previously-inhabited talus patches that did not support pikas in our surveys. Summer daily maximum air temperatures at these taluses averaged more than 2°C warmer than occupied taluses, and taluses that pikas occupied in some years but not in others were intermediate in temperature. Sites with no evidence of past pika occupancy averaged warmest of all. We suggest aboveground air and surface temperatures, rather than temperatures within talus, pose a greater challenge to pika persistence, through effects on foraging and dispersal. Our results indicate that the thermal refuge provided by talus is likely to be necessary and beneficial to American pikas, but sufficient only to partially offset the ongoing impacts of warming ambient temperatures on waning pika distribution.

Key words: American pika, climate warming, distribution, extirpation, microclimate, talus, temperature logger

Conserving biodiversity in the face of climate change requires that we know how species will respond over the coming decades and centuries. Accurate predictions inform smart conservation planning, such as identifying species and populations vulnerable and not vulnerable, emphasizing the conservation of corridors important for climate-mediated range shifts, and protecting refugial habitat areas projected to remain suitable for taxa of concern as climate change proceeds.

The American pika (*Ochotona princeps*) has emerged as a model organism for investigating the impact of climate change on animal population viability and distribution (Galbreath et al. 2009, Beever et al. 2010, 2011, Guralnick et al. 2011, Stewart et al. 2015, Wilkening et al. 2015a, Castillo et al. 2016, Mathewson et al. 2017). Pikas are small lagomorphs of the family Ochotonidae, with a single living genus. Two species occur in North America, with only the American pika within the continental USA (see <https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=2359&inline=1>, Smith and Weston 1990 for species accounts). Montane habitat use and cold adaptation are widespread in the genus (Leach et al. 2015, Yang et al. 2008). In response to a state listing petition, which presented climate change as a primary threat (Wolf et al. 2007), the California Department of Fish and Wildlife in 2007 and in 2013 reviewed the status of pikas in California and recommended against listing, but indicated monitoring and more information were needed (CDFW 2013). The pika is currently included by the State as a Species of Greatest Conservation Need.

Much of American pikas' sensitivity to global warming appears to be due to direct thermal-physiological limitations. Thermal metabolic experiments and thermal models have indicated that the species' susceptibility to mortality is due to a poor ability to shed excess body heat (MacArthur and Wang 1973, 1974, Moyer-Horner et al. 2015). Death at temperatures 25.5 – 30° C has been observed in small studies (Smith 1974, $n=2$ pikas; MacArthur and Wang 1973, $n=2$ pikas). Field observations have shown pika hours of activity are restricted by warmer ambient temperatures commonly experienced by the animal, particularly at lower elevation sites or during the peak of summer (MacArthur and Wang 1974, Smith 1974, Henry et al. 2012, Otto et al. 2015, Moyer-Horner et al. 2015). Staff and O'Connor (2015), studying American pikas in southeastern British Columbia, Canada, found foraging activity decreased by 3% for each 1°C increase in aboveground air temperature, declining to near inactivity at 20°C. Wilkening et al. (2015b) found summertime stress metabolite concentrations were greater in fresh pika scat from an area that experienced both higher within-talus temperatures in summer and more extreme within-talus cold conditions during the preceding winter. Increasing temperatures or declining snowpack due to local effects of global warming have widely been implicated in shrinking pika distribution in the North American Great Basin and California (Beever et al. 2013, 2016, Nichols et al. 2017, Stewart and Wright 2012, Stewart et al. 2015, 2017, Wilkening et al. 2011).

We investigated the ability of subsurface talus temperatures to predict pika occupancy and persistence patterns in mid to low elevation talus patches in the northern Sierra Nevada. Millar and others (Millar and Westfall 2010, Millar et al. 2014b, Smith et al. 2016) have suggested pikas may be resilient to local climate warming because they have a thermal refuge in cool taluses, allowing them to thermoregulate behaviorally. Stable thermal refuge in talus also was suggested as the reason for pika persistence in seemingly anomalous, low-elevation lava habitats (Rodhouse et al. 2017). Millar et al. (2014a) offered an interesting counterpoint, suggesting Great Basin taluses are less likely to be strong thermal refugia and expecting continuing pika range contraction there. Mathewson et al. (2017) built a mecha-

nistic model of pika response to their various thermal microenvironments and estimated the thermal refuge provided by talus would protect against pika population loss at 8 to 19% of sites where extirpation would otherwise be expected—conversely, talus would not protect against pika loss at 81 to 92% of sites.

MATERIALS AND METHODS

We sampled in 46 talus habitats across the northern Sierra Nevada extending from Yosemite National Park to central Sierra County (37.7 – 39.6° latitude) and ranging in elevation from 1208 to 2933 m (Figure 1). Fifteen were sites we visited in studies of historical and other pika locations (Stewart and Wright 2012, Stewart et al. 2015, Stewart et al. 2017), 31 others we selected for accessibility, apparent suitability for pikas in terms of rock size, depth and amount of talus, and for adequate representation of taluses at a variety of elevations (Figure 2). In order to focus on the “hot zone” of potentially tenuous pika viability near the lower edge of its elevation range, we worked relatively low in the elevational range of the pika (which extends to well above 4000 m in the Sierra Nevada: Millar et al. 2010, Stewart et al. 2015). We included sites across a range of elevations in areas like the Yosemite Valley/Merced River drainage, Mariposa County, and the Lovers Leap/Horsetail Falls area, El Dorado County, that have abundant talus throughout both low and higher elevations. Unlike many authors, because we wanted to determine whether within-talus temperatures at low elevation sites were limiting the distribution of pikas, we included sites lower in elevation and warmer than the occupied range.

Temperature loggers (Lascar “EasyLog USB”), programmed to record hourly and housed in waterproof aluminum cases, were wired to a surface rock and lowered into the talus—typically a depth of 0.5–1 m. Often talus is deeper than this, but it was rarely feasible to reach lower depths. We took care that loggers would not be exposed to direct sunlight from any angle. We recorded logger locations on a handheld Global Positioning System (GPS) unit and thoroughly photographed each site of placement to enable relocation of the site for retrieval. Each talus patch received one logger, placed where fecal pellets were abundant relative to other areas sampled within the talus—or, at sites without pika evidence, at locations that resembled pika-preferred microhabitat in our experience, based on rock size, talus depth, and rock niche geometry. Temperatures have been shown to vary within talus patches in other studies (Millar et al. 2014b, Rodhouse et al. 2017, Wilkening et al. 2011); however examining multiple locations per site was beyond the scope of this study. Instead we used consistent, unbiased sampling at many sites to maximize power in detecting trends across locations. Each logger remained in place and recording for approximately one year, depending on site revisit schedule. At many locations loggers were replaced upon retrieval with another logger and recording continued for another year.

We surveyed for pika following the methods of Stewart and Wright (2012, also Stewart et al. 2015) upon each occasion of logger placement or retrieval. We searched for both current sign and relict sign (old pika fecal pellets can remain for decades on rocks or in soil or duff collecting in pockets in the talus: Nichols 2010, Stewart et al. 2017). For analysis, each site was categorized as having current pika sign (pikas present), old pika sign only (buried pellets, old surface pellets), no pika sign, or as “marginal”. We defined marginal sites as those that had current pika sign in at least one year of survey but only old sign in at least one other year. Current pika sign included visual confirmation, auditory confirmation,

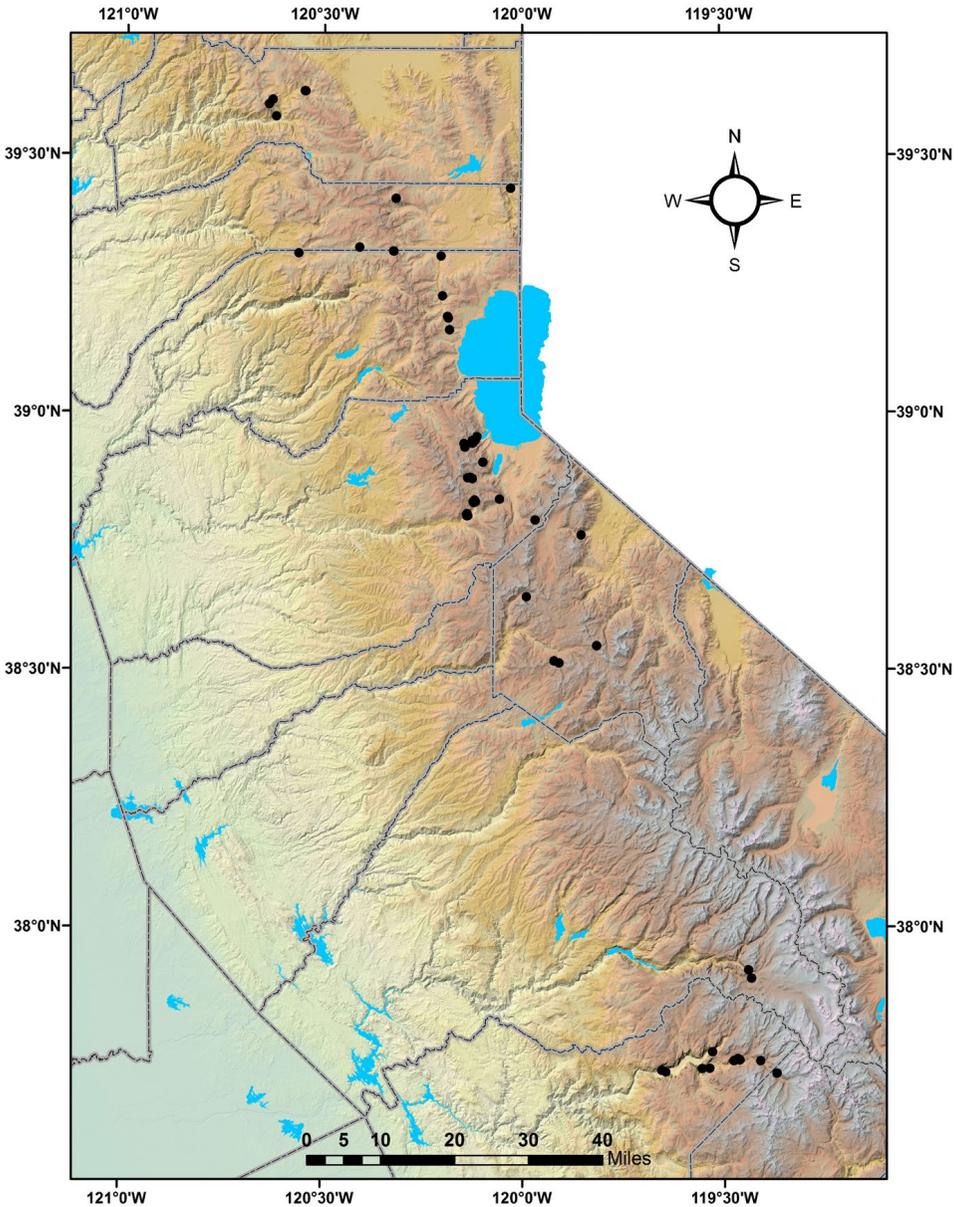


FIGURE 1.—Map showing locations of 46 sites (black dots) in northern California where temperature loggers were placed within talus that appeared appropriate for pika. Lake Tahoe is at north center of the figure; California county boundaries are also shown.

green haypiles, or fresh scat (pikas give distinctive calls, stockpile harvested vegetation in piles for winter consumption, and have distinctive scat: Smith and Weston 1990, Elbroch 2003). We commonly detected more than one type of current sign when pikas were present. Pikas have widely been reported to be highly detectable (Beever et al. 2008, 2011, Rodhouse et al. 2010, Hall et al. 2016).

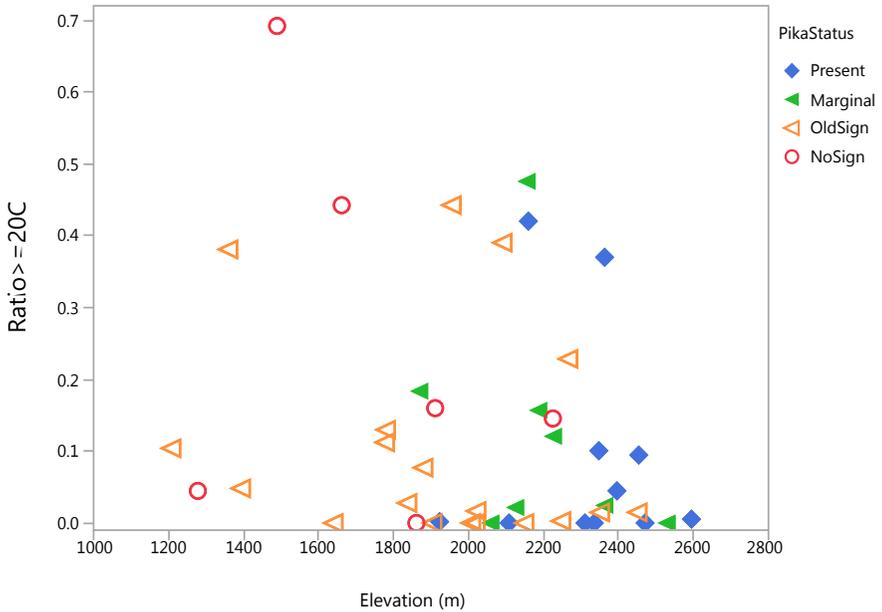


FIGURE 2.—Warm temperature exceedances (ratio of within-talus hours $\geq 20^{\circ}\text{C}$ to all hours June 1 through September 30 in the record [R20+]), versus elevation, in meters. Symbol color and shape shows pika population status. R20+ was not strongly related to elevation (Spearman $\rho = -0.22$, $n = 44$, $P = 0.15$). Sites with few or no temperatures reaching 20°C occurred at all elevations. Pika-occupied (blue diamonds), marginal (intermittently occupied: green triangles) and absent (open triangles and circles) sites overlapped greatly, with many unoccupied and formerly occupied sites similar to occupied sites in within-talus 20°C temperature exceedances.

Logger data were downloaded using Lascar software and analyzed using JMP 9.0.2 statistical software (SAS Institute, Inc.). Because dates of placement and retrieval varied between sites and years, logger records covered differing durations of the summer months. For this reason, we report exceedances of warm and cold temperature thresholds as a ratio: the number of hourly records equal to or exceeding a given threshold, divided by the total number of hours recorded during the warm or cold season. We defined the warm season as June, July, August and September (“JJAS”); and the cold season as December, January, February and March (“DJFM”). We denote these ratios as R20+, R24+, R(-2.5)-, and R(-5)- ($\geq 20^{\circ}\text{C}$, $\geq 24^{\circ}\text{C}$, $\leq -2.5^{\circ}\text{C}$, and $\leq -5^{\circ}\text{C}$, respectively). We chose exceedance thresholds based on values investigated previously in the literature as potentially significant to pika (Beever et al. 2010, Moyer-Horner et al. 2015, Yandow et al. 2015, Wilkening et al 2011). Ratio values were Box-Cox transformed before analysis if needed to correct non-normal distribution, adding 0.0001 to all values to prevent errors due to transforming zero values.

To check whether warm exceedances were biased by time of placement or retrieval of loggers, we assessed the correlation of Julian day of placement (start of record) and retrieval (end) with elevation, latitude, and with the most sensitive talus warm exceedance response variable: R20+. Elevation, for example, might reasonably be expected to interfere with timing of logger placement in a non-random way through delay of fieldwork by lingering snowpack at high elevations. If any factor related to temperatures was biasing logger timing we would expect a relationship between timing and R20+.

We used the Basin Characterization Model (BCM; Flint et al. 2013) data to estimate aboveground climatic conditions at sites. The BCM dataset is an interpolated, spatially continuous, downscaled climate dataset for the watersheds of California (270-m resolution). In addition to minimum and maximum temperature and precipitation, BCM has a variety of useful variables such as estimated water balance and snowpack, and provides past, recent, and future estimates of all climate variables for each 270-m cell.

In multi-variable analyses, we excluded moderately to highly correlated variables (nonparametric Spearman $|\rho| > 0.5$) from occurring together in the same model. We followed Vittinghoff and McCulloch (2007) in limiting the complexity of our statistical models to prevent overfitting. Model comparisons were performed using AIC_C , and we used $\Delta AIC_C \leq 2$ as an indication of a well-fitting model (Anderson et al. 2000, Burnham and Anderson 2002).

RESULTS

Within-talus temperature records were obtained from 46 sites (Figure 1, Appendix I). Full cold-season records were obtained at all sites, but we excluded two sites from analyses of warm temperature exceedences because battery failure curtailed their warm season records to fewer than 70 days.

Day of the year of logger placement correlated differently in different years with elevation, the correlation being negative in 2010 (Spearman rank test, $P = 0.02$, $n = 14$), non-significant in 2011 ($P = 0.16$, $n = 45$), and positive in 2012 ($P = 0.02$, $n = 13$). Day of logger retrieval was negatively correlated with elevation in 2012 ($P = 0.03$, $n = 45$) and non-significant in other years (2011, $P = 0.35$, $n = 14$; 2013, $P = 0.08$, $n = 13$).

To check whether these effects might bias our assessment of warm season temperature exceedences, we examined effects of start and end day of the record on the most sensitive temperature metric, R20+: the ratio of within-talus hourly temperature records $\geq 20^\circ\text{C}$ to total hourly records during the warm season (transformed to approximate normality). Because elevation and latitude affect temperatures, we also included these variables and year in an all-combinations model comparison to evaluate variable importance (Burnham and Anderson 2002). The best model included elevation and year, only, explaining about 18% of the variance in transformed R20+ (Table 1). Eleven models had $\Delta AIC_C \leq 2$ (Table 1); of these, none of the top 5 ($\Delta AIC_C < 1.4$) included start or end day. Variable importance among the 11 models with $\Delta AIC_C \leq 2$ highlighted year and elevation (relative importance 0.75 and 0.72, respectively) and latitude (0.45), followed by end day and start day (0.23 and 0.15, respectively). The best single-factor models were year of survey ($\Delta AIC_C = 0.81$), elevation ($\Delta AIC_C = 1.92$), and latitude ($\Delta AIC_C = 2.37$), followed distantly by start day ($\Delta AIC_C = 5.99$) and end day ($\Delta AIC_C = 7.87$, which trailed the no-variable model ΔAIC_C of 7.06). We concluded that start and end dates had effects on R20+, but these effects were small relative to effects due to elevation and year.

Acute warm temperature extremes.—Acute warm temperature extremes within talus were uncommon. Only two of 44 sites experienced within-talus temperatures equal to or above 28°C , and both had ≤ 12 hourly exceedences of this threshold in any sampled year. Old pika sign was detected at one of these sites, and the other was currently occupied. More than two-thirds of sites (32 of 44: 73%) experienced ≤ 3 hours of within-talus temperature $\geq 24^\circ\text{C}$ in any year of sampling.

TABLE 1.—Best models ($\Delta\text{AICc} \leq 2$) explaining within-talus warm temperature exceedances ($\geq 20^\circ\text{C}$: R20+, transformed to approximate normality). Dots indicate variables included in each model.

Model Rank	Model:					ΔAICc	Weight
	Year	Elevation	Latitude	Start Day	End Day		
1	•	•				0.00	0.103
2		•	•			0.73	0.072
3	•					0.81	0.069
4	•		•			1.09	0.060
5	•	•	•			1.29	0.054
6	•	•	•		•	1.41	0.051
7		•	•		•	1.43	0.050
8	•	•		•		1.47	0.049
9	•			•		1.56	0.047
10	•	•			•	1.79	0.042
11		•				1.92	0.040

Acute cold temperature extremes.—Extremely cold temperatures were also uncommon within talus. Only two sites of 46 experienced temperatures at or below -10°C in any year, each for fewer than 10 hours in a year. Pikas were present at one of these sites, and we detected old pika sign at the other.

Temperatures between -5° and -10°C were more common, with 25 sites (54%) experiencing ≥ 10 hours in at least one year of recording. These sites ranged widely in elevation, from 1278 – 2933 m. Other studies have associated within-talus temperatures substantially below 0°C or having wide fluctuations below 0°C with lack of snow cover (Kreuzer and Huntly 2003, Millar et al. 2014b, Beever et al. 2010, 2011).

Comparing a heavy and a light snow winter.—California's water year 2010 – 2011 was generally wetter than average, while 2011 – 2012 was dry. Snowpack during March 2011 averaged about 3 times the snowpack during March 2012, as estimated by BCM for the 13 sites we sampled in both years (mean \pm standard deviation across sites: 1180 ± 173 mm in 2011, 370 ± 75 mm in 2012). Within-talus temperature loggers during 2010 – 2011 showed fewer warm temperature extremes in the warm season, and longer periods of winter temperatures hovering around 0°C as is typical under an insulating snow layer. There were fewer cold exceedances under this heavy snowpack: 0.7% vs. 3.1% of cold season hours $\leq -5^\circ\text{C}$ in 2010-2011 vs. 2011-2012 (Wilcoxon signed ranks test, $Z = 3.56$, $P = 0.0004$); and 2.6% vs. 23.4% of hours $\leq -2.5^\circ\text{C}$ ($Z = 3.83$, $P = 0.0001$).

Patterns in 2011 – 2012 within-talus temperatures.—Here we restricted across-sites analysis to summer 2011 through summer 2012 ($n = 44$ sites), to control for weather differences between years. Variation among sites in within-talus temperature exceedances was considerable, and exceedances did not explain pika status.

Warm temperature exceedances in the talus hourly records were only very weakly negatively correlated with elevation (R20+ vs. elevation, Spearman $\rho = -0.22$, $P = 0.15$;

R24+ vs. elevation, $\rho = -0.15$, $P = 0.33$; $n = 44$). Correlation of talus warm temperature exceedances with BCM estimates of summer daily maximum air temperatures at each site (Jun through Sep, 2001 – 2010 averages) were still rather weak (R20+ vs. T_{max} , $\rho = 0.30$, $P = 0.05$; R24+ vs. T_{max} , $\rho = 0.19$, $P = 0.22$, due to great variation in within-talus temperatures that was not strongly tied to ambient air temperature: the well-known buffering effect of talus. For example, thirteen sites ranging from 1641 to 2530 m elevation logged zero hours $\geq 20^\circ\text{C}$ within talus. There was substantial variation across elevations in the ratio of hours $\geq 20^\circ\text{C}$ (Figure 2). Pika-occupied and pika-absent sites overlapped extensively in $\geq 20^\circ\text{C}$ exceedances within talus (Figure 2).

Low temperatures within talus during 2011 – 2012 were also resistant to simple categorization. There was a significant but high-variance positive correlation of cold exceedances with elevation (R(-5)- vs. elevation, $\rho = 0.55$, $n = 45$, $P = 0.0001$; Figure 3). Of 45 sites, 16 had zero hourly records $\leq -5^\circ\text{C}$, and these sites ranged broadly in elevation: 1208 – 2530 m. Two sites with many hours $\leq -5^\circ\text{C}$ were at modest elevations (1792 and 2156 m), one of which seemed topographically likely to be subject to cold air drainage. Patterns in R(-2.5)- were similar (R(-2.5)- vs elevation, $\rho = 0.62$, $P < 0.0001$). Correlation of within-talus cold exceedances with BCM's 2001 – 2010 average winter T_{min} (average daily minimum temperature DJFM) gave correlations of -0.30 (for both R(-5)- and R(-2.5), $n = 45$, $P = 0.05$,). We doubt -2.5°C is acutely challenging to pikas, which routinely live for months at approximately 0°C , during snow cover, but subzero temperatures within talus may increase long-term winter energy demand (cf. Otto et al. 2015 Figure 1, MacArthur and Wang 1973 Figure 3).

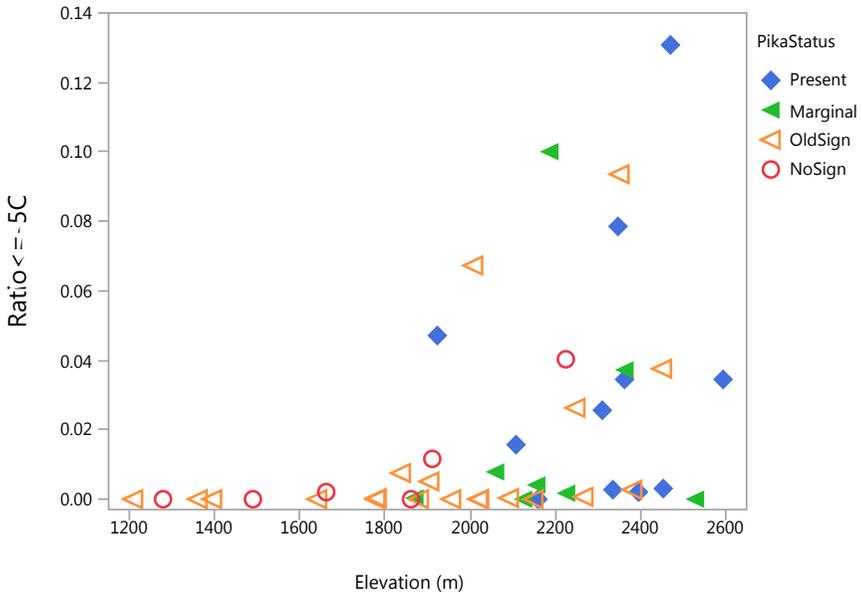


FIGURE 3.—Cold temperature exceedances (R(-5)-: the ratio of within-talus hours $\leq -5^\circ\text{C}$ to all recorded hours December 1 through March 30, versus elevation. Symbol color and shape shows pika population status. R(-5)- was positively related to elevation (Spearman $\rho = 0.55$, $n = 45$, $P = 0.0001$). Sites with few or no temperatures $\leq -5^\circ\text{C}$ occurred at all elevations. Pika-occupied (blue diamonds), marginal (intermittently occupied: green triangles) and absent (open triangles and circles) sites overlapped greatly, with many unoccupied and formerly occupied sites similar to occupied sites in within-talus -5°C temperature exceedances.

Comparisons in relation to pika status at sites.—Pika status was negatively associated with warm aboveground temperatures and positively with elevation. Sites where pika were present averaged higher elevation and cooler aboveground than marginal sites, sites with old sign, or sites lacking any sign, in that order (Figure 4). Model comparison of ordinal logistic regression on factors related to pika status, in which pika status was ranked no sign < old sign < marginal < present, showed aboveground average warm season daily maximum temperature (T_{max}) to be the best single predictor examined (effect likelihood ratio chi-square 21.4, 1 df , $P < 0.0001$). Elevation and mean annual temperature also performed reasonably well ($\Delta AICc = 0.77$ and 2.10, respectively), although each was strongly correlated with T_{max} ($r = -.96$ and $.92$, respectively). Along with aboveground average cold season daily minimum temperature (T_{min} : $\Delta AICc = 8.8$), these four were the only factors related to pika status with $\Delta AICc < 10$.

Warm exceedances within talus did not effectively explain pika status (R_{20+} , $\Delta AICc = 17.6$; R_{24+} , $\Delta AICc = 18.9$). The direction of the effect of within-talus cold extremes ($R(-2.5)$ -, $\Delta AICc = 11.3$) on pika status was not as expected from a hypothesis of cold stress—more cold extremes were positively associated with pika presence—but was consistent with its correlation with air temperatures, including T_{max} . No quadratic effect was supported: pika presence was not maximized at intermediate values of cold exceedances within the limits of our study. The direction of the $R(-5)$ - effect also was not consistent with a cold stress hypothesis within our data set, and a quadratic effect was not supported.

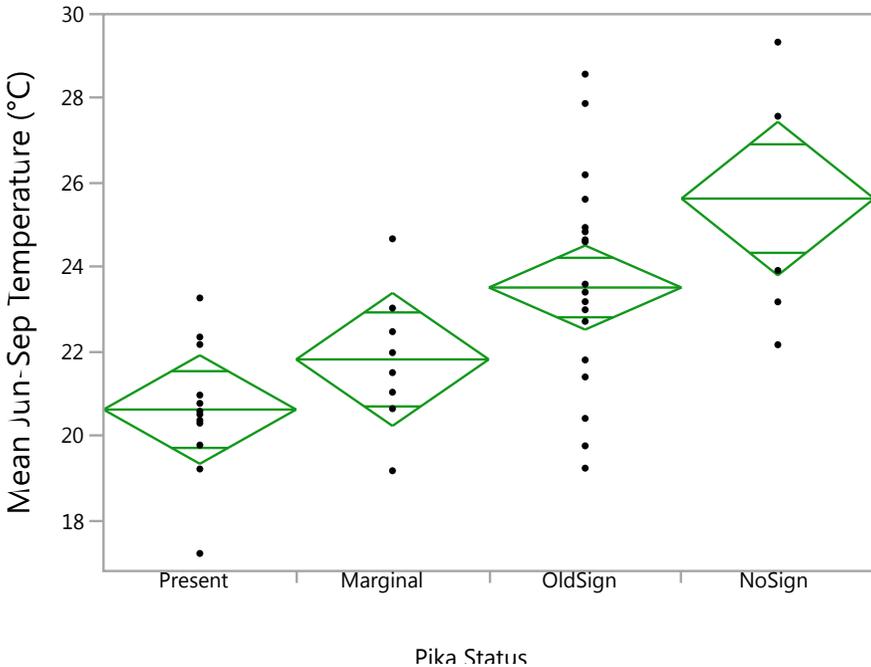


FIGURE 4.—Mean daily-maximum air temperature June-September during 2001-2010, from BCM (Flint et al. 2013) for each site, versus pika status at that site. Cooler daily maximum warm season temperatures were the best predictor of pika occurrence in our study (ordinal logistic regression, $\chi^2 = 21.4$, 1 df , $P < 0.0001$). Green diamonds center on the mean and extend vertically to the upper and lower 95% confidence limits of the mean; short internal horizontal lines show significant differences where not overlapping the internal lines of other diamonds. Dots show individual sites.

DISCUSSION

Soil acts to buffer deeper ground layers from variation in air temperature, and to an extent this has been proven true of talus as well (Millar et al. 2014b). The deeper one goes underground, the more variations in air temperature are buffered—first daily variations disappear, and ultimately annual variation is also smoothed to a constant value: the mean annual temperature of the site, barring geothermal effects (Hillel 1982). Pikas presumably are capable of exploring talus deposits to their very bottoms in many places, a freedom human researchers lack. Yet even at very modest depths within talus, typically less than 1 meter, we found substantial buffering of temperatures. We may presume pikas are capable of reaching depths within talus that are even more equable than we have documented. Remarkably, Smith et al. (2016) found pikas occurring at a site with summer within-talus temperatures (1 m depth) up to 30°C, albeit with some of the lowest feeding, haying, and other activity rates known for American pikas. The authors mention a possibility of subsurface permafrost at the site, which in combination with pikas' presumed ability to move deep within talus or lava formations, might explain toleration of such warm temperatures at intermediate depths of their talus refuge.

Even at the modest depths where we were able to place recorders, temperatures did not appear particularly challenging to pikas. Otto et al. (2015) estimated 28°C as the lower limit of the thermal neutral zone for resting pikas from Colorado and Wyoming, while MacArthur and Wang (1973) observed a mortality at this temperature. Moyer-Horner et al. (2015) suggested American pika activity would likely be restricted at temperatures above 20°C, due to the extra heat production of activity above resting metabolism, solar insolation, and the limited capability of pikas to shed that heat. All but two of our sites never reached 28°C within talus even at only 0.5-1 m depth, and nearly one-third of 45 sites sampled during 2011-2012 never reached 20°C within talus. Further, many of our sites are at elevations lower than/experience air temperatures higher than sites where pikas currently occur, yet had within-talus temperatures that were suitable for pikas. We did not observe evidence these equable within-talus temperatures were related to the rock-ice features discussed by Millar et al. (2014b) as contributing to pika resiliency. We believe rock-ice features, which retain year-round ice beneath the talus surface, are rare or absent in the "hot zone" of the lower elevational limit of pika distribution within our study area. Instead, equable within-talus temperatures in or below the hot zone were likely the result of the buffering effects of depth.

Amount of talus in the vicinity may be a factor that affects pika status at sampled taluses (Stewart and Wright 2012, Stewart et al. 2015), but seems unlikely to be the whole story. We elected to survey in and around Yosemite Valley and Lovers Leap/Horsetail Falls because there are large areas of talus present, more than is typically found at elevations below 2000 m. The abundance of talus there did not support pikas, even though temperatures within many of those taluses sampled were suitable; the lowest current pika occupancy we found in Yosemite was at 2352 m, and near Horsetail Falls was at 2029 m (marginal). We also know from old sign that, in the past, pika have reached and probably lived at many taluses we sampled. These taluses overwhelmingly still have moderate within-talus temperatures, yet are not currently occupied, suggesting that within-talus temperatures are not what excludes pikas from these locations. These findings echo those of Stewart et al. (2017), who found a large, apparently recently extirpated area of former pika occupation north of Lake Tahoe,

California, where air temperatures have become increasingly challenging for pikas.

The tendency of researchers to study microclimates—such as subsurface temperatures within talus—only where pikas occur may be responsible for unjustified optimism about pika resilience to climate change (Millar and Westfall 2010, Smith et al. 2016). Varner and Dearing (2014), based on more moderate within-talus temperatures at lower elevations, suggested that lower elevation taluses might even provide better climate change refugia than higher elevations. We found, however, by examining elevations below where pikas currently occur, that pikas have been present in the past at low elevation taluses but appear extirpated there now, despite generally suitable within-talus temperatures. These lower taluses have warmer aboveground climates. Lower and warmer yet, we found no evidence of pika occurrence at all, despite comparable below-talus temperatures, even in taluses that appeared to be within pika dispersal range (e.g., Yosemite Valley, Lovers Leap).

As opposed to within-talus temperatures, aboveground summer temperatures appear more relevant to pika occupancy in our region. Elsewhere we argued that, among available climatic variables, mean summer temperature had mechanistic appeal as an index of chronic summer heat stress (Stewart et al. 2015), and it was a strong explanatory factor in this study as well. Several authors have shown negative correlations of pika activity with ambient aboveground temperature (MacArthur and Wang 1974, Smith 1974, Moyer-Horner et al. 2015, Otto et al. 2015, Staff and O'Connor 2015). Warm aboveground temperatures may impair pikas' ability to forage or to disperse (Smith 1974, Wilkening et al. 2011), both essential activities contributing to reproductive rate and metapopulation persistence. Heat restricts foraging activity due to pikas' heat sensitivity and limited ability to shed body heat (MacArthur and Wang 1973, Otto et al. 2015). Moyer-Horner et al. (2015), based on a biomechanical heat flux model, estimated that American pika activity generally would be limited by ambient temperatures above about 20°C. Above this temperature, brief bouts of activity (as opposed to resting metabolism) might still be possible, but would generate body heat load that would have to be dissipated quickly to avoid stress and perhaps death. Mathewson et al (2017), exploring further the consequences of the same heat flux model, calculated under a "moderate" climate change scenario (mean western USA temperatures, summer +2.6°C, winter daily minimums +0.8°C) that by the year 2070 the American pika would be extirpated at 53 of 616 sites. A purely associative temperature model (i.e., not incorporating pika morphology, physiology or behavior) under the same conditions projected extirpation at more sites (69 of 616), the difference implying pika resilience—including use of the thermal refuge of talus—would reduce but not eliminate pika range retraction in the face of climate change.

Finding and establishing new territories is a potentially heat-sensitive period in the life of juvenile pikas. Svendsen (1979) reported that subadult American pikas near Gothic, Colorado, before they dispersed to find and establish their own territories, attempted to use "ephemeral home ranges" within their natal talus that sometimes overlapped adult territories. Territorial adults harassed them at times when the adults were active. Svendsen observed that subadults took advantage of times of day when adults were less active—prior to 0700 hours, during midday, and beyond dusk—to have greater use of these areas without harassment. Under conditions of high daytime air temperatures, subadult pikas might be less able to be active aboveground during the warmest midday hours, which could affect their ability to forage and avoid aggression by adults, and therefore to survive through the dispersal phase of their life cycle. In addition, subadult dispersal to new territories sometimes involves

movement through areas lacking thermal refugia such as deep talus, and if temperatures are too warm, dispersing individuals may be subjected to stress or mortality during this essential life stage (Smith 1974, Smith et al. 2016).

Within-talus winter cold stress has emerged repeatedly as another possible climate-related factor leading to pika extirpations (Beever et al. 2010, 2011, Erb et al. 2011, Ray et al. 2012, Yandow et al. 2015), but was not strongly supported as an explanation of pika occupancy in our study. Instead, we found colder within-talus temperatures correlated to higher pika occupancy within our scope of study. This correlation must not be taken too literally because pikas can no doubt access more equable places within talus than those where our loggers were placed—warmer during winters and cooler during summers. Nevertheless, low temperatures within talus—below our focal thresholds—were weakly less frequent with increasing mean air temperature and with decreasing elevation, which ran counter to a cold-stress hypothesis to explain the broad absence of pikas at our lowest, warmest sites.

Overall, our results indicate, in agreement with Mathewson et al. (2017), that the thermal refuge provided by talus is likely to be necessary and beneficial to American pikas, but sufficient only to partially offset the ongoing impacts of warming ambient temperatures on waning pika distribution.

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APPENDIX I.—Study sites.

Site	Latitude (°)	Longitude (°)	Years	Elevation (m)	Pika Status
Deadman M	39.6254	-120.5495	2010-2012	1923	Present
Sardine L. Uppr.	39.6086	-120.6310	2011-2012	1861	NoSign
Sierra Buttes	39.5997	-120.6402	2011-2012	2225	NoSign
Sierra City NE	39.5760	-120.6220	2011-2012	1489	NoSign
Hwy.80 nr.border	39.4368	-120.0288	2011-2012	1662	NoSign
Carpenter Ridge	39.4170	-120.3183	2011-2012	2595	Present
Donner W_14	39.3219	-120.4100	2010-2013	2008	OldSign
Donner E	39.3140	-120.3233	2010-2012	2187	Marginal
Cisco Butte NW	39.3101	-120.5632	2011-2012	1911	NoSign
Hwy.89 Bridge 6	39.2279	-120.2005	2011-2012	1880	OldSign
Mt. Watson 2	39.1875	-120.1877	2011-2012	2267	OldSign
Mt. Watson 1	39.1844	-120.1855	2011-2012	2248	OldSign
Big Bear	39.1619	-120.1825	2011-2012	2022	OldSign
Eagle Fls. 4	38.9537	-120.1134	2010-2013	1905	OldSign
Eagle Fls. 20	38.9473	-120.1172	2011-2012	2150	OldSign
Eagle Fls. 15	38.9470	-120.1197	2011-2012	2108	Present
EagleFls_100	38.9467	-120.1248	2010-2012	2157	Marginal
Eagle Lk.	38.9414	-120.1245	2010-2012	2160	Present
Velma Lk. Lower	38.9409	-120.1459	2010-2012	2382	OldSign
Mt. Tallac	38.9048	-120.0984	2010-2013	2933	Present
Heather Lk. Blw, S	38.8755	-120.1294	2010-2012	2363	Present
Heather Lk.	38.8745	-120.1365	2010-2012	2454	Present
Heather Lk. Below	38.8727	-120.1244	2010-2013	2311	Present
Echo Lk. S	38.8331	-120.0561	2010-2012	2336	Present
Pyramid Ck. E	38.8285	-120.1223	2011-2012	2126	Marginal
Twin Bridges NNE	38.8282	-120.1166	2011-2012	2364	Marginal
Pyramid Ck. SE2	38.8267	-120.1212	2011-2012	2060	Marginal
Hogback LL3	38.8050	-120.1375	2011-2012	1781	OldSign
American R., S fork	38.8028	-120.1392	2011-2012	1778	OldSign
Lovers Leap 2	38.8007	-120.1358	2011-2012	1838	OldSign
Hwy.89 WM	38.7926	-119.9671	2011-2012	2352	OldSign
Carson R. W	38.7633	-119.8519	2011-2012	1870	Marginal
Round Top	38.6435	-119.9891	2010-2012	2348	Present
Mosquito Lk. NW	38.5189	-119.9203	2011-2012	2530	Marginal
Pacific Gr. Summ. 10	38.5147	-119.9074	2010-2012	2452	OldSign
Calif. Falls N	37.9176	-119.4379	2011-2012	2396	Present
McGee Lk.	37.9014	-119.4311	2011-2012	2471	Present
HalfDome,CloudsR	37.7589	-119.5284	2011-2013	1394	OldSign
Bunnell Pt.	37.7454	-119.4652	2011-2013	2092	OldSign
Bunnell Crossing	37.7428	-119.4607	2011-2013	2020	OldSign
Moraine Dome	37.7412	-119.4763	2011-2013	1956	OldSign
Merced Lk. Camp	37.7410	-119.4098	2011-2013	2227	Marginal
Nevada Fall, Tr.Blw.	37.7269	-119.5354	2011-2013	1641	OldSign
Vernal Fall Tr.	37.7265	-119.5539	2011-2013	1360	OldSign
El Capitan SW	37.7233	-119.6543	2011-2013	1278	NoSign
Bridalveil E	37.7206	-119.6448	2011-2013	1208	OldSign