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Thermal components of American pika habitat—How does a small lagomorph encounter climate?

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A B S T R A C T

Anticipating the response of small mammals to climate change requires knowledge of thermal conditions of their habitat during times of the day and year when individuals use them. We measured diurnal and seasonal temperatures of free air and of six habitat components for American pikas (*Ochotona princeps*) over five years at 37 sites in seven mountain ranges in the western Great Basin, United States. Talus matrices (subsurfaces) had low daily variances and, in the warm season, remained cool during the hottest times of the day relative to surfaces and free air. During winter, matrices were warmer than free air. Talus surfaces were warmer than free air in the warm and cold seasons, and had large daily variances. Summer forefield and dispersal environments were warmest of all habitat components. Talus surfaces in summer were highly responsive to solar radiation over the course of the day, warming quickly to high midday temperatures, and cooling rapidly in the evening. By contrast, matrices lagged the daily warm-up and remained warmer than free air at night. These differences afford diurnal and seasonal opportunities for pikas to adapt behaviorally to unfavorable temperatures and suggest that animals can accommodate a wider range of future climates than has been assumed, although warming of the dispersal environment may become limiting. Climate envelope models that use or model only surface air measures and do not include information on individual thermal components of pika habitat may lead to errant conclusions about the vulnerability of species under changing climates.

INTRODUCTION

The effect that climate change will have on species depends on how individuals encounter daily weather over the course of their lives. Influencing factors include species longevity, mobility, dispersal capacity, behavioral plasticity, and social structure, as well as habitat characteristics. Because most species use a diversity of microhabitats for their daily and seasonal activities, the corresponding microclimates of these habitat components, and the way those respond to regional climate change, will influence survival of individuals and, ultimately, populations. An accurate climate envelope for a species should

reflect the cumulative conditions encountered in all habitat components and, thus, should include all relevant microclimates. Because of the differences in the way organisms encounter weather, even species with identical geographic ranges can have very different climate envelopes depending on how they partition and use microhabitats (Gordon et al., 1968).

Assessments of species' vulnerability to climate change, by contrast, commonly use projections of free-air temperatures without taking habitat components into account. To the extent that free-air temperature correlates with microhabitats, these can be useful proxies. As components of habitat

become decoupled from free air, however, proxies become less meaningful. Fuller understanding of responses to climate change, and better anticipation of future responses, requires knowledge of conditions in each tessera of the habitat mosaic.

American pikas (*Ochotona princeps* Richardson) are small generalist herbivores that inhabit patchily distributed, rocky landforms of mountains in western North America (Smith and Weston, 1990). Relatives of rabbits and hares (Order Lagomorpha), pikas tolerate cold climates through a combination of microhabitat selection and physiological adaptations that also renders them sensitive to direct heat, with lethal temperature only a few degrees above body temperature (MacArthur and Wang, 1973; Smith, 1974b). Pikas do not hibernate, and they spend winters active near stores of vegetation (“haypiles”) that they collect during the warm season. While snow typically insulates talus and haypiles in winter, decreasing snowpacks expose haypiles to extreme cold, which is another potential stressor (Beever et al., 2010). These sensitivities, coupled with low reproductive rate, poor dispersal capability, low population density, and use of scattered mountain habitat, have raised concern for the persistence of pikas in the face of warming climates (Beever et al., 2003, 2011). While pika populations persist in the major cordillera of the Cascade Range, Sierra Nevada, and Rocky Mountains (Hafner, 1994; Millar and Westfall, 2010; Erb et al., 2011; Stewart and Wright, 2012), some warm-margin and isolated populations in the Great Basin are declining rapidly (Beever et al., 2003, 2010; Wilkening et al., 2011).

Pika habitat is partitioned into distinct above- and below-surface components (described in the next section). While prior studies have begun to dissect the relationship of talus internal thermal regimes to pika physiological and behavioral constraints, key components of pika habitat have been ignored. In particular, little is known about seasonal temperatures at haypiles, talus surfaces, and dispersal environments. In the current study, we sought to improve understanding of thermal conditions and thresholds for key components of pika habitat as they relate to pika life history. In addition, we assessed thermal relationships of pika habitat relative to free-air temperature, commonly used to project vulnerability to future climate change. We asked the following questions: Do thermal regimes of pika

habitat components differ from free air (decoupled), and, if so, do they afford refuge from temperature extremes? How do temperatures in pika dispersal areas differ from those in their primary habitat components? How do these relationships differ diurnally and seasonally? Is surface air temperature a reliable proxy for the climate envelope of pikas?

PIKA HABITAT COMPONENTS AND PRIOR REPORTS ON THERMAL RELATIONS

Pikas’ primary habitat is talus or similar fractured-rock landforms having coarse, open, and deep matrices (interstices below the surface). Pikas are considered talus-dependent, in that they live, breed, and reproduce in talus. Talus habitat can be subdivided into elements used by pikas. Pikas are active on the talus surface during the daytime. They take refuge from predators or severe weather in the talus matrix. Haypiles are often located under a large boulder or distinct configuration of rocks; matrices below haypiles appear to be not as deep as other parts of talus fields (personal observation). While pikas will forage opportunistically within the talus, they more often foray a few meters into adjacent forefields, which are vegetated with forbs and/or shrubs (Huntly et al., 1986). A final habitat component is the dispersal environment, which is the ground surface between talus slopes. In some situations, taluses are close together and the dispersal environment is small, in others, taluses are disjunct and dispersal areas are large. Pikas have been observed to disperse ~3 km (Tapper, 1973), which sets a threshold on effective dispersal distance; more commonly, pikas disperse far shorter distances, <300 m (Smith, 1974a; Smith and Ivins, 1983; Smith, 1987).

Talus matrices have been the focus of limited prior thermal monitoring (MacArthur and Wang, 1973; Beever et al., 2010; Wilkening et al., 2011; Henry et al., 2012). These studies concluded that talus matrices in summer were cooler than surfaces during middays and afternoons, warmer at night, and had attenuated extremes relative to talus surfaces. Winter conditions have been less monitored: whereas talus temperatures were buffered when snow-covered, when snow-free, their cold extremes were similar to free air (Beever et al., 2010; Wilkening et al., 2011). Our prior in-

tensive study of talus surface, matrix, and forefield thermal regimes, conducted over three years in the Sierra Nevada for eight pika habitats, gave systematic information on a subset of components (Millar et al., 2014). Seasonal patterns were apparent: summer matrix temperatures were cool and attenuated relative to the talus surface and free air; forefields were cool on average, but had high diurnal fluctuations. Coolest talus positions were at the base of the slope adjacent to the forefield. In winter, the base of the talus was snow-covered longer than the upper talus and maintained greater protection against extreme winter cold. Seasonal decoupling of matrix from free-air temperatures and lag effects of surface-matrix were suggested as contributing to pika habitat quality.

While prior studies have begun to dissect thermal regimes, haypile positions and dispersal environments in particular have not been investigated. Increasing temperature of dispersal environments has been implicated as a contributing factor for population extirpation: Smith (1974a) observed that distances >300 m (or 200 m in Smith, 1979) posed difficult barriers for dispersal under warm locations of the Bodie Mountains, California, relative to cooler locations, such as high elevation sites in the Sierra Nevada, where pikas dispersed as far as 2 km (Peacock, 1997). Dispersal is further challenged by conditions of daytime heat in that pikas are primarily diurnal, whereas other small mammals that use the same dispersal environments, such as *Neotoma* spp., benefit from a nocturnal habit, thus moving routinely during cooler nighttime conditions (Smith, 1974a). Pikas are philopatric and disperse only if natal talus is unavailable (i.e., fully occupied by existing animals; Smith and Ivins, 1983); most commonly juveniles disperse (Smith, 1987), and dispersal occurs during the warmest time of year, midsummer through early autumn (Tapper, 1973; Smith and Ivins, 1983; Smith, 1974a, 1987). In recognizing that metapopulation persistence depends on ongoing recolonization among talus patches, and that increasing temperature of the dispersal environment reduces the distance over which dispersal is successful, Smith (1974b, p. 1375) concluded that “temperature apparently is the primary environmental factor contributing to initial success of dispersing juveniles.”

METHODS

Study Sites, Habitat Components, and Temperature Monitoring

We conducted the study at 37 locations in the western Great Basin, California and Nevada, United States (Fig. 1, Table 1). Study sites were centered on a talus, eroding bedrock, or lava flow landform (hereafter, “talus”) that was either currently occupied by pikas (34 sites) or potentially extirpated during the course of our study (3 sites; Table 1). Of the 37 sites, we consider 34 to be distinct pika metapopulations, with groups of talus patches separated from adjacent talus groups by ≥ 3 km distance. The sites extend across 1.5° latitude, 2.9° longitude, 1468 m elevation, and seven mountain ranges. We observed annual occupancy and scored sites as extant by the presence of haypiles with green vegetation, pika sightings, and vocalizations.

Temperature was measured for six components of pika habitat: haypile surface (on the vegetation); haypile matrix (~0.5–1 m within talus below the haypile); talus surface (>10 m from the haypile but in the same talus and near the lower border of the talus); talus matrix (~1 m below the surface position); talus forefield (ground surface ~2 m in front of the lower talus border); and dispersal environment (ground surface ~25 m from the talus, positioned toward the nearest suitable talus habitat). In addition, we measured free-air temperature at 2 m height, with thermochrons attached on the north side of trees. Eight sites were the same as those used in our prior talus thermal study (Millar et al., 2014); these had the most comprehensive monitoring in the present study. Due to access and time constraints, not all sites had the same number and type of monitoring positions (Table 1).

We measured temperature with Maxim (www.maxim-ic/products/ibutton) DS1921 and 1922 iButton thermochrons, following methods of Millar et al. (2014), programming instruments to record at 4-hr intervals starting at noon on the day they were deployed. All thermochrons were inserted into white PVC T-fittings, which had openings to allow air-flow; iButton locations were shaded from direct sun by shrubs, tree canopy, or rock cover. Dispersal iButtons were deployed in midsummer 2012; iButtons at other positions were deployed in midsummer 2009. Data were downloaded and instruments

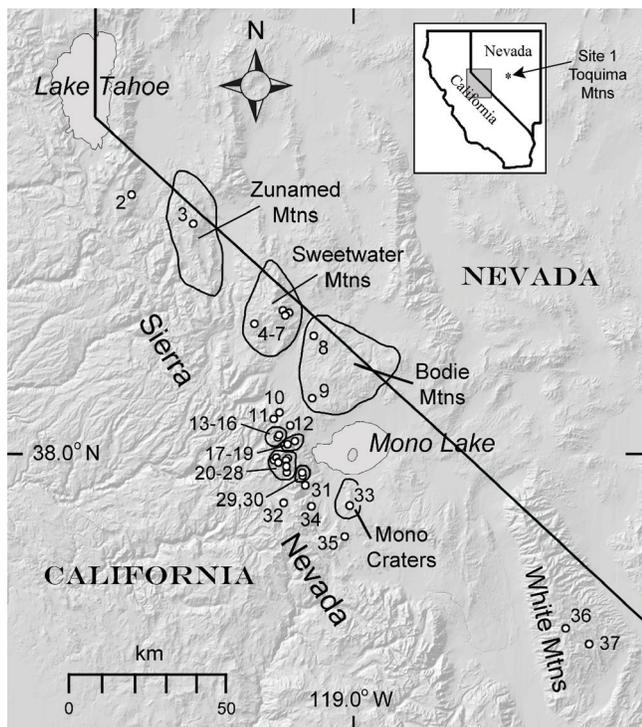


FIGURE 1. Map of the study region, with monitoring locations and mountain ranges. Numbers correspond to site labels in Table 1. Inset shows location of the main map (shaded box) and Site 1, Toquima Mountains, which is outside the main map.

reprogrammed annually or biannually until October 2014, when the study was terminated.

Analyses

Temperature analyses were calculated for habitat components and free-air temperature across all years of available data, annually and seasonally. For seasonal and annual analyses, daily mean temperatures and standard deviations were calculated from the seven (4-hr interval) thermochron daily measurements, and from these, seasonal and annual means were computed. Seasons were designated by dates that represent regional and talus conditions rather than conventional intervals: summer (1 June–30 September), autumn (1 October–31 December), winter (1 January–31 March), and spring (1 April–31 May), following Millar et al. (2014). We conducted a mixed-model analysis of variance (ANOVA) on means and standard deviations of habitat positions for extant sites by location and season (JMP; SAS Institute, 2015). Because the data

were highly imbalanced (Table 1), we limited the full model ANOVA to the haypile surface, haypile matrix, and dispersal positions. Analysis methods for temperature patterns for the free air, forefield, and talus surface and matrix were presented in Millar et al. (2014). The model included latitude and elevation as covariates (where the parameter for elevation reflected mean annual lapse rate), and habitat position, season, aspect, and substrate color (dark, medium, light) as fixed effects. Included in the model were two-way interactions (higher-order interactions were nonsignificant), including those with elevation (heterogeneity of slopes).

To obtain seasonal lapse rates for each measurement position, we ran ANOVAs by season and extracted appropriate rates for habitat positions. To evaluate multivariate temperature differences among locations, we ran principal components analysis (PCA) of absolute and mean minima and maxima and mean temperatures for January and July for the surface and matrix positions (SAS Institute, 2015). For the purpose of this analysis, we combined the talus surface with the haypile surface and talus matrix with haypile matrix positions. Joint temperature differences among locations will create covariances among temperature variables, and principal components (PCs) will reflect those joint differences. We also tested paired differences in daily temperatures between positions to determine the uniformity of these differences over time periods. However, we found that daily temperatures were highly auto-correlated, persistent, and long-memory, effectively resulting in repeated data. So we first fit the data with an autoregressive, moving average (ARMA) model, and then used the predicted ARMA values as weights in pairwise tests. ARMA modeling and paired tests were done in JMP (SAS Institute, 2015).

To better understand the role of topographic influence on temperature of pika habitats, and the possibility of future cool-climate refugia (Millar et al., 2014, 2015), we analyzed the relative strength of cold-air pooling (CAP) for each site. We intersected in geographic information system (GIS) (ESRI, 2011) talus locations with CAP values that have been calculated across the Sierra Nevada by Curtis et al. (2014, GIS rasters). Index values are 1.0 (strong CAP), 0.5 (uncertain CAP), and 0.0 (no CAP; Lundquist et al., 2008). To compare differences between PRISM-modeled data (commonly used in projections of future tem-

peratures) and observed values at the pika sites, we first adjusted 800-m grid PRISM data (Daly et al. 1994) for the difference of the tile elevation and that of the talus location by the PRISM location-specific lapse rate (as in Millar and Westfall, 2010). Then we computed differences between observed January and July maximum and minimum talus position temperatures and adjusted PRISM values.

RESULTS

We recovered temperature records for 43 haypile surfaces and matrices (33 sites), 16 forefields (8 sites), 18 non-haypile talus surface and matrix positions (10 sites), 78 dispersal positions (21 sites), and 11 free-air positions (10 sites) (Table 1). Temperatures were warmest on southern aspects and coolest on northern. Temperatures decreased most rapidly with elevation in the dark and medium-colored substrates; dark and medium-colored substrates were significantly warmer than light substrates at low elevations (10 °C vs. 6 °C; $p < 0.001$), but not at high elevations. Dispersal positions were significantly warmer than the matrix positions (4.7 °C vs. 3.9 °C; $p < 0.001$). The elevation*position interaction was not significant ($p = 0.08$), but temperature decreased most rapidly with elevation at the dispersal positions. Temperatures decreased most rapidly with elevation in the spring. Diurnal variances in temperature for all habitat positions decreased with increasing elevation and were highest on south and west aspects. Light-colored substrates had lowest diurnal variances.

In the principal components analysis, the first three components composed 75% of the variation. In this PCA, locations with high PCA scores tend to have high values for variables highly and positively correlated with a PC and low values for those negatively correlated and vice versa for those locations with low negative scores. In the first component (43% of variation), the highest correlations (mostly $r > 0.9$, and positive for the first two components) were for summer minimum matrix temperatures, mean temperatures in the matrix and haypile/talus surfaces, and late summer mean maximum matrix temperatures. Locations with high scores in PC1 included Chemung, Lower Star City, Lundy S, and Lee Vining S, whereas locations with low negative scores were Virginia Lks Canyon (all sites), and Pine Creek. Correlations were low and nonsignificant in

early winter and increased in late winter. In the second principal component, correlations were highly positive in mean and minimum winter temperatures and weakly negative in summer maxima for haypile matrices and surfaces. Highest positive scores were to Warren Fork Canyon (E Fk and Confluence) and Saddlebag (Main), and low negative scores were to County Line Hill (White Mountains), and Mono Craters. Correlations in the third component were moderate ($r > |0.6|$), with the highest correlations negative for summer minimum temperatures for surfaces and matrices and positive for autumn/winter maximum temperatures for the talus/haypile surfaces. Locations with high scores in PC3 were Obsidian Dome, Saddlebag Lk, Virginia Lks Cyn (Moat Lake and Moat Trail, Blue Lk Low), and Warren Fork Cyn, and those with low negative scores were Carson Pass, Lundy Cyn (Main Talus N and Lake Cyn Trail), Parker Lk Trail, and County Line Hill. Correlations noted were highly significant ($p < 0.001$).

Means and standard deviations calculated for the periods of record varied by habitat component and season (Table 2). During summer, the temperature ranks, from coldest to warmest, trended as: talus matrices < free air < forefield < dispersal area < haypile and talus surfaces. Differences between the warmest and coldest means were 2.1–2.8 °C (significant at $p < 0.0001$). Large differences in standard deviation (SD) occurred for all elevations: talus matrices had the lowest SDs (1.9 °C), and dispersal areas had the highest (7.2 °C). Free air, and the haypile and talus surfaces, had intermediate variability.

Winter temperatures had different patterns, with trends from coldest to warmest position varying by elevation. At low elevations, free-air temperatures were warmer than all talus and ground positions except the dispersal area; at middle and high elevations, free-air temperatures were coldest. Matrix temperatures averaged warmer than surfaces. Free air and dispersal area had the highest SDs, ranging 3–20 times larger than other positions.

Spring and autumn mean temperatures had values and trends intermediate to summer and winter patterns. Annual means, averaged over the periods of record, of both ground-level positions (forefield and dispersal area) were warmer than free air and warmer than haypile and talus positions.

Seasonal relationships are illustrated by 5-yr graphs from representative low-, mid-, and high-elevation sites

TABLE 1

Study site locations, with habitat components assessed, occupancy status, and cold-air pooling values (based on Lundquist et al., 2008, and data from Curtis et al., 2014). Locations are ordered from north to south.

Location	Mountain range	Map code ¹	Occupancy status ²	Sample sizes by habitat component ³				Elev (m)	Elev zone ⁴	Aspect	Cold air pooling ⁵
				Haypile	Non-haypile	Forefield	Dispersal				
Pine Creek	Toquima	1	O	S(2), M(2)		4	2	3292	H	S	NA ⁶
Carson Pass, Woodfords	Sierra Nevada	2	O	S, M				1837	L	N	1.0
Monitor Pass, Leviathan Pk	Zunnamed	3	O	S, M				2686	M	S	0.0
Ferris	Sweetwater	4	O	S		2		3136	H	E	0.0
Lower Star City	Sweetwater	5	O	S, M		3		2602	M	S	0.0
Upper Star City	Sweetwater	6	O	S, M		3		2836	M	E	0.0
Electronic Site	Sweetwater	7	O	S(2), M(2)		3		2950	M	E, W	0.0
Chemung Mine	Bodie	8	E	S, M		3		2528	L	S	0.0
SR 270	Bodie	9	E	S, M				2202	L	S	0.0
Green Cr Cyn, Moraine	Sierra Nevada	10	O	S, M		3		2665	M	S	0.0
Green Cr Cyn, Main Talus	Sierra Nevada	11	O		S(2), M(2)	2	1	2586	M	S	1.0
Benjamin Buttes	Sierra Nevada	12	O	S(2), M(2)		3		2801	M	N, S	0.5
Virginia Lks Cyn, Moat Lk	Sierra Nevada	13	O	S, M				3190	H	S	0.5
Virginia Lks Cyn, Moat Trail	Sierra Nevada	14	O	S, M				3182	H	S	0.5
Virginia Lks Cyn, Blue Lk Low	Sierra Nevada	15	O	S, M				3059	M	S	1.0
Virginia Lks Cyn, Main Talus	Sierra Nevada	16	O		S(2), M(2)	2	1	3158	H	N	1.0
Lundy Main Talus S	Sierra Nevada	17	O	S(2), M(2)		2	1	2371	L	S	1.0
Lundy, Lake Cyn Trail	Sierra Nevada	18	O	S, M				2387	L	N	1.0
Lundy Main Talus N	Sierra Nevada	19	O	S(2), M(2)		2	1	2401	L	N	1.0
Warren Fork Cyn, Main Talus	Sierra Nevada	20	O	S(2), M(2)		2	1	3206	H	S	0.5
Saddlebag Lk, Main Talus	Sierra Nevada	21	O	S(2), M(2)		2	1	3119	H	S	0.5
Greenstone Lk, Main Talus	Sierra Nevada	22	O	S(2), M(2)		2	1	3093	H	N	1.0
Warren Fork Cyn, E Fork	Sierra Nevada	23	O	S, M				3064	H	E	0.0
Saddlebag Lk, Trail E	Sierra Nevada	24	O	S, M				3099	H	W	1.0
Warren Fork Cyn, Confluence	Sierra Nevada	25	O	S, M				3005	M	S	0.5
Saddlebag Lk, Trail W	Sierra Nevada	26	O	S, M				3091	H	E	0.5

TABLE 1
(Continued)

Location	Mountain range	Map code ¹	Occupancy status ²	Sample sizes by habitat component ³					Aspect	Cold air pooling ⁵	
				Talus		Forefield	Dispersal	Air			Elev zone ⁴
				Haypile	Non-haypile						
Warren Fork Cyn, Gardisky C	Sierra Nevada	27	O	S, M				2922	M	SE	0.0
Ellery Lake	Sierra Nevada	28	O	S(2)		3		2944	M	S	0.0
Lee Vining Cyn, S	Sierra Nevada	29	O	S, M				2305	L	S	0.0
Lee Vining Cyn, Main Talus	Sierra Nevada	30	O	S, M	S(2), M(2)	2	1	2319	L	N	1.0
Gibbs Cyn	Sierra Nevada	31	O	S, M		3		2837	M	N	0.0
Kuna Lake	Sierra Nevada	32	O	S				3305	H	SE	1.0
Mono Craters	Mono Craters	33	O	S, M	M		2	2573	L	S	0.0
Parker Lk Trail	Sierra Nevada	34	E	S, M				2546	L	N	1.0
Obsidian Dome	Sierra Nevada	35	O	S, M	M		2	2491	L	SW	1.0
County Line Hill	White	36	O	S(4), M(4)		6	1	3207	H	W	0.0
Roberts Ranch	White	37	O	S, M				2466	L	S	1.0

¹Refer to Figure 1 for map codes.

²O = occupied; E = potentially extirpated during the course of the study.

³S = surface (haypile or talus); M = talus matrix. Numbers indicate the number of haypile, talus (1.0 m below talus surface), forefield (ground), dispersal (ground), and air (2.0 m above ground) iButtons deployed at each site. In the case of haypiles, the values refer to the number of individual haypiles monitored as well. Empty cells indicate no iButtons deployed; for surface and matrix positions, where no number is added, only one iButton was deployed.

⁴Low (L, <2580 m); Mid (M, 2580–3060 m); High (H, >3060 m).

⁵Cold-air pooling (CAP) values: 1.0 is strong CAP; 0.5 is uncertain CAP; 0.0 is no CAP.

⁶CAP values not available for central Nevada.

TABLE 2

Annual and seasonal temperature and diurnal standard deviation means (°C) for 37 pika sites by habitat component and elevation zone. Contrasts between means are significant ($p < 0.001$) where differences are $\geq |1|$ °C.

Elevation zone	Free Air		HP Surface		HP Matrix		Talus Surface		Talus Matrix		Talus Forefield		Dispersal	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
(1) Low elevation (<2580 m; 12 sites)														
Summer	16.70	4.41	17.30	4.79	15.74	2.18	18.18	4.81	16.63	1.51	17.88	6.39	17.51	7.52
Autumn	2.89	3.52	1.74	2.55	2.01	1.20	2.36	2.47	2.39	0.95	2.02	2.83	2.44	4.86
Winter	0.39	3.49	-0.67	1.61	-0.51	0.77	-0.51	1.26	-0.23	0.54	-0.18	1.48	0.64	3.59
Spring	7.55	3.95	6.64	3.72	5.71	1.78	7.14	3.81	6.30	1.52	8.46	5.62	8.80	7.46
Annual	6.88	3.85	6.25	3.17	5.74	1.48	6.79	3.09	6.27	1.13	7.04	4.08	6.94	5.87
(2) Mid elevation (2580–3060 m; 12 sites)														
Summer	14.15	6.07	15.77	4.77	14.50	2.42	16.09	3.76	13.48	1.15	14.52	5.47	14.88	7.09
Autumn	0.91	4.62	1.54	2.61	1.45	1.39	1.51	1.91	1.49	0.56	0.28	2.55	1.81	4.27
Winter	-1.73	4.34	-0.86	1.20	-0.93	0.66	-0.14	0.58	0.22	0.21	-1.25	0.50	-0.21	2.13
Spring	5.48	5.21	4.24	2.92	3.33	1.61	5.62	2.62	3.87	0.84	4.71	3.82	5.73	5.22
Annual	3.46	3.54	4.87	2.77	4.54	1.51	5.07	2.54	4.20	0.80	4.64	3.11	5.13	4.70
(3) High elevation (>3060 m; 13 sites)														
Summer	10.73	3.52	13.13	4.26	12.99	3.02	11.90	4.70	10.39	1.36	10.70	5.69	12.53	6.86
Autumn	-1.33	2.86	0.11	2.40	-0.03	1.53	-0.35	1.84	-0.06	0.55	0.71	2.49	-0.17	3.72
Winter	-4.31	2.89	-2.02	0.62	-2.14	0.35	-1.27	0.26	-0.84	0.09	-0.68	0.33	-2.27	0.94
Spring	1.07	3.27	1.55	1.80	1.10	1.18	0.69	0.91	0.55	0.29	0.71	1.04	2.33	3.41
Annual	1.54	3.13	3.19	2.27	2.98	1.52	2.75	1.93	2.51	0.57	2.86	2.39	3.10	3.73

for haypile and talus surface, talus matrix, and dispersal positions (Fig. 2). During the warm season, the pattern of temperature attenuation and cold aspect of the matrices relative to the haypile/talus surfaces was expressed at all sites, with the contrast especially marked at low elevation Obsidian Dome. Haypile surface temperatures often reached maxima $>30\text{ }^{\circ}\text{C}$ during the warm season. Dispersal zone temperatures had highest temperatures of all positions, with absolute maxima exceeding $40\text{ }^{\circ}\text{C}$, even in the high elevation sites. Winter temperature series for the same sites illustrate that haypile surface and

matrix positions, by contrast to summer, were similar, and both positions had attenuated extremes relative to free-air and ground locations (Fig. 2). In some years winter temperatures flat-lined near $0\text{ }^{\circ}\text{C}$ ($<1\text{ }^{\circ}\text{C}$ daily fluctuation), interpreted as snow-covered (Millar et al., 2013, 2014); in other years, substantial temperature fluctuation suggested little or no snow cover at these positions. As with talus surfaces and matrices, haypile temperatures settled into winter equilibria below $0\text{ }^{\circ}\text{C}$ early in winter (Millar et al., 2014). In contrast, when snow-covered, dispersal locations remained near $1\text{ }^{\circ}\text{C}$,

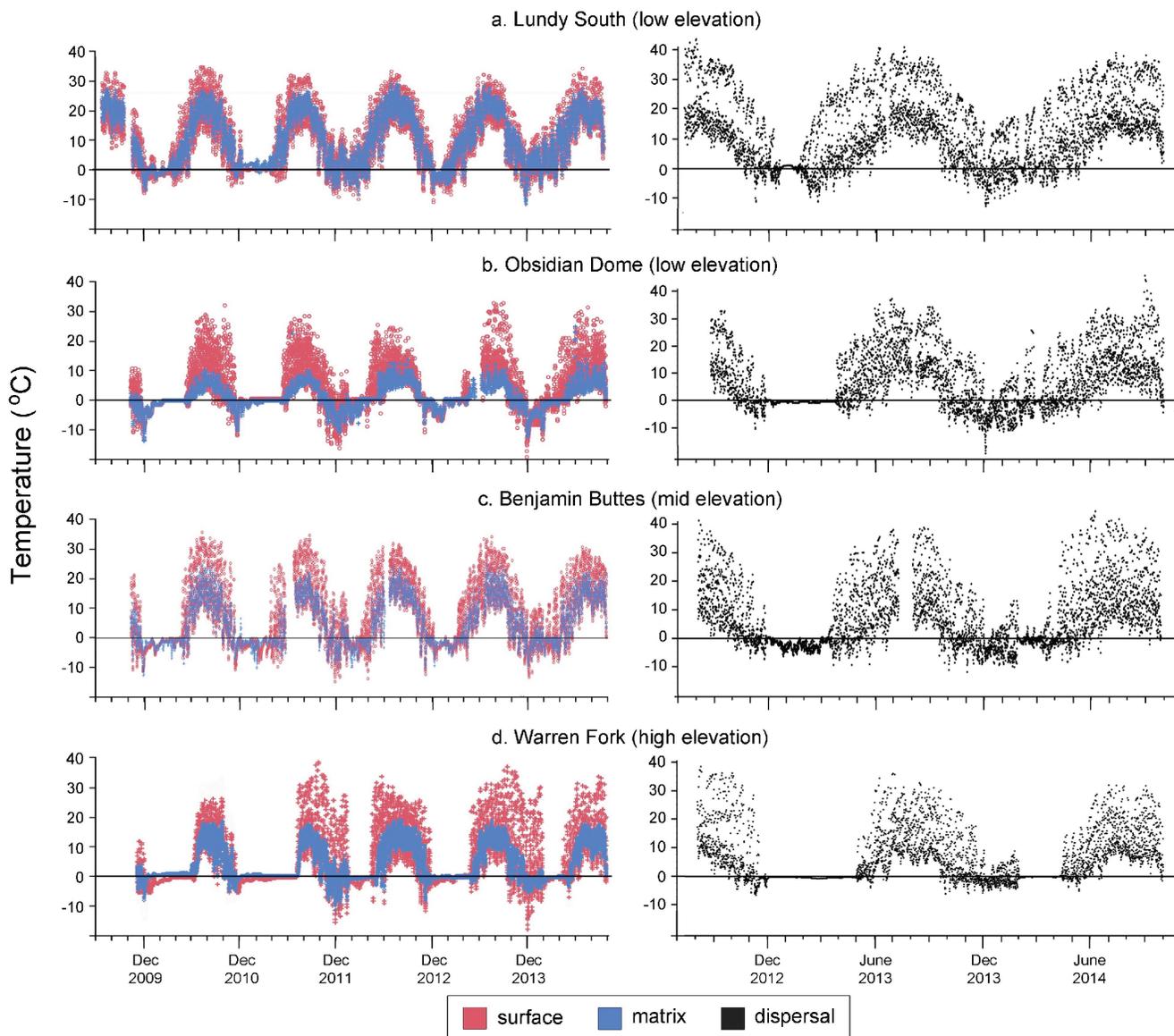


FIGURE 2. Temperature time series for periods-of-record; haypile surfaces versus talus matrices (left graphs), and dispersal areas (right graphs) at representative low, mid-, and high elevation sites. (a) Low elevation: Lundy South (2371 m); (b) low elevation: Obsidian Dome (2491 m); (c) mid-elevation: Benjamin Buttes (2801 m); and (d) high elevation: Warren Fork (3206 m).

as expected for soil surface temperatures (Lundquist and Lott, 2008). During snow-free periods, acute minimum temperatures on the talus surfaces fell below -15°C .

The extent of mean versus extreme thermal stress is further illustrated by scatter plots of mean and absolute daily extreme temperatures, which represent regional and seasonal climate envelopes for these habitat components. Mean maximum temperatures in summer (Fig. 3, parts a, c, and e) underscore that many extant sites exceeded 28°C (considered a thermal threshold; MacArthur and Wang, 1973; Beever et al., 2010) for all positions except talus matrices; dispersal areas had the warmest mean maximum temperatures. By contrast, win-

ter matrix mean minima were warmer than haypile surfaces and ground positions (Fig. 3, parts b, d, and f). In absolute extreme temperatures, many sites had haypile surface temperatures, but far fewer matrix or free-air temperatures, that exceeded 35°C in summer (Fig. 4, parts a, c, and e). Dispersal areas at many sites had extreme summer heat, exceeding 35°C , with some days warmer than 45°C . Winter absolute extremes indicate that matrix temperatures were a subset of the distribution of talus surface temperatures, with many sites reaching cold extremes below -5°C (considered a thermal threshold; Beever et al., 2010), and some below -25°C , mirroring cold extremes of free air (Fig. 4, parts b, d,

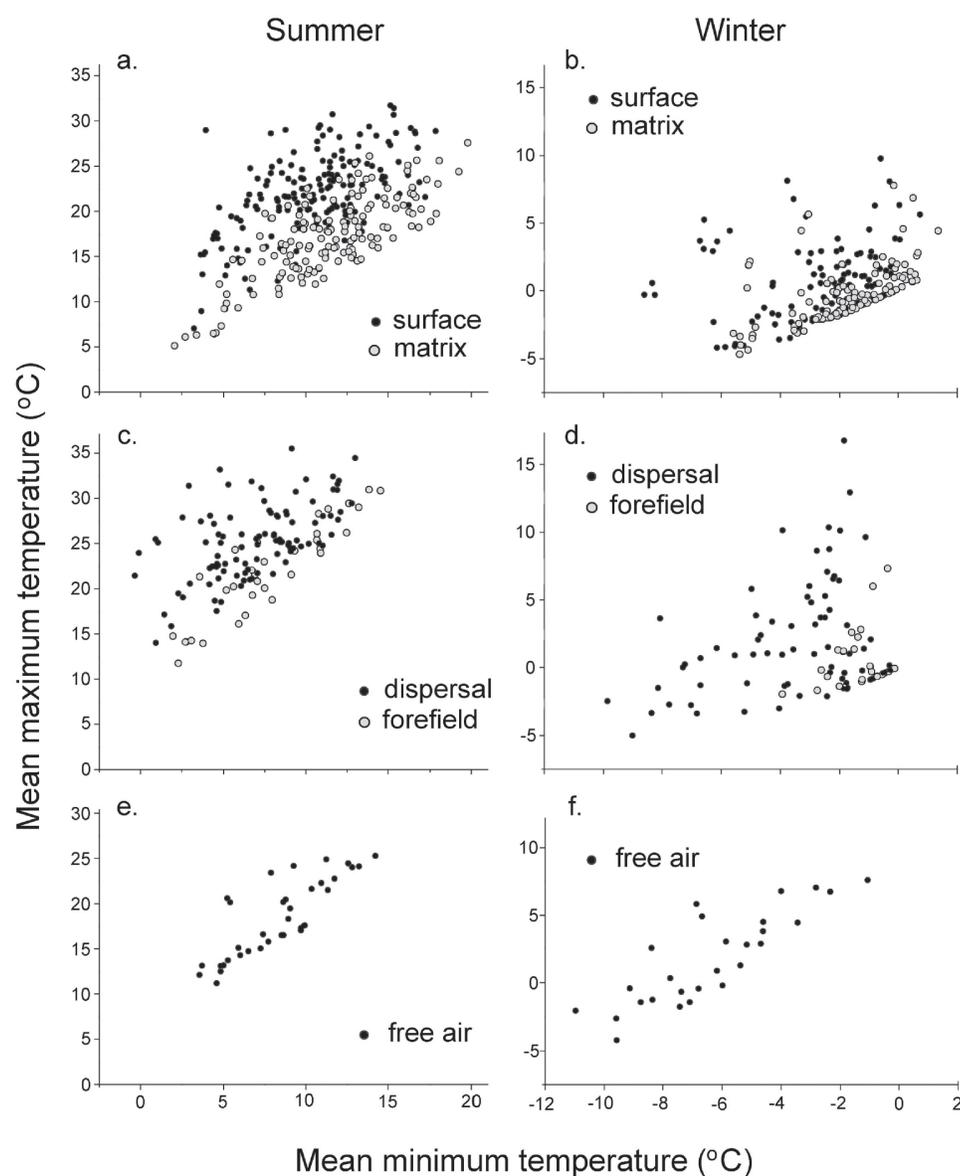


FIGURE 3. Mean minimum and maximum temperatures over the period of record for habitat components by season over all sites for (a, c, and e) summer and (b, d, and f) winter. (a and b) Haypile surface and matrix. (c and d) Dispersal and forefield. (e and f) Free air. Plots are generated as the mean extreme value for each month of summer or winter, by site and habitat component, over the period of record.

and f). The three potentially extirpated sites did not cluster in extreme climate space: two (Chemung, SR 270) had moderately high maximum summer and winter temperatures, whereas one (Parker) was at the cool margins of both seasonal extremes.

Important differences in temperature among the positions evolved over the course of day and night that are masked by seasonal means. Representative summer plots from low and high elevation sites illustrate common responses of diurnal temperature evolution (Fig. 5, parts a and b). By 0400 hrs, all positions had lost the greatest amount of thermal mass from the prior day and showed an “equilibrium” pattern: Dispersal and forefield environments were coldest; free-air temperatures remained warmer than the ground positions; talus surfaces were similar or slightly warmer than ground positions; and matrices were warmest of all. By noon, all positions had warmed, but the ranks changed: matrices had the coolest temperatures and dispersal environments were warmest. Relative heat continued

to grow in all talus positions into late afternoon, especially in the low elevations, while dispersal areas were cooling. By 2000 hrs and midnight, the “0400 hrs equilibrium” rank orders were attained, although temperatures dropped in absolute degree through the course of the evening and night. These summer diurnal patterns illustrate the buffering character of the matrix (warmer at night, cooler in the day, lags over the course of the day) contrasting to the high sensitivity of the dispersal environment (quick to warm during the day and cool at night; large extremes).

In winter, haypile talus matrices were warmer than haypile surfaces and free air during cold times of the day at both low and high elevations (Fig. 5, parts c and d). The Toquima high-elevation plots show the moderating effect of talus matrices even when the talus is not snow-covered. Where taluses were snow-covered, the haypile surface and matrix positions remained between 0 °C and -2 °C, with the matrix warmer than the surface, even when

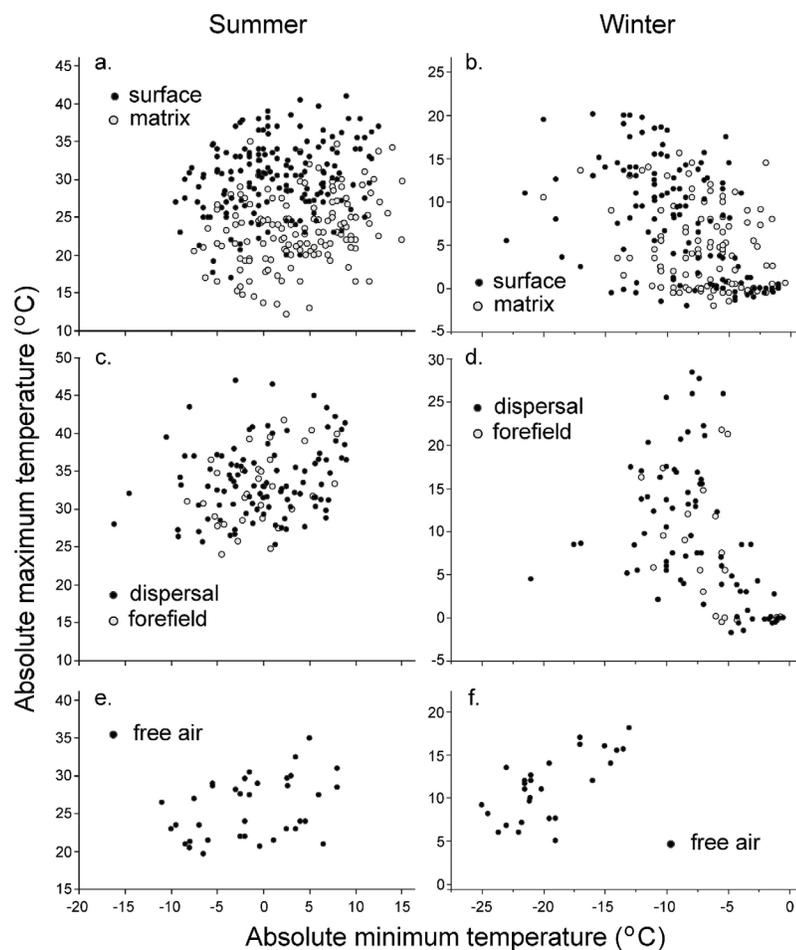


FIGURE 4. Absolute minimum and maximum temperatures over the period of record for habitat components by season over all sites for (a, c, and e) summer and (b, d, and f) winter. (a and b) Haypile surface and matrix. (c and d) Dispersal and forefield. (e and f) Free air. Plots are generated as the absolute extreme value for each month of summer or winter, by site and habitat component, over the period of record.

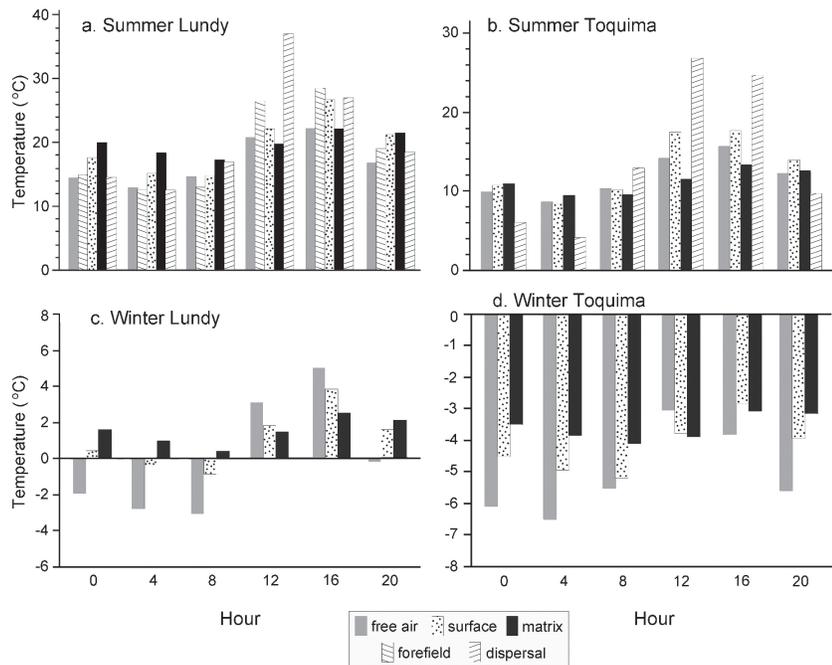


FIGURE 5. Hourly temperatures for habitat components at representative sites by season and elevation. Summer: (a) low elevation: Lundy-South; (b) high elevation: Toquima. Winter: (c) low elevation: Lundy-South; (d) high elevation: Toquima.

free-air temperatures dropped below -15°C (not shown).

Diurnal differences among positions are summarized over all sites for the warmest times of the day in summer (1200 and 1600 hrs) and the coldest times of the night in winter (2400 and 0400 hrs) (Table 3). Position had a large influence, including the significantly cooler matrix in summer than talus surface and free air, much warmer dispersal environment than matrix, and the relative heat of the talus and haypile surface compared to free air. In the coldest times of winter nights, the matrix warmth relative to the surface, and the relative warmth of all talus positions relative to free air, are prominent.

Lapse rates estimated over the elevation ranges of our sites differed among habitat position and season; annual free-air rates approximated the regional expectation and all lapse rates were negative as expected ($-6.5^{\circ}\text{C km}^{-1}$) (Table 4). Winter lapse rates had the greatest discrepancy among positions. Lapse rates for all habitat positions in that season were smaller than free air, and those for haypile matrices were lowest. Values for CAP extracted from the Sierra-wide data set indicate that our sites are about equally situated in CAP and uncertain or no CAP environments, without obvious relation to elevation or aspect (Table 1).

TABLE 3

Mean and standard deviation of differences in temperatures between pairs of habitat components. In summer, the differences were computed for the warmest recording of the day (either noon or 4:00 p.m.); in winter, the differences were computed for the coldest recording of the night (either midnight or 4:00 a.m.). All differences are significant ($p < 0.001$).

	Talus/HP surface minus matrix ($^{\circ}\text{C}$)		Free air minus matrix ($^{\circ}\text{C}$)		Free air minus talus/HP surface ($^{\circ}\text{C}$)		Dispersal minus matrix ($^{\circ}\text{C}$)	
	mean	std dev	mean	std dev	mean	std dev	mean	std dev
Summer	6.1	2.3	3.5	1.8	-7.8	13.1	8.4	4.8
Winter	-2.3	1.8	-9.3	15.1	-8.4	16.8	-1.2	1.2

HP = haypile.

TABLE 4

Lapse rates estimated from temperature means and mean standard deviations across the elevation range of the study sites, and by habitat component and free air.

Position	Lapse rate (°C km ⁻¹)					Std Dev Annual
	Annual	Summer	Fall	Winter	Spring	
Free air	-6.33	-7.09	-4.97	-5.53	-7.76	-1.11
Haypile surface	-3.72	-4.86	-2.22	-1.69	-6.12	-0.85
Haypile matrix	-3.44	-3.78	-2.69	-1.83	-5.44	-0.25
Talus surface	-5.50	-8.33	-3.35	-1.13	-9.11	-1.47
Talus matrix	-4.84	-7.93	-3.14	-0.90	-7.38	-0.71
Forefield	-5.24	-8.99	-1.57	-0.64	-9.75	-2.08
Dispersal area	-6.00	-7.08	-3.83	-4.20	-8.83	-2.74

Compared to elevation-corrected temperatures extracted from the PRISM model, mean observed talus temperatures had strong seasonal differences (Table 5). In summer and winter, observed matrices were cooler than PRISM maximum temperatures and warmer than minima, whereas observed talus surfaces in summer were warmer in minima and maxima. In winter, observed surfaces were cooler than PRISM maximum temperatures but warmer than minima.

DISCUSSION

Our study of thermal regimes across a span of 1468 m elevation and seven mountain ranges of California and Nevada systematically investigated important components of pika habitat over 2–5 yr. Aside from our previous 3-yr study in the eastern Sierra Nevada (Millar et al., 2014), most other studies of observed temperatures have been of short duration, limited to a few months in summer, conducted at one to two sites, and measured free-air

temperature (MacArthur and Wang, 1973; Smith, 1974b; Simpson, 2009; Henry et al., 2012). Beever et al. (2010) and Wilkening et al. (2011) conducted the most widespread instrumental study of temperatures in the vicinity of 25 pika locations across the Great Basin. In most studies, temperatures were estimated from distant climate stations or used modeled data (Hafner, 1994; Erb et al., 2011; Stewart and Wright, 2012; Jeffress et al., 2013; Stewart et al., 2015; Smith and Nagy, 2015). By measuring habitat components continuously over five years, we accrued data sets that could be analyzed for times of the day and seasons when pikas are known to use parts of their environment. This allowed us to develop a more nuanced understanding of climate envelopes than has been reported.

Chronic and acute heat stresses have been suggested as important determinants of pika extirpation (Beever et al., 2010; Wilkening et al., 2011). Regarding the 28 °C threshold for talus, which Beever et al. (2010) found on <1 day yr⁻¹ at extant sites in 2005–2006, our sites regularly exceeded

TABLE 5

Differences between observed temperatures at pika habitat positions and elevation-corrected temperatures extracted from the 800 m grid PRISM model (Daly et al., 1994).

	Observed temperatures minus PRISM temperatures (°C)			
	Matrix T max	Matrix T min	Surface T max	Surface T min
July differences	-2.4	8.1	3.1	7.2
January differences	-2.7	8.4	-1.9	7.6

this heat threshold for talus surfaces. For instance, at the Mono Craters site, all years had more than 45 days $>28^{\circ}\text{C}$ (maximum of 67 days in 2010); at Lee Vining N, all years had more than 48 days $>28^{\circ}\text{C}$ (maximum of 74 in 2011); and at Lundy S all years had more than 44 days $>28^{\circ}\text{C}$ (maximum 79 in 2010). For talus matrices, two of our low-elevation sites (Mono Craters and Lundy S) exceeded the threshold annually at measured depths: at Mono Craters, >6 days every year and 14 days during two years. These exceedances suggest that a threshold $>28^{\circ}\text{C}$ is acceptable pika habitat.

In the few studies where winter temperatures were measured on-site, acute cold stress was reported to be a constraint, distinguishing extant from extirpated populations (Beever et al., 2010; Wilkening et al., 2011). Although snowcover insulates taluses and haypiles at many high and cool locations, diminishing snowpacks have been reported to expose pikas to extreme cold of winter air temperatures, contributing to population decline. Beever et al. (2010) observed a mean of 21.2 days yr^{-1} colder than -5°C for extant sites. Surface temperatures at our high elevation sites exceeded this rate in all years (many >25 days yr^{-1}) in winter and autumn. For instance, in winter 2011, Greenstone and Virginia N sites both had 27 days that were colder than -5°C and Saddlebag had 33 days. A high elevation site situated in a cold-air pool (Kuna) was colder than -5°C for 28 days in 2010, 44 days in 2011, 97 days in 2012, 40 days in 2013, and 31 days in 2014. These exceedances further suggest that pikas can tolerate more than 21 days per winter that are $\leq -5^{\circ}\text{C}$, and may tolerate as many as 97 days or more below this value.

Free-air temperatures are the most widely estimated proxies for pika habitats. Hafner's (1994) estimates for rangewide temperature thresholds are widely cited, and regional modifications have been added (e.g., Henry et al., 2012). Hafner's weather map-based estimates emphasize the cool nature of pikas' range, with fewer than 20 days per year where maximum temperatures exceed 35°C and more than 180 days per year when maximum temperatures are below 0°C . In general, our measurements of free-air temperatures support Hafner's estimate for summer limits: only three of our sites exceeded 35°C (Lee Vining Cyn N, Lundy N, and Lundy S), and for these only once in five years; interestingly,

the three potentially extirpated sites did not reach this threshold. Our cool temperatures, however, do not match those in Hafner's envelope: While air temperatures often were colder than 0°C , there were far fewer days than 180 per year with air temperatures remaining below freezing. Even during the coldest and longest winter of the five years we measured (2011), the greatest number of days $<0^{\circ}\text{C}$ was 136 days; other sites and other years ranged 37–83 days $<0^{\circ}\text{C}$. Days $<0^{\circ}\text{C}$ also were not consecutive: only at one high-elevation site (Virginia N) were there as many as 20 consecutive days below this threshold in one year. Differences between our study and Hafner's may relate less to pika tolerance range but to the warm nature of Pacific-dominated winters in the western Great Basin region of our study as compared to cold continental climates of more interior parts of the species distribution.

Compared to other studies, mean air temperatures were warmer at all elevations (relative to pikas' regional range) than those measured along an elevation gradient at the north end of the species' range (Henry et al., 2012). Jeffress et al. (2013) estimated temperatures from the PRISM model for pika sites within eight national parks across western North America. Their mean summer temperature range (~ 7.9 – 17.8°C) compares with our mean values, while their mean summer maximum temperature range (~ 16.5 – 28°C) was warmer than ours (15.2 – 25.6°C). Maximum summer temperatures estimated for a low-elevation and high-elevation site in California (22.8°C and 14.5°C , respectively; Smith, 1974b) were cooler than our temperature range. PRISM estimated July–August maximum air temperatures (adjusted to years > 1980) of 13.9 – 23.4°C measured along an elevation gradient in the southern Rocky Mountains (Erb et al., 2011) were slightly cooler than our free-air measurements.

Further, free-air temperatures do not estimate important daily variances of habitat components that likely influence pika daily activities. Even at sites where mean warm-season matrix temperatures were similar to free-air means, the daily variabilities of the matrices were one-half to one-third those of free air, underscoring the important buffering capacity of talus matrices. The summer means of other habitat components were poorly estimated by free air: haypile and talus surfaces, forefields, and dispersal environments were 2 – 3°C warmer than

free air. When assessed at warmest times of the day in summer, matrices were 3.5 °C cooler than free air, whereas talus surfaces and dispersal environments were as much as 8 °C warmer. Taken together, these differences suggest that free air temperatures do not consistently relate to temperatures of pika habitat components, and are likely unreliable proxies for pika climate envelopes.

Whereas the buffering capacity and relative cool of talus matrices have been suggested previously to provide thermal refugia in summer, the stability of internal talus temperatures across elevation gradients has not been documented. Although cold-air pooling has been suggested as a possible factor for the relative cool and stability of pika habitats (Hafner, 1994), our estimates of CAP do not bear out that it is a regular feature of pika environments. More the decoupled internal thermal processes unique to rocky ecosystems maintain relative cool and stable conditions (Millar et al., 2013, 2014). Not only is the rate of temperature increase in the matrices less than those at the talus surface, but above 10 °C at the surface, matrix temperatures become decoupled further, especially in periglacial features that retain permafrost or ice (Millar et al., 2013). Our estimates that matrix lapse rates across ~1500 m elevation are less than half those of free air and have very low variance suggest a potential explanation for how pikas are able to persist in locations where free-air temperatures appear prohibitively warm. Further, these attenuated lapse rates give reason to speculate that the effect of global and regional warming in the future might not affect talus matrices as rapidly as other habitat components: that is, matrices might be buffered from rising temperatures or, at least, lag in warming across a range of elevations. If pikas are able to behaviorally adapt so as to forage and collect vegetation during cool times of warm days (Smith, 1974b), internal matrices may continue to provide thermal refugia longer than anticipated from projections of air temperature change.

Thermal regimes of dispersal environments have been least investigated of pika habitat components. Frequent dispersal and recolonization are essential under the metapopulation dynamics that characterize pika behavior and habitat (Smith and Gilpin, 1997; Smith and Nagy, 2015), making condition of the dispersal environment a key limiting factor affecting metapopulation persistence (Smith, 1974b;

Peacock, 1997; Castillo et al., 2014). Smith (1974a, 1974b, 1979) documented that increasing air temperatures reduced the capacity for pikas to disperse, but he did not measure actual dispersal temperature values or report thresholds. In our measurements during the time of year when pikas disperse, mean and maximum temperatures of the dispersal environment were warmest of all habitat components, commonly attaining mean maximum temperatures >30 °C, with many sites having absolute maximum temperatures of 40–45 °C. Despite the high mean summer/autumn temperatures of these environments, the high variances and cool temperatures during morning, night, and evening suggest that pikas have an opportunity to disperse even during very hot days and chronically warm years, as suggested by Smith and Nagy (2015). Further, high spatial variability in the dispersal environment makes this habitat component the most difficult to assess. Inherent variation in dispersal environments, and pikas' sensitivity to temperature, means animals will be highly selective in how and when they move.

CONCLUSIONS

Understanding the response of species to climate change requires knowing how species partition their environment, climatic conditions of the habitat components, and microclimatic processes affecting each component. This is especially important for small mammals, which have climate niches that differ significantly from those of larger and more mobile mammals. Being small, their thermal environment relates to ground surfaces and subsurfaces, which for many situations are likely decoupled from free-air temperatures. For pikas, six habitat components important for survival and reproduction include haypile surface, haypile matrix, talus surface, talus matrix, forefields, and dispersal environments. Each of these has specific thermal regimes that vary daily, seasonally, and interannually. Important for thermally sensitive species such as pikas, talus matrices are highly buffered against external summer heat and provide important refuges where pikas can escape high temperatures that develop on talus surfaces and foraging grounds. In winter, talus surfaces at snow-covered haypiles provide protection against severe cold temperatures of free air; whether snow-covered or not, talus matrices are warmer yet,

offering warm refuges during cold nights. Cumulatively, the thermal nature of these habitat components offers opportunities for pikas to behaviorally adapt to temperature extremes throughout the year. Dispersal environments may present the most limiting constraints for pikas thermally. Pikas disperse at a time of year when air temperatures are warmest and ground surface temperatures for much of the day are extremely high. Although nights are cooler in the dispersal habitats, and significant spatial variability exists that provides opportunity for heat avoidance, avoidance of extreme heat reliably would require a shift in pikas' dispersal season. In that dispersal is cued to other seasonal and annual events in pikas' life history (reproduction, juvenile development, haying), however, such a shift is less likely within the scope of behavioral plasticity than other habitat-use modifications. Thus, while talus environments in general provide pikas significant opportunity to behaviorally adapt on daily and seasonal scales, critical thresholds of rising dispersal area temperatures during the time of year used by pikas could contribute to metapopulation decline in marginal and disjunct contexts in the future. Overall, we show that accurate understanding of pikas' responses to climate and to climate change requires knowledge of climate regimes of all habitat components. Free-air temperature, used commonly to project future status of pikas to regional warming, is likely an inaccurate proxy for the conditions these animals actually encounter.

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