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RESEARCH ARTICLE

Revisiting talus and free-air temperatures after 50 years of change at an American pika (*Ochotona princeps*) study site in the Southern Rockies

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Abstract

Climate change in mountain regions has exposed high-elevation species to rapidly changing temperatures. Although climate exposure can be reduced in certain microclimates, the quality of microclimatic refugia might also degrade with climate change. The American pika (*Ochotona princeps*) often inhabits high elevations, and is considered climate-sensitive due to its narrow thermal tolerance and recent extirpations in some warmer portions of its range. Pikas behaviorally thermoregulate by taking refuge in the subsurface microclimates found in taluses and other rocky habitats, where daily thermal fluctuations are attenuated and somewhat decoupled from free-air temperatures. Changes in microclimate might reduce the efficacy of this behavioral thermoregulation. This study compares recent (2009–2021) subsurface temperatures at a long-term pika study site with a rare instance of historical (1963–1964) data from the same location. We also place historical and recent microclimates in context using long-term data on free-air temperatures from the same area. Recent free-air temperatures were often warmer than historical records, and subsurface temperatures exhibited even stronger warming between periods. Temperatures measured in the talus were often dramatically warmer in recent records, especially at the deeper of two subsurface sensor placements in this study. Winter months showed the greatest changes in both talus and free-air temperatures. Differences between historical and recent microclimates were not explained by the precise placement of sensors, as recent temperatures were similar across a wide variety of subsurface placements, and temporal changes in free-air temperatures at the historical study site were also reflected in data from nearby weather stations. Together, these results suggest that subsurface microclimates important for pika thermoregulation have changed over the past few decades, perhaps even faster than observed changes in free-air temperatures. The generality of these results and their potential ramifications for ecosystem processes and services should be explored.

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Data Availability Statement: All data and analyses can be found in the GitHub repository, https://github.com/emilymonk/50_Years_of_Change_Pikas.git. Data from the primary study site is provided in a supporting zip file. Data used in analyses of surrounding sites can be found in the EDI Portal at the following DOI's: https://doi.org/10.6073/pasta/6b8288f9498b00cf4f2156a3fefc1b72; https://doi.org/10.6073/pasta/1b62f2cda71579c4870ac5c1af71e6f3; https://doi.org/10.6073/pasta/edd9e457fd22a703a587cc8608d54bde; https://doi.org/10.6073/pasta/1e9f40409e69299b1a41f98ac767bcd7; https://doi.org/10.6073/pasta/0a786c99fe3d4e1dfb8c57424ce79091.

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Introduction

Changes in temperature, precipitation, and extreme weather events are impacting ecosystems across the globe, altering the abiotic conditions experienced by many species [1–3]. High elevation areas may be warming at rates that exceed the global average [4–6], leaving mountain species more exposed to changes in temperature than their lowland counterparts [7]. However, climate exposure can be mediated by access to microclimates or small-scale variation in climate. Microclimatic variation can result in local differences in biotic processes and species distributions [8–10], and can explain nuances in how populations experience and are vulnerable to climate change [11, 12]. Further, microclimates have been shown to provide refuge for animals in times of extreme climate events [13]. There have been calls for greater focus on microclimates to better understand local impacts of climate change [10, 14], especially at high elevations [15]. Microclimatic studies are increasingly common, in part due to advances in remote sensing [16], but records of subsurface and historical microclimate are sparse [17], limiting our understanding of how climate exposure might be changing for many species [18].

Microclimates are produced by effects of topography and land cover [19, 20], such as exposure to sun and wind on ridgelines or shade under a forest canopy. In alpine and sub-alpine environments, rock-matrix landforms such as taluses offer a three-dimensional habitat that harbors a subsurface microclimate significantly decoupled from free-air temperatures [21]. Thermal buffering in taluses can resist changes induced by variation in external air temperature, providing favorable temperature refugia for many plants and animals, and altering how these species experience variations in climate [15, 21, 22]. Rock-matrix landforms, including taluses, rock glaciers, block fields and lava beds, can experience depressed average temperatures that allow permafrost to persist in locations otherwise precluded by free-air temperatures [21, 23]. Such rock-ice features are important in the persistence of many cold-adapted species, such as the American pika [22].

The American pika (*Ochotona princeps*) ranges across much of western North America, and is often considered a microclimatic indicator species [24, 25] and a sentinel species for detecting effects of climate change [26, 27]. These designations derive in part from the fact that pikas have disappeared from some remote and rugged areas in a pattern that suggests effects of climate rather than other anthropogenic impacts such as removal or fragmentation of habitat through land-use change [28–31]. *Ochotona princeps* inhabits taluses and other rock-matrix habitats that harbor the microclimates they require for behavioral thermoregulation [32, 33]. Pikas have evolved superb adaptations for retaining heat, allowing them to survive winter–without hibernating–in the coldest reaches of their range [25, 34]. Their specialization is so complete that they lack common adaptations for shedding excess heat, such as evaporative cooling (panting, sweating or self-grooming with saliva), and they have no bare skin available to accelerate cooling through conduction or convection [35]. Heat gained during the physical activities of summer–such as territorial defense and the stockpiling of "haypiles" (forage) to sustain them over the winter–must be shed passively through their thick fur during time spent resting in cool spaces under the surface of the rock matrices in which they live [35].

Because the pika's persistence is so closely coupled with talus microclimates, it will be useful to understand how–and how quickly–these microclimates might be changing. The rapid loss of permafrost in arctic and alpine habitats [36, 37] indicates that subsurface microclimates are strongly affected by atmospheric climate change, but little is known about how subsurface microclimates are changing in the rock-matrix features used by pikas and many other cold-adapted vertebrates, such as wolverines, North American porcupines, golden-mantled ground squirrels, bushy-tailed woodrats and several species of ptarmigan, marmots, chipmunks and weasels, as well as many plants and arthropods [15]. Pikas are especially associated with rock glaciers [22], which consist of rocky debris covering a debris-ice mixture [38]. The ice hidden in rock glaciers can persist long after glaciers have disappeared from a warming landscape, but just how long is poorly understood [39]. Here, we examined changes in free-air and subsurface temperature using data from a rock glacier on Niwot Ridge (Boulder County, Colorado, USA) where pikas have been studied intermittently over the past 50 years. We leveraged a rare dataset to compare "historical" temperatures recorded in 1963–1964 with "recent" temperatures recorded during 2009–2021, and we compared the apparent changes in microclimate with changes recorded by two climate stations on the same ridge. We expected changes in free-air and subsurface temperature over the past 50 years to be positive, in keeping with many observations worldwide. However, we expected changes in temperature within the rock matrix to be smaller in magnitude than changes in free-air temperature, especially if changes in microclimate lag changes in climate by multiple years and if processes controlling subsurface air temperature are more localized than those controlling free-air temperature. Because this study site is located within a former rock glacier, we assumed local processes support some degree of subsurface cooling, while free-air temperatures might reflect more heterogeneous influences. We also predicted the deepest temperature measurements would show the smallest change over time, assuming the deeper portions of a rock matrix would be more buffered from fluctuations in free-air temperature. Finally, we predicted that changes in subsurface temperature would be more pronounced in summer than in winter. Precipitation on Niwot Ridge—which falls mainly as snow—has not declined over our study period [40], so we expected the insulating effect of snow to be active in both historical and recent times, allowing subsurface temperatures to remain decoupled from free-air temperatures during the winter.

Methods

Study site

This microclimatic study was conducted in Boulder County, Colorado, USA (40˚ 3'24.31"N, 105˚35'44.59"W) at an American pika study site within the Front Range of the Rocky Mountains, on the north slope of Niwot Ridge, below treeline at an elevation of 3,300 meters (Fig 1). The study site is situated in a talus slope recently described as a "fossil" rock glacier [41, 42], meaning it no longer harbors permafrost or interstitial ice deposits that could lead to active downslope flow of this rocky debris. However, in a study published 50 years ago [43], permafrost was detected on the ridge immediately above this study site, and was also encountered at elevations as low as 3,140 meters. Today, the talus at this site might harbor seasonal ice that melts each summer; in recent years, water has been heard flowing beneath the rocks during mid-summer at some locations within the site.

Historical study

In the early 1960s, Harry Robert Krear used this site to conduct one of the first intensive ethological studies of the American pika [44]. Krear's study also included the first temperature monitoring project specific to the microclimates used by pikas. Recognizing the talus microclimate as critical to pika survival, Krear measured temperatures in free air and within the talus using equipment that required weekly servicing year-round. Although his preparation for this research included solo work in the arctic and training in the Tenth Mountain Division [45], his remarks suggest this year-long task was nevertheless difficult given the tools available at that time. "It is a relatively simple matter to observe and record the climatic conditions that impinge upon a fossorial mammal in its external habitat. It is much more difficult to measure accurately the climate of the mammal's microhabitat, which is the climate on which the mammal is dependent for its maximum security and general survival, inasmuch as it has access to

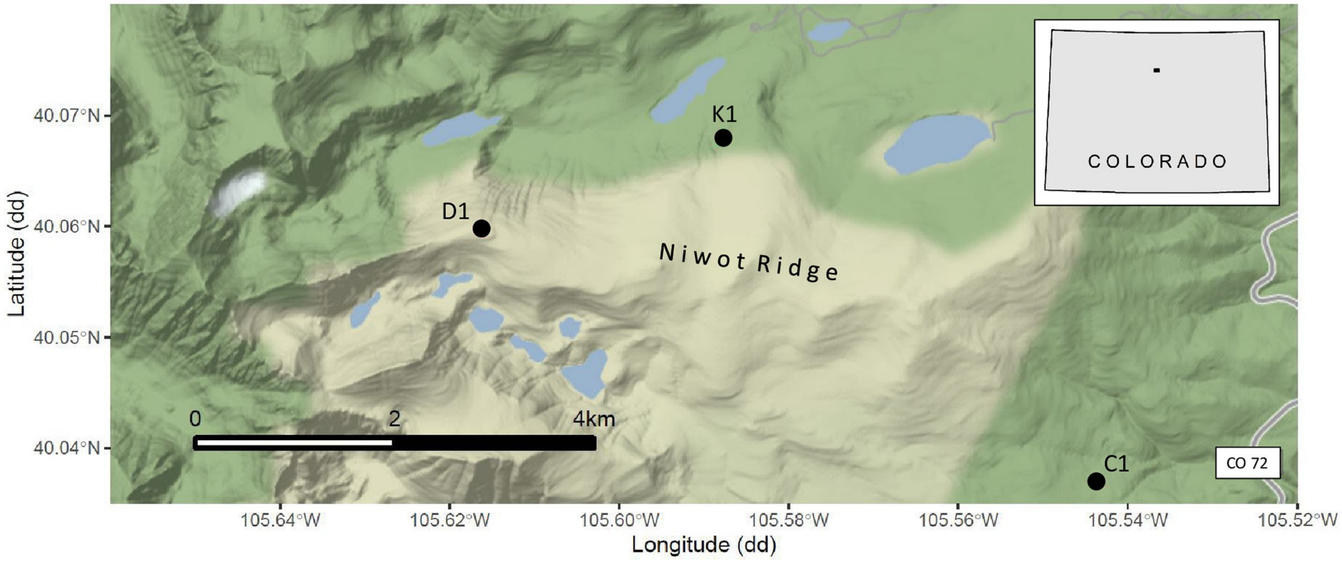

Fig 1. Map of study site. Stations providing recent and historical microclimatic data (K1) and long-term climatic data (C1 and D1) on Niwot Ridge, Boulder County, Colorado, west of Colorado Highway 72 (CO 72). Map tiles by Stamen Maps (http://stamen.com) provided under CC BY 3.0 (http://creativecommons.org/licenses/by/3.0). Data by OpenStreetMaps (http://openstreetmap.org) provided under ODbL (http://www.openstreetmap.org/copyright).

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no more favorable conditions" [43 p. 69]. Krear's temperature monitoring station (hereafter, K1) is still marked by a post left *in situ* at the study site, allowing precise replication of sensor locations and facilitating the direct comparisons made in this study. Hereafter, we refer to Krear's temperature monitoring station as K1, and the approximately 3-hectare pika study site surrounding K1 as the Krear site.

Krear recorded temperatures from July of 1963 to June of 1964 using two chart recorders, each capable of continuous operation over a seven-day period. Free-air temperatures were measured using a Friez thermograph (Model 77, Julian P. Friez Company, Baltimore, Maryland), while talus temperatures were measured using a Dickson thermograph (Minicorder Model 42–2, Dickson Company, Chicago, Illinois). The Dickson thermograph was supplied with two external sensors, which Krear used to measure temperatures at shallow and deep positions in the talus, 0 and 1.37 m below the surface, respectively. External sensors in the talus were shaded from direct sunlight by the rocks themselves, while thermographs were sheltered in a custom screen [43 pp. 20–22]. Free-air temperature was measured at a position "several feet above the talus" [43 p.17]. We have no record of the exact height of this free-air measurement, but our on-site observations of an *in-situ* pole bearing notches and hardware for placement of Krear's equipment suggests it was roughly 1.5 meters above the talus surface. This height approximates the height of nearby weather stations with which Krear was familiar, as referenced in his statement on the calibration of thermographs, which "were continuously checked with the use of two standard U.S. Weather Bureau maximum and minimum thermometers. . . generously loaned to my research project by the University of Colorado, Institute of Arctic and Alpine Research, which has maintained continuously recording weather stations. . .on Niwot Ridge, adjacent to my research area. . .since 1952 [44, 46]".

The weather stations referenced by Krear are still in operation and include C1, located in a subalpine forest at 3022 m, and D1, located in alpine tundra at 3739 m. Previous results from C1 and D1, which offer the longest continuous high-elevation record of climate in the US, have shown a strong warming trend over the past 70 years in both subalpine (C1) and alpine (D1) environments [47, 48]. We expected the change between historical and recent

Table 1. Datasets used to compare recent and historical temperatures at an American pika study site on Niwot Ridge, Colorado, USA.

Temperature station	Elevation (m)	Recent period	Historical period
K1 free air	3312 + 1.5[a]	2013–2021	1963–1964
K1 shallow	3312	2009–2021	1963–1964
K1 deep	3312–1.37[b]	2011–2021	1963–1964
Krear site haypiles	3276 to 3342	2009–2021	NA
C1 free air	3022	2009–2020	1958–1969
D1 free air	3739	2009–2020	1958–1969

[a] 1.5 m above the surface of the talus.

[b] 1.5 m below the surface of the talus.

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temperatures at K1 to reflect this warming trend, given the proximity of these stations and their similar elevations (Table 1).

Recent temperature recording and analysis

To characterize recent temperatures at the Krear site, we measured temperatures at K1 during 2009–2021 using datalogging sensors (HOBO models H and U, Onset Computer Corp.; hereafter, “sensors”) with an accuracy +–0.2˚C. Sensors were programmed to record data every hour or two–the maximum sampling rate we could achieve given our year-long deployments and the different memory limits of each sensor model. Sensors were placed in deep, shallow and free-air positions approximating those used by Krear in 1963–1964 (Table 1). We serviced sensors annually during the fall and occasionally replaced them with sensors more recently tested for calibration.

The continuous data recorded by Krear’s thermographs captured daily maximum and minimum temperatures that our discrete (e.g., hourly) records could easily miss. To estimate these daily extremes, we used a generalized additive model (GAM) to fit a smooth curve through each single day of data recorded by a sensor. Given a set of daily temperature records y_i, where $i = 1, \ldots, N$ and $N = 12$ or 24, we modeled the expected temperature in continuous time as $g(E(y_i)) = \beta_0 + f(x_i) + \varepsilon_i$, (Equation 1), where β_0 was a constant intercept, $f(x_i)$ was a cyclic cubic-spline smooth function of the time of day x_i corresponding to each record, $\varepsilon_i \sim N(0,\sigma^2)$ was a normally distributed random error with mean zero, and g was the identity link corresponding to our assumption that y was normally distributed. When fitted to (1), the short series of data from a single day typically showed little evidence of residual autocorrelation, based on model-specific calculation of the autocorrelation function (ACF) and partial autocorrelation function (*p*ACF). Fitting a GAM with up to N knots and a cyclic cubic-spline smooth term allowed us to capture the typical daily “peak-and-trough” pattern of temperature fluctuation at free-air and snow-free subsurface sensors This peak-and-trough pattern consisted of relatively low temperatures each morning followed by relatively high temperatures in the afternoon (Fig 2). GAMs were not used, however, when temperatures varied by less than 2˚C over a 24-hour period (indicating significant snow cover). In these cases, the observed maximum and minimum temperatures represented the full daily temperature range, and were used directly in our analyses, without prior modeling.

Using the observed or modeled daily maxima and minima from the recent period, we calculated recent monthly statistics patterned on each of the monthly statistics provided in Krear’s study (Table 2). For a given statistic S, our goal was to compare each monthly value S_m from the historical data-year to the distribution of S_m values calculated from recent data-years. The recent sample size for S_m was determined by the number of years of recent data, and ranged 8–12 years (Table 1).

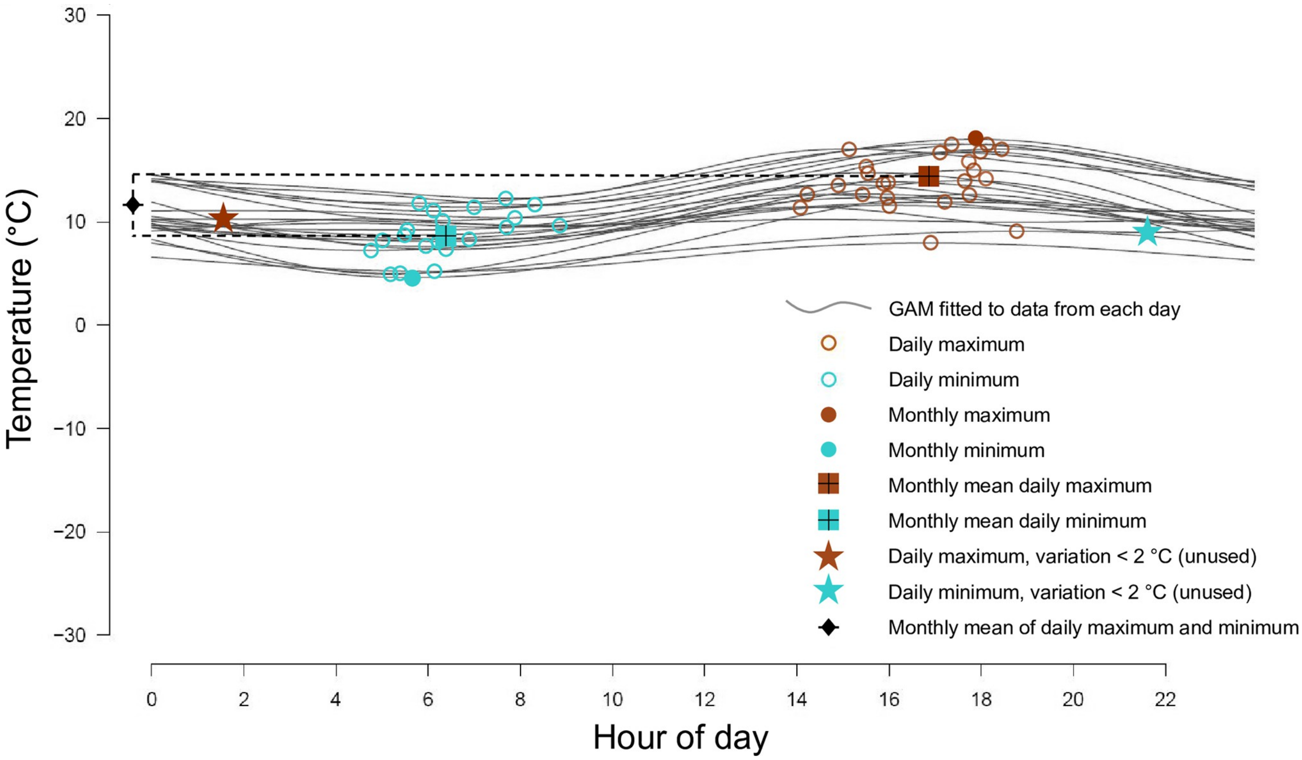

Fig 2. Temperature statistics calculated from recent data. Discrete (timed-interval) data from each day at the K1 site were interpreted as continuous data using a cubic-spline smooth in a generalized additive model (GAM), to allow direct comparisons with historical data, which were recorded continuously by thermographs. This example shows GAM fits for August 2013. Symbols represent statistics calculated from each daily fit, as defined in Table 2.

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Table 2. Temperature statistics compared between historical and recent datasets.

Statistic	Calculation from historical data	Calculation from recent data*
Monthly maximum or minimum temperature	The maximum or minimum temperature observed on chart recorders across all days of month *m* in the historical data-year (1963–1964)	The maximum or minimum temperature derived from cubic-spline smooths of each day's temperature data** from month *m* in recent year *t*
Monthly mean of daily maximum or mean of daily minimum temperature	The daily maximum or minimum temperature observed on chart recorders, averaged across all days of month *m* in the historical data-year	The daily maximum or minimum temperature derived from cubic-spline smooths of each day's temperature data** and averaged across all days of month *m* in recent year *t*
Monthly mean of daily maximum and minimum temperature	The daily average of maximum and minimum temperatures observed on chart recorders, averaged across all days of month *m* in the historical data-year	The daily average of maximum and minimum temperatures derived from cubic-spline smooths of each day's temperature data** averaged across all days of month *m* in recent year *t*
Number of days above freezing	The number of days on which the maximum temperature observed on chart recorders rose above zero celsius	The number of days on which the maximum temperature derived from a cubic-spline smooth of the day's temperature data** rose above zero celsius

*See Fig 2 for illustration of each definition.

**For days with variation in temperature $< 2^{\circ}$C, observed maximum and minimum temperature were used to calculate each recent statistic.

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Recent temperature comparisons with historical, weather station, and surrounding site data

To compare historical with recent data from K1, we first calculated $S_{m(y)}$, where S was the focal statistic (Table 2), month $m = 1, \ldots, 12$ and year $y = 2009, \ldots, 2021$. To characterize the time series of expected S_m throughout a typical year in the recent period, we grouped values of $S_{m(y)}$ by month and then fitted a GAM to this time series of 12 groups as $g(E(S_{m(y)})) = \beta_0 + f(m) + \varepsilon_{m(y)}$ (Equation 2). The smooth in Eq. 2 was a simple—rather than cyclic—cubic spline, to allow for the typically large difference between June and July temperatures, which represented either end of the historical time series. We plotted the data along with the fitted curve, to illustrate this structure in the data. The link function g in Eq. 2 was either the identity link (for normally distributed response variables such as monthly maximum temperature) or the log link (for the number of days above freezing, which was modeled using a Poisson error distribution). Although ACF/*p*ACF analyses revealed some evidence of residual autocorrelation (typically of order 1) in preliminary fits of Eq. 2, we found little support for autoregressive (AR) models when compared with (nested) non-AR models using a generalized likelihood ratio test. For this reason, we dropped the residual covariance matrix from our final fits of Eq. 2. Finally, we noted historical statistics whenever they fell far outside the 95% confidence interval estimated for recent mean values. Although Krear's raw data were not available, all historical monthly statistics were provided within his dissertation, and were used for the present comparison.

To compare historical with recent data from C1, and similarly to compare historical with recent data from D1, we applied the same approaches as described above for K1, except that we fitted a GAM to the historical data as well, because each climate station provided multiple years of historical data. To construct a fair comparison with similar sample size at either end of our 50-year study period, we included 10 years of historical data (1958–1969) that spanned the historical year of data collected by Krear.

Finally, we also compared recent temperature data recorded in the shallow position at K1 with recent temperature data recorded at haypiles throughout the ~3-ha Krear site. For this comparison, we applied the same approach as described above for C1 or D1: for each statistic, a GAM was fitted through the monthly values calculated from all years of shallow temperature data, and another GAM was fitted through the monthly values calculated from all years of haypile temperature data. We expected broad overlap between the means and 95% confidence intervals of these two fits, indicating that shallow temperatures at K1 were similar to haypile temperatures throughout the Krear site. Expected similarities would also suggest that sensor placement at K1 was representative of other possible placements, such that any differences we detected between historical and recent temperatures at K1 were not due to any slight difference between our recent placement and Krear's historical placement of the shallow sensor.

Dataset and regulatory information

Data from weather stations C1 and D1, including the daily maximum and minimum temperatures, were provided by the Niwot Ridge Long-Term Ecological Research site [49–52]. Temperature data from the Krear site is archived with the Environmental Data Initiative (package knb-lter-nwt.8.4) [53]. This study was conducted under temporary special use permits from the USDA Forest Service (authorizations BOU 283, 341, 362, 390, 412, 538, 567, 584, 621 and 651), and animal research was carried out in strict accordance with protocol #2681, approved by the University of Colorado-Boulder Institutional Animal Care and Use Committee. All data were analyzed in the R environment for statistical computing (S1 and S2 Files) [54]. The site map was produced using the ggmap package [55]. GAMs were fitted using the package mgcv [56],and visualized using the ggplot2 package [57].

Results

Monthly means for each focal statistic (defined in Table 2) were summarized across recent years (2009–2021) to characterize the annual progression of microclimatic conditions at K1 throughout a typical year in the recent period (Table 3, Tables A and B in S1 Text). Similar statistics from the historical year were published in Krear (1965) and are reproduced here in graphical comparisons of historical and recent data.

Historical versus recent temperatures at K1

For sensors within the talus, monthly maximum and minimum temperatures were higher in winter months of recent years than in winter months of the historical year (Fig 3A and 3B). Monthly maximum temperatures were also higher across the summer months of recent years, but mainly for deep sensors (Fig 3B). Surprisingly, free-air temperatures (Fig 3C) appeared more similar between recent and historical time periods than were subsurface temperatures in the talus. At all sensor positions, recent temperatures were generally higher than historical temperatures more often for monthly minima than maxima.

Monthly means of the daily maximum temperature and the daily minimum temperature were higher in the talus for summer, winter, and spring in recent years when compared to the historical year (Fig 3D and 3E). However, similar to the monthly maxima and minima, this pattern was less pronounced in the free-air temperatures (Fig 3F). Free-air temperatures were higher than historical temperatures mainly in the winter months for both the mean of the daily maximum and mean of the daily minimum.

Table 3. Monthly summary statistics from recent (2009–2021) microclimatic data collected by the shallow sensor at K1, just below the surface of the talus.

Month	Summary	Mean daily max T	Mean daily min T	Mean of Daily Max and Min	Month Maximum	Month Minimum	Days above freezing
Jul	Mean	16.7	10.1	13.4	22.1	5.8	31.0
	SD	2.0	1.4	1.6	3.5	0.8	0.0
Aug	Mean	15.3	8.6	11.9	19.6	4.3	29.9
	SD	1.8	1.9	1.8	2.6	1.6	2.8
Sep	Mean	11.2	4.1	7.7	16.5	-2.4	28.7
	SD	1.7	2.5	2.0	2.9	2.6	3.3
Oct	Mean	3.5	-3.9	-0.2	8.3	-9.1	20.5
	SD	1.7	2.8	2.1	3.2	1.8	3.7
Nov	Mean	-2.2	-10.3	-6.3	0.7	-14.1	9.2
	SD	1.8	2.0	1.8	2.5	2.0	9.8
Dec	Mean	-6.4	-14.7	-10.5	-4.4	-17.2	0.0
	SD	2.2	3.1	2.4	2.5	4.1	0.0
Jan	Mean	-6.7	-12.9	-9.8	-5.4	-14.2	0.0
	SD	1.2	1.7	1.1	1.6	2.3	0.0
Feb	Mean	-5.6	-11.5	-8.6	-5.0	-12.2	0.0
	SD	1.6	2.4	1.8	1.9	2.6	0.0
Mar	Mean	-2.7	-7.9	-5.3	-1.7	-9.0	4.5
	SD	2.4	1.7	1.6	4.5	3.0	10.5
Apr	Mean	0.0	-4.5	-2.2	0.9	-5.1	12.5
	SD	2.0	1.2	1.1	4.0	2.0	14.6
May	Mean	6.0	-0.8	2.6	7.9	-2.1	22.5
	SD	5.4	1.3	3.1	7.6	1.5	14.4
Jun	Mean	15.1	6.6	10.8	21.3	-0.4	29.9
		2.4	2.3	2.3	3.0	2.1	0.3

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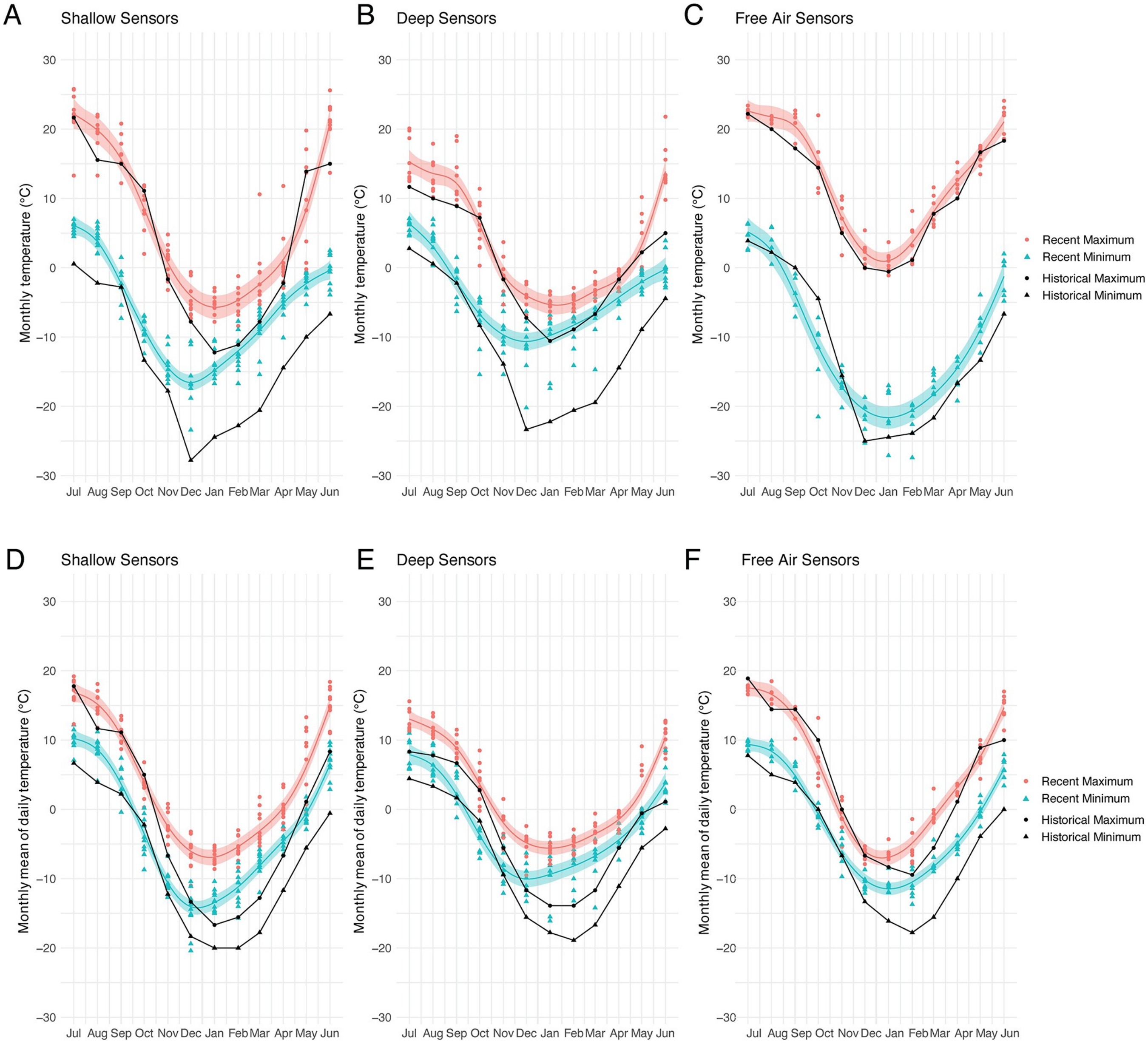

Fig 3. Recent and historical monthly maximum and minimum temperature metrics. Values shown are absolute monthly maximum or minimum temperatures (panels A-C) as well as monthly averages of daily maximum or minimum temperature (panels D-F). All data were recorded at K1 in a pika study site on Niwot Ridge (Boulder County, Colorado, USA). Time periods for historical data (black symbols) and recent data (colored symbols) are shown in Table 1. Historical maximum temperatures (black dots) and minimum temperatures (black triangles) are compared with recent maximum temperatures (red dots) and minimum temperatures (blue triangles) using a cubic-spline smooth to estimate recent means (colored curves) and 95% confidence intervals (shaded regions).

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Although the differences between historical and recent talus temperatures summarized in Fig 3 varied by season and were perhaps strongly influenced by the single year of historical data, it is worth noting that some of these differences were quite large. Historical talus temperatures were often 10˚C lower than the lower bound of the 95% confidence interval on recent estimates of minimum and maximum temperatures, especially in late winter (Fig 3).

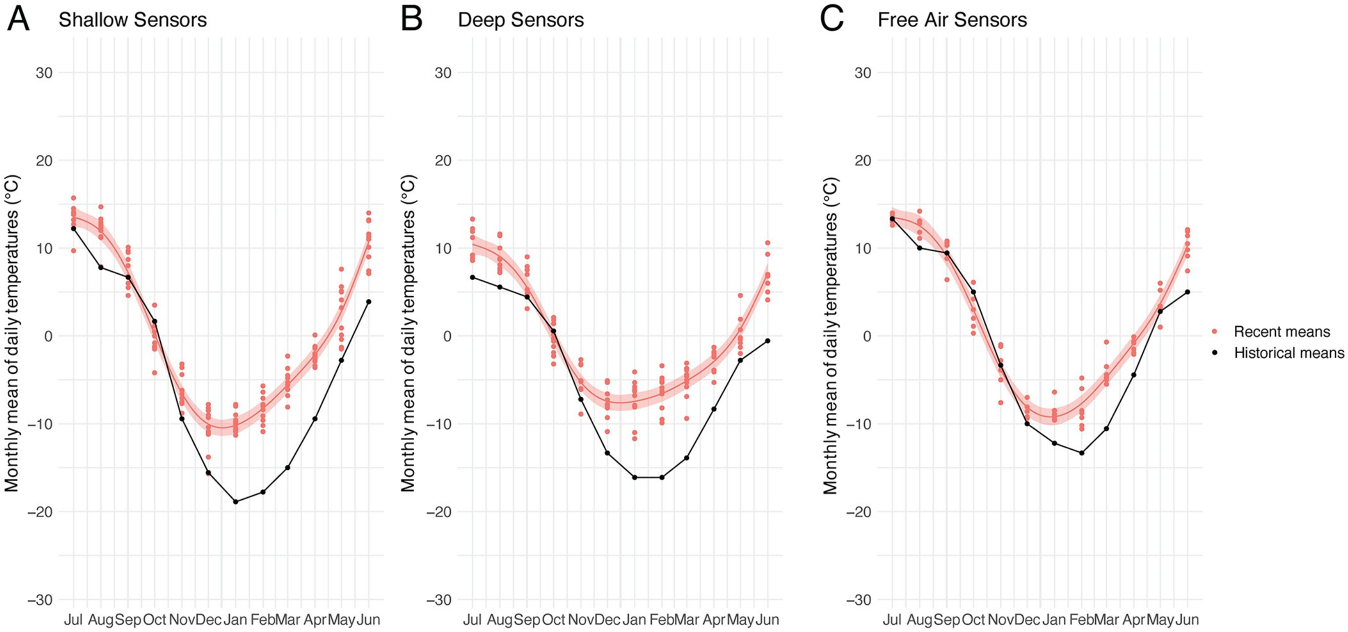

Fig 4. Recent and historical monthly mean temperatures. Values shown are the daily means of the absolute maximum and minimum temperature, averaged across the days in each month (Table 2). All data were recorded at K1 in a pika study site on Niwot Ridge (Boulder County, Colorado, USA). Time periods for historical data (black symbols) and recent data (colored symbols) are shown in Table 1. Historical mean daily temperatures (black dots) are compared with recent mean daily temperatures (red dots) using a cubic-spline smooth to estimate recent means (red curves) and 95% confidence intervals (shaded regions).

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For the mean of the daily maximum and minimum temperature, all values in talus were warmer in recent years except the fall months of September and October (Fig 4A and 4B). Compared with free-air temperatures, talus temperatures showed a greater magnitude of change between historical and recent values of this mean difference (Fig 4C). Again, the largest changes appeared in winter months.

The number of days above freezing in recent years was similar to the number of days above freezing from the historical data set, with pronounced differences in fall and spring (Fig 5). Free-air sensors recorded the greatest difference in counts, with more days above freezing in fall, winter, and spring months of recent years. Deep and shallow sensors each showed differences in the number of days above freezing in fall and spring, but did not differ in summer or winter.

Recent temperatures at pika haypiles surrounding K1

Temperatures were monitored at pika haypiles throughout the Krear site during 2009–2021, resulting in 22 year-long temperature records suitable for comparison with recent shallow temperatures from K1. Sensor placements at haypiles varied with the natural structure of the talus, and were often up to 10 cm deeper than the shallow placement at K1, yet temperatures from these two sources broadly overlapped (Fig 6). When compared to shallow temperatures at K1, haypile site temperatures were somewhat less variable across the year, being up to 8˚C warmer in winter and up to 5˚C cooler in spring (Fig 6A–6C). The number of days above freezing differed between haypile sites and the shallow K1 placement only during spring, when haypile sites were cooler (Fig 6D).

Recent and historical temperatures at weather stations near K1

Recent metrics of maximum and mean free-air temperature at K1 tended to be lower than comparable metrics at the lower-elevation weather station, C1 (Fig 7A and 7C), and higher

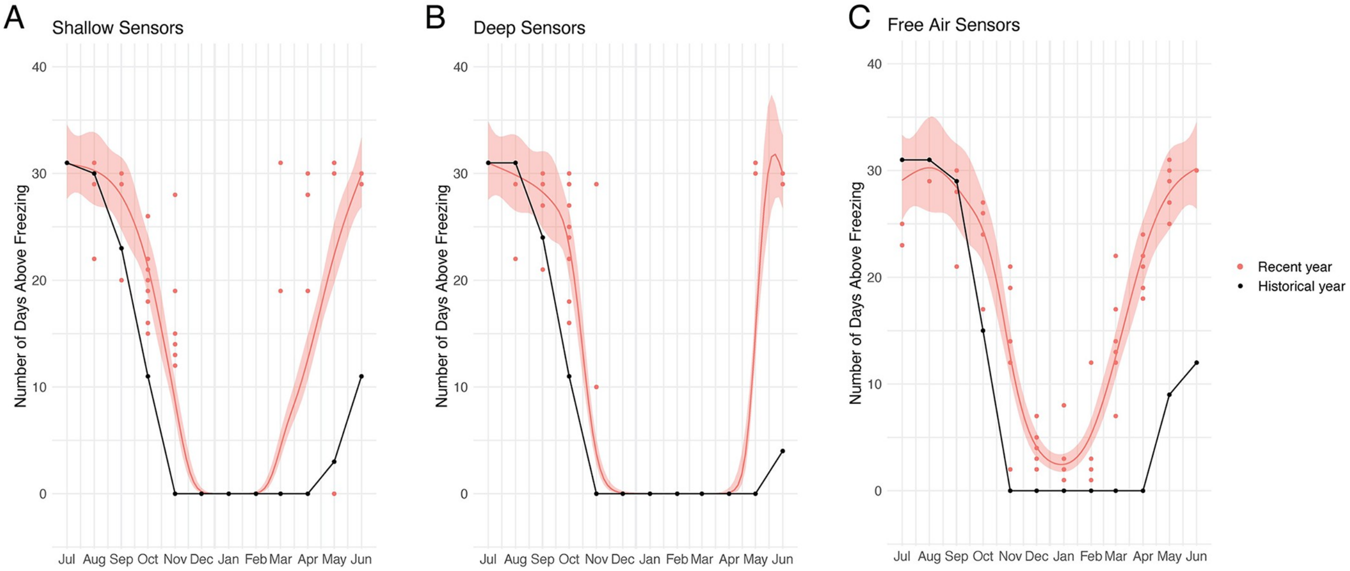

Fig 5. Recent and historical days above freezing (0˚ C). All data were recorded at K1 in a pika study site on Niwot Ridge (Boulder County, Colorado, USA). Time periods for historical data (black symbols) and recent data (red symbols) are shown in Table 1. Historical data (black dots) are compared with recent data (red dots) using a cubic-spline smooth to estimate recent means (colored curves) and 95% confidence intervals (shaded regions).

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than comparable metrics at the higher-elevation weather station, D1 (Fig 8A and 8C). Similar patterns of intermediate temperature were observed for historical metrics of maximum and mean free-air temperature, with the possible exception of the relationship between historical D1 and K1 temperatures (Figs 7B, 7D, 8B and 8D). The range of recent maximum and minimum temperatures at C1 also tended to be more extreme than the same range of recent temperatures at K1 (Fig 7A and 7C). The range of recent maximum and minimum temperatures at D1 was more similar in breadth to those at K1, although recent temperatures at this higher-elevation weather station tended to be lower than those at K1 (Fig 8A and 8C).

The recent number of days above freezing at K1 was also intermediate between the lower- and higher-elevation weather stations (Fig 9). In the recent period, confidence intervals on days above freezing overlapped most often in summer and fall; in winter and spring, K1 usually recorded significantly fewer days above freezing than C1 (Fig 9A), and significantly more days above freezing than D1 (Fig 9C). In the historical year of data from K1, the number of days above freezing was generally lower than observed at C1 and D1 during the historical period, except for July-September at both weather stations and January at D1 (Fig 9B and 9D).

A comparison of data between the two weather stations without reference to K1 showed a similar pattern of change between recent and historical metrics (S1 and S2 Figs). At the subalpine station (C1), monthly maximum temperatures were higher during summer months in the recent period, but no other monthly maxima or minima differed between historical and recent years. At the alpine station (D1), no monthly maxima or minima differed between historical and recent years. C1 recorded higher mean daily maximum values for some spring and summer months in recent years, and higher mean daily minimum values for some fall and early winter months in historical years. D1 recorded higher mean daily maximum and mean daily minimum temperatures in summer months of recent years. At both C1 and D1, the mean of daily maximum and minimum temperatures was higher in only a few months of the year during the recent period. Neither weather station recorded a change in the number of days above freezing between recent and historical years.

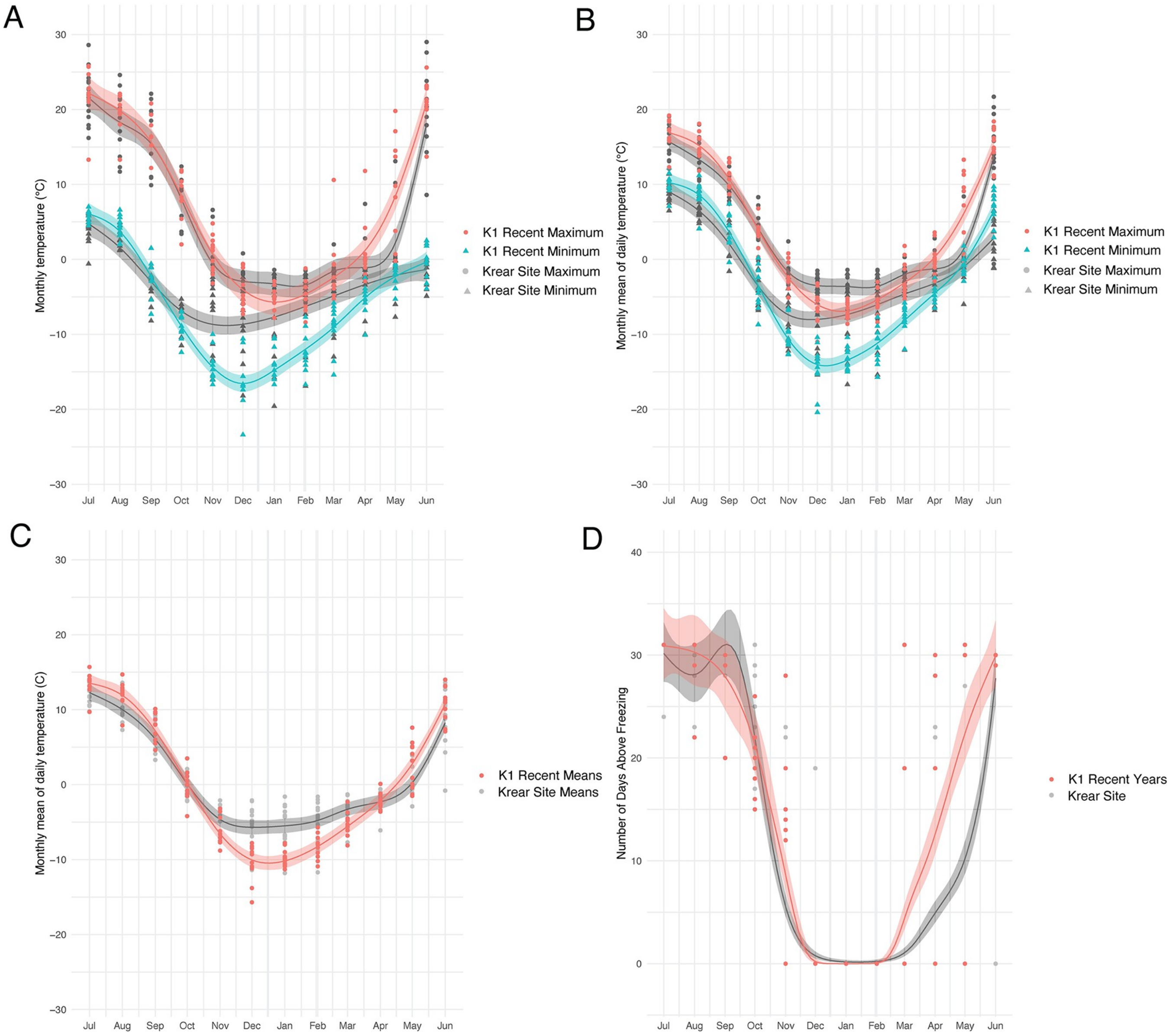

Fig 6. Recent temperatures recorded at K1 and surrounding pika haypiles. All data were recorded during 2009–2021 at shallow positions in talus within a pika study site on Niwot Ridge (Boulder County, Colorado, USA). Temperature metrics (Table 2) at K1 (colored symbols) and at pika haypiles throughout the surrounding Krear study site (gray symbols) are compared using a cubic-spline smooth to estimate means (colored curves) and 95% confidence intervals (shaded regions).

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Discussion

This study offers a glimpse at the recent rate of subsurface temperature change within one rock glacier in the southern Rocky Mountains, and suggests that talus temperatures have warmed more than free-air temperatures during the past 50 years at this site. Due to the small sample size and non-standard methods employed in this study, we present these results in a qualitative manner (providing graphical rather than numerical estimates of change) as a starting point for further research.

Assuming our qualitative results are robust, measurable changes in talus temperature have occurred in the last 50 years, and–contrary to our expectations–warming below the surface of

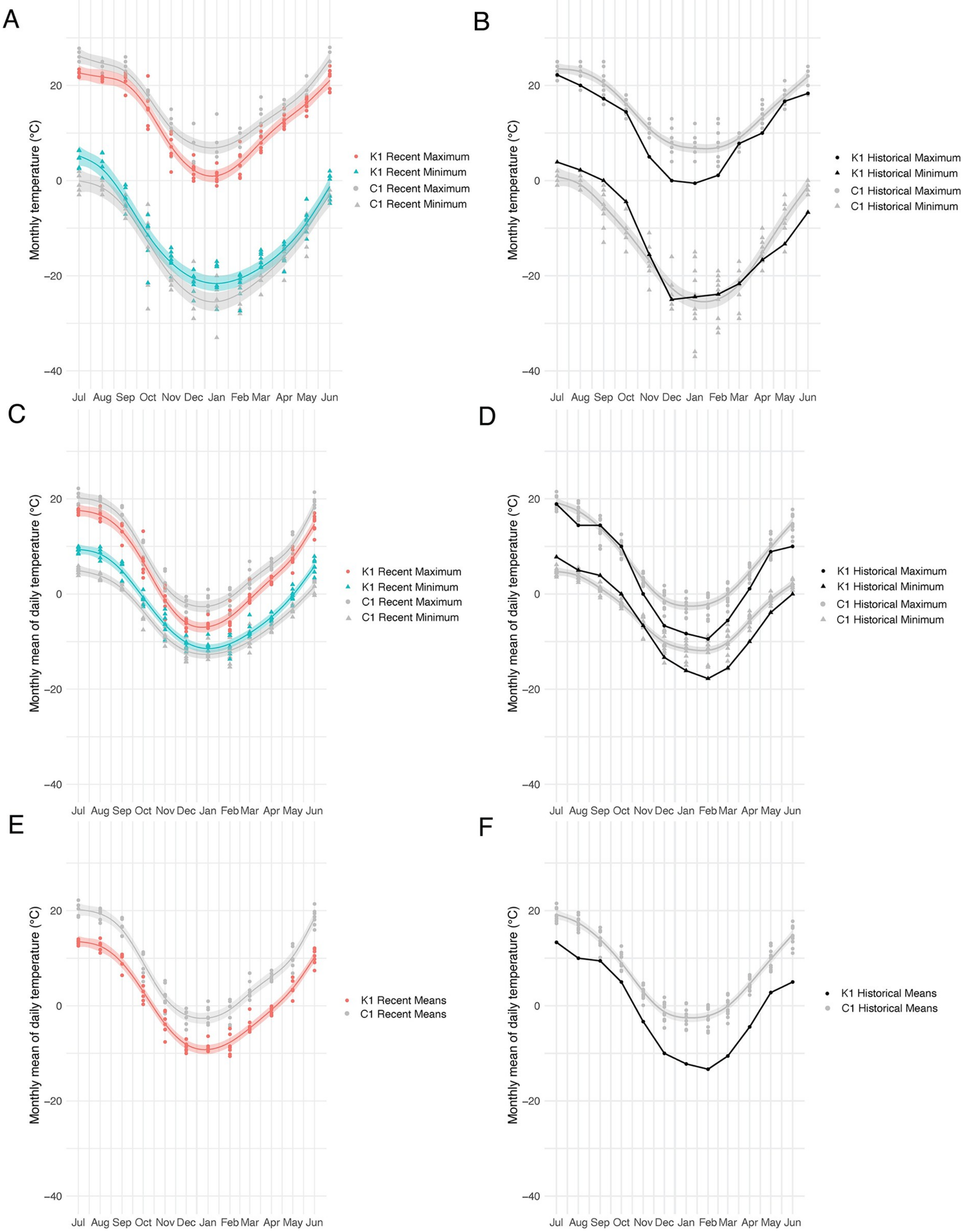

Fig 7. Recent and historical free-air temperatures at K1 and C1. Data recorded at the K1 pika study site and C1 subalpine weather station on Niwot Ridge (Boulder County, Colorado, USA). Means (curves) and 95% confidence intervals (shaded regions) were estimated using a cubic-spline smooth. See Table 1 for years associated with each period, and Table 2 for temperature metrics.

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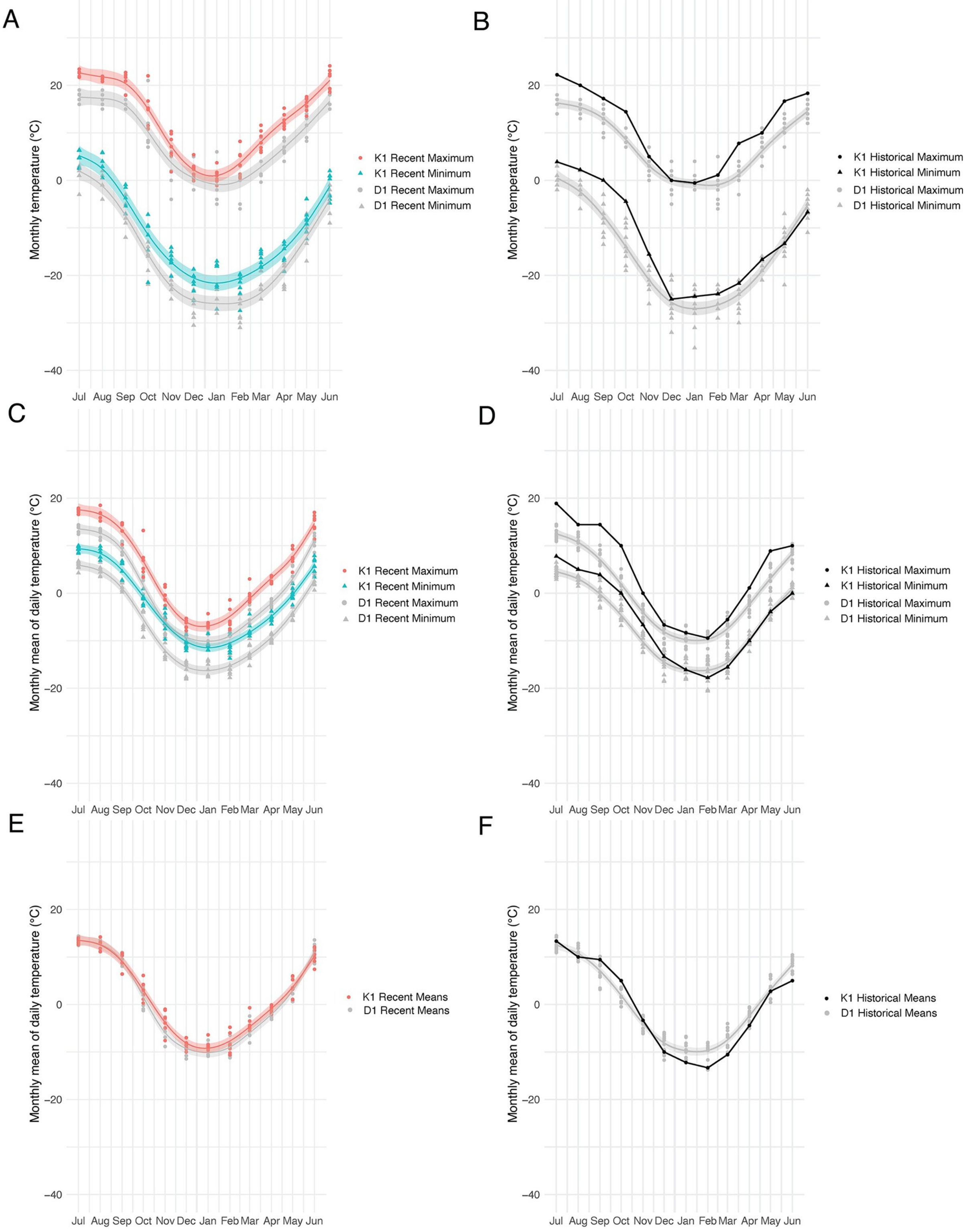

Fig 8. Recent and historical free-air temperatures at K1 and D1. Data recorded at the K1 pika study site and D1 alpine weather station on Niwot Ridge (Boulder County, Colorado, USA). Means (curves) and 95% confidence intervals (shaded regions) were estimated using a cubic-spline smooth. See Table 1 for years associated with each period, and Table 2 for temperature metrics.

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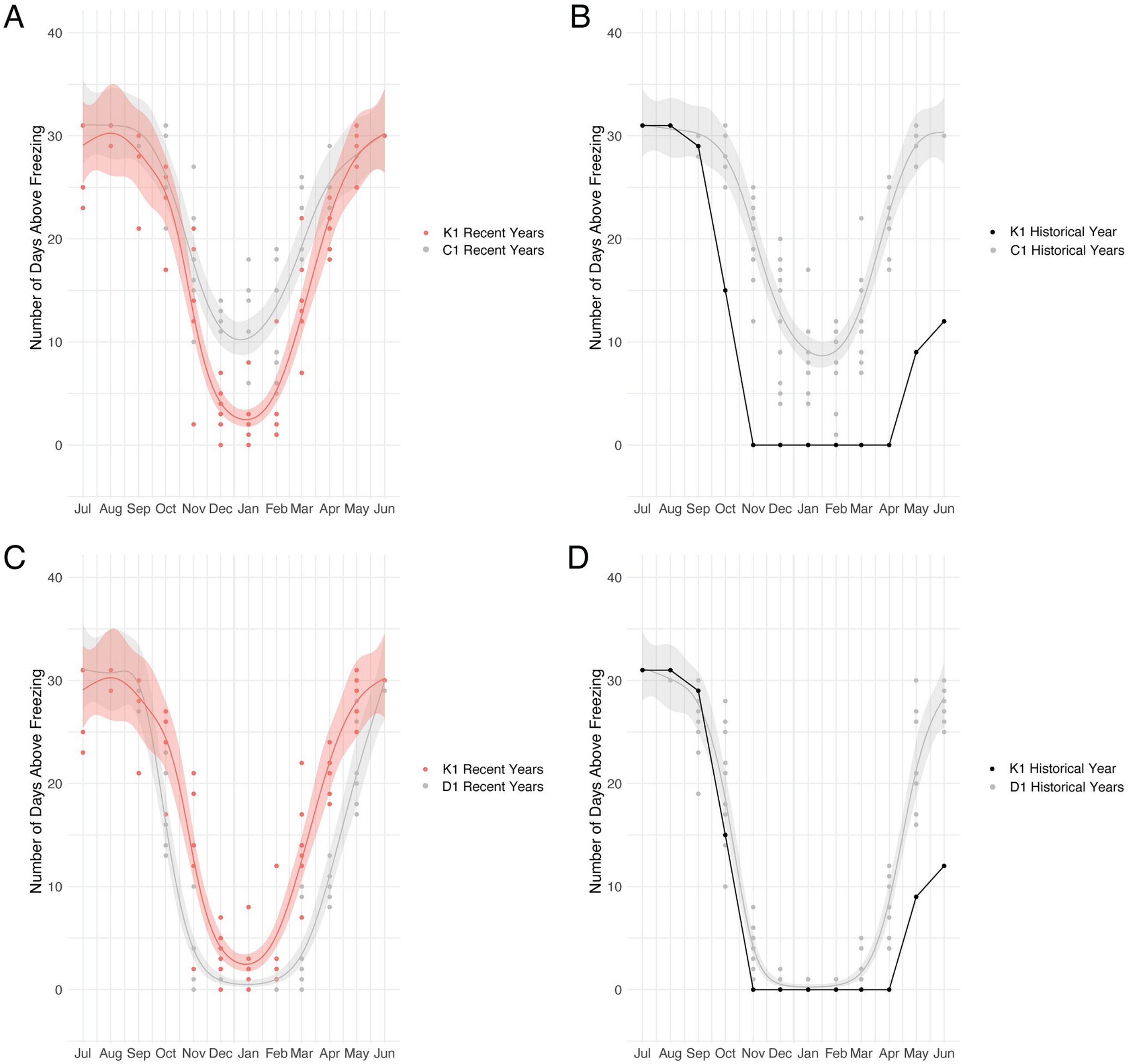

Fig 9. Recent and historical number of days above freezing (0˚ C). Data from the K1 pika study site and weather stations C1 (subalpine) and D1 (alpine) on Niwot Ridge (Boulder County, Colorado, USA). Recent weather station data (gray dots) were compared with recent K1 data (red dots) in panels A and C, while historical weather station data (gray dots) were compared with historical K1 data (black dots) in panels B and D. Means (curves) and 95% confidence intervals (shaded regions) were estimated using a cubic-spline smooth. See Table 1 for years associated with each period, and Table 2 for temperature metrics.

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this rock glacier appears to have exceeded warming in free-air temperature at this site and at two weather stations on the same ridge. Multiple metrics of talus temperature were warmer in recent years than in 1963–1964, most notably during the winter, at both shallow and deep positions. This apparent trend was greatest at the deeper placement, 1.37 m below the talus surface. Shallow sensors showed similar temperature shifts with a slightly reduced magnitude. Free-air temperatures also appeared to warm between 1964 and 2013, but did not experience the magnitude of change apparent in talus temperatures.

This warming trend was also supported by patterns in the number of days above freezing, which increased at K1 between periods, especially in fall and spring. In winter, K1 talus temperatures never rose above freezing, due to sufficient snow cover during both historical and recent periods. Snow cover can buffer subsurface temperatures, and a reduction in this buffering effect might explain why more warm days were recorded in the talus during the recent period. During the span of this study, the Western US has seen a significant decline in snow cover, especially in the spring [58, 59], although records from Niwot Ridge show more interannual variation than trends in precipitation [40].

While every attempt was made to place sensors consistently across years and to replicate historical methods based on information in Krear's dissertation and artifacts at the site, we acknowledge that there were slight differences in sensor position and important differences in sensor type between periods. Even small changes in instrumentation or the immediate environment surrounding a weather station can cause detectable variations in time-series data [60].

However, we used two methods to corroborate the apparent changes in temperature at K1 over the past 50 years. First, we used an independent set of shallow talus temperatures, recorded at pika haypiles surrounding the K1 temperature station, to show that the shallow temperatures at K1 were comparable to other shallow temperatures recorded in the same rock glacier from 2009 to 2021. Although winter temperatures were notably warmer in haypiles than in the shallow position at K1–possibly due to pika selection of suitable microclimates–this distinction means that the shallow K1 placement offered a conservative benchmark for change, and strengthens our finding that temperatures in shallow talus at this site were warmer in recent years than during 1963–1964. Second, we compared free-air temperatures at K1 during both historical and recent periods with temperatures at two weather stations on the same ridge. During the historical data-year, free-air temperatures at K1 were intermediate between those recorded at the two weather stations, as expected given the intermediate elevation of K1, and a similar pattern of intermediate temperatures at K1 was observed for recent temperatures. These results, along with the tight clustering of historical temperature metrics calculated from 1958–1969 records at each weather station, suggest that 1963–1964 was not an outlier with respect to temperature. A further concern involves thermal exchange issues that can be introduced by the use of a solar shield [61]. This issue applies only to the free-air sensors in this study, because sensors deployed in the talus were placed in the complete shade and drafty spaces among the rocks, requiring no shield. No data are available to assess how the effects of solar-shielding on free-air sensors might have differed between historical and recent periods. However, the fact that free-air temperatures at K1 were intermediate between C1 and D1 temperatures during both periods suggests that any difference in solar-shielding between periods did not cause a qualitative shift in the temperature record at K1. Finally, no outliers were identified in our review of the K1 data. We conclude that the qualitative pattern of change in temperature reported here did not result from changes in temperature monitoring equipment or variations in sensor placement between periods, although future studies would benefit from additional focus on how variations in sensor placement within the talus environment might affect results.

While rising temperatures are a particularly influential component of climate change, other factors such as shifting phenology and precipitation may be just as important [62, 63], and have measurable effects on species such as pikas [64]. However, precipitation metrics are typically more variable than temperature metrics, and monthly precipitation is predicted to become even more variable with climate change [65]. This relative variability can make it more difficult to detect trends in precipitation than trends in temperature, especially over short time scales. Research is needed on precipitation and its changing effects on pikas in this system, but will require more years of data to achieve confidence intervals as narrow as we achieved using temperature data.

Several results of this study align with previous work on both mountain climates and pika microclimates. Mountain climates are predicted to change faster than previously recorded, with impacts on both abiotic and biotic systems [66]. Pika range retraction and recent extirpations have been explained by temperature changes in both microclimate and regional climate [31, 64]. However, the potential for behavioral thermoregulation might allow the persistence of pikas at lower elevations and on their range periphery [67, 68]. Recent modeling has indicated that variability in the talus microclimate helps determine climate change response in pikas [69]. Although one study suggests that free-air temperature may be more important than subsurface temperature as a determinant of pika occupation and persistence in some regions [70], our study suggests that a warming trend in free air might be associated with disproportionate subsurface warming, an additional consideration that might not be evident from a study of short-term temperature records. The amount of subsurface warming required to stress pikas should be related to the amount of heat they need to shed, which should be related to surface temperature and the amount of required surface activity–variables that would vary in space and time. In a recent study that included the Krear site and other sites on and near Niwot Ridge, pika surface activity varied with the differential between shallow and deep temperatures in the talus [71]. The fact that this relationship could be detected in recent years suggests that recent subsurface temperatures in this region are at least somewhat limiting for pikas.

A relevant question is whether changes in pika density have been associated with the apparent changes in temperature documented at K1. Although the year-round occupancy of all territories was not tracked during the recent period as it was during the historical study, recent observations during late summer strongly suggest that several territories occupied during the historical study were no longer occupied in most recent years. Krear placed markers near the central haypile in each occupied territory [43, p. 18], and all recent haypiles were located near such markers, but almost half of his markers appeared to lack active haypiles in most years of the recent study—even in late summer and fall when haying activity should be greatest. These observations suggest that the trends seen in the temperature data might be having a negative impact on pika populations. However, additional factors such as forage availability, predation, snow cover, and precipitation were not considered in this analysis; a change in climate is likely to have an effect on other potential population drivers through mechanisms that are beyond the scope of this study. It has also been suggested that pikas may be able to deal with temperature changes by altering certain behaviors [72]; future studies at this site would benefit from ethological observations similar to those of Krear [44], allowing a temporal analysis of pika behavior. Beyond pikas, our results highlight the need for research on the relationships between macro- and microclimates in this system, to explore the potential for disproportionate warming and its consequences for thermal refugia that affect a variety of species and hydrological processes.

Results counter to our hypotheses should also be explored. Although we expected deeper portions of the talus to be less impacted by changes in air temperature, deeper sensors appeared to record larger changes in some metrics, relative to historical values. These results might be due to a loss—over the past 50 years—of processes with disproportionate effects on deep talus, such as cold-air drainage, Balch effect or permafrost cooling [73]. Our prediction that changes in temperature would be more pronounced in summer than in winter was also overturned. Although precipitation on Niwot Ridge—which falls mainly as snow—has not declined over the past 70 years, perhaps key properties of the snowpack have changed, such as the timing or duration of snow cover and frequency of freeze-thaw events, all of which can drive warming in the rock matrix through processes related to convection, advection, evaporation and sublimation, or by reducing the period of shallow snow cover that can lead to supercooling [73]. Addressing these hypotheses through further monitoring and modeling of rock-matrix microclimates should suggest where and when these landforms might fail to buffer species and permafrost from changes in climate.

Conclusion

Climate change is a global and persistent threat that has already impacted many living systems. Although organisms might escape some of these impacts by exploiting microclimates, little is known about how microclimatic refugia will respond to current changes in climate. This study utilizes a rare historical dataset to assess temporal changes in temperature within a subsurface microclimate, relative to changes in free-air temperature in the same vicinity. Temperatures experienced by animals using this microclimatic niche have increased dramatically over the past 50 years, perhaps even more than local free-air temperatures have increased over the same period. Our results suggest that subsurface microclimates, which provide a critical thermal refuge for many plants and animals, could be changing more rapidly than might be projected based on observed changes in climate. We encourage further research into historical records of microclimate and characterization of the relationships between climate and microclimate, which will affect myriad species and ecosystem processes.

Supporting information

S1 Fig. Recent and historical free-air temperatures at weather stations C1 and D1. Data recorded at subalpine (C1) and alpine (D1) weather stations on Niwot Ridge (Boulder County, Colorado, USA). Means (curves) and 95% confidence intervals (shaded regions) were estimated using a cubic-spline smooth. See Table 1 for years associated with each period, and Table 2 for temperature metrics.
(TIF)

S2 Fig. Recent and historical mean free-air temperatures and days above freezing at weather stations C1 and D1. Data recorded at subalpine (C1) and alpine (D1) weather stations on Niwot Ridge (Boulder County, Colorado, USA). Means (curves) and 95% confidence intervals (shaded regions) were estimated using a cubic-spline smooth (A and B). Recent data (green dots) and historical data (gray dots) on days above freezing are compared using bootstrapped 95% confidence intervals (C and D). See Table 1 for years associated with each period, and Table 2 for temperature metrics.
(TIF)

S1 File. Data from K1 sensors for recent years.
(ZIP)

S2 File. Code for K1 analysis in R.
(R)

S1 Text. Monthly summary statistic tables from recent (2009–2021) microclimatic data collected at K1 in deep subsurface portions of the talus and the free air.
(DOCX)

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Formal analysis: Emily M. Monk, Chris Ray.

Funding acquisition: Emily M. Monk, Chris Ray.

Investigation: Emily M. Monk, Chris Ray.

Methodology: Emily M. Monk, Chris Ray.

Resources: Chris Ray.

Software: Emily M. Monk, Chris Ray.

Writing – original draft: Emily M. Monk, Chris Ray.

Writing – review & editing: Emily M. Monk, Chris Ray.

References

1. Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. Nature. 2003 Jan; 421(6918):37–42. https://doi.org/10.1038/nature01286 PMID: 12511946
2. Brodie JF, Post ES, Doak DF. Climate Change and Wildlife Conservation. In: Brodie JF, Post ES, Doak DF, editors. Wildlife Conservation in a Changing Climate. Chicago: The University of Chicago Press; 2012. p. 1–14.
3. IPCC. Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. 2019.
4. Cannone N, Diolaiuti G, Guglielmin M, Smiraglia C. Accelerating climate change impacts on alpine glacier forefield ecosystems in the European Alps. Ecol Appl. 2008 Apr; 18(3):637–48. https://doi.org/10.1890/07-1188.1 PMID: 18488623
5. Mountain Research Initiative EDW Working Group. Elevation-dependent warming in mountain regions of the world. Nat Clim Change. 2015 May; 5(5):424–30.
6. Gao L, Deng H, Lei X, Wei J, Chen Y, Li Z, et al. Evidence of elevation-dependent warming from the Chinese Tian Shan. The Cryosphere. 2021 Dec 20; 15(12):5765–83.
7. Freeman BG, Lee-Yaw JA, Sunday JM, Hargreaves AL. Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. Glob Ecol Biogeogr. 2018 Nov; 27(11):1268–76.
8. Löffler J, Pape R. Thermal niche predictors of alpine plant species. Ecology. 2020 Jan; 101(1). https://doi.org/10.1002/ecy.2891 PMID: 31509230
9. De Frenne P, Lenoir J, Luoto M, Scheffers BR, Zellweger F, Aalto J, et al. Forest microclimates and climate change: Importance, drivers and future research agenda. Glob Change Biol. 2021 Jun; 27(11):2279–97. https://doi.org/10.1111/gcb.15569 PMID: 33725415
10. Riddell EA, Iknayan KJ, Hargrove L, Tremor S, Patton JL, Ramirez R, et al. Exposure to climate change drives stability or collapse of desert mammal and bird communities. Science. 2021 Feb 5; 371(6529):633–6. https://doi.org/10.1126/science.abd4605 PMID: 33542137
11. Storlie C, Merino-Viteri A, Phillips B, VanDerWal J, Welbergen J, Williams S. Stepping inside the niche: microclimate data are critical for accurate assessment of species' vulnerability to climate change. Biol Lett. 2014 Sep; 10(9):20140576. https://doi.org/10.1098/rsbl.2014.0576 PMID: 25252835
12. Stark JR, Fridley JD, Gill J. Microclimate-based species distribution models in complex forested terrain indicate widespread cryptic refugia under climate change. Glob Ecol Biogeogr. 2022 Mar; 31(3):562–75.
13. Scheffers BR, Edwards DP, Diesmos A, Williams SE, Evans TA. Microhabitats reduce animal's exposure to climate extremes. Glob Change Biol. 2014 Feb; 20(2):495–503. https://doi.org/10.1111/gcb.12439 PMID: 24132984
14. Lembrechts JJ, Nijs I, Lenoir J. Incorporating microclimate into species distribution models. Ecography. 2019 Jul; 42(7):1267–79.

15. Millar CI, Westfall RD, Evenden A, Holmquist JG, Schmidt-Gengenbach J, Franklin RS, et al. Potential climatic refugia in semi-arid, temperate mountains: Plant and arthropod assemblages associated with rock glaciers, talus slopes, and their forefield wetlands, Sierra Nevada, California, USA. Quat Int. 2015 Nov; 387:106–21.

16. Zellweger F, De Frenne P, Lenoir J, Rocchini D, Coomes D. Advances in Microclimate Ecology Arising from Remote Sensing. Trends Ecol Evol. 2019 Apr; 34(4):327–41. https://doi.org/10.1016/j.tree.2018.12.012 PMID: 30651180

17. National Research Council. Surface Temperature Reconstructions for the Last 2,000 Years: Chapter 2, The instrumental record [Internet]. Washington, D.C.: National Academies Press; 2006 . Available from: http://www.nap.edu/catalog/11676

18. Varner J, Dearing MD. The Importance of Biologically Relevant Microclimates in Habitat Suitability Assessments. Moreau CS, editor. PLoS ONE. 2014 Aug 12; 9(8):e104648. https://doi.org/10.1371/journal.pone.0104648 PMID: 25115894

19. Sharpe DM. Microclimatology. In: Climatology Encyclopedia of Earth Science. Dordrecht: Kluwer Academic Publishers; 1987. p. 572–81. (Encyclopedia of Earth Science).

20. Hoylman ZH, Jencso KG, Hu J, Martin JT, Holden ZA, Seielstad CA, et al. Hillslope Topography Mediates Spatial Patterns of Ecosystem Sensitivity to Climate. J Geophys Res Biogeosciences. 2018 Feb; 123(2):353–71.

21. Millar CI, Westfall RD, Delany DL. Thermal and hydrologic attributes of rock glaciers and periglacial talus landforms: Sierra Nevada, California, USA. Quat Int. 2013 Oct; 310:169–80.

22. Millar CI, Westfall RD. Distribution and Climatic Relationships of the American Pika (*Ochotona princeps*) in the Sierra Nevada and Western Great Basin, U.S.A.; Periglacial Landforms as Refugia in Warming Climates. Arct Antarct Alp Res. 2010 Feb; 42(1):76–88.

23. Juliussen H, Humlum O. Thermal regime of openwork block fields on the mountains Elgåhogna and Sølen, central-eastern Norway: Thermal Regime of Openwork Block Fields in Central-eastern Norway. Permafr Periglac Process. 2008 Jan; 19(1):1–18.

24. Hafner DJ. North American Pika (*Ochotona princeps*) as a Late Quaternary Biogeographic Indicator Species. Quat Res. 1993 May; 39(3):373–80.

25. Hafner DJ. Pikas and permafrost: post-Wisconsin historical zoogeography of Ochotona in the southern Rocky Mountains, USA. Arct Alp Res. 1994; 24(4):375–82.

26. Grayson DK. A brief history of Great Basin pikas. J Biogeogr. 2005 Dec; 32(12):2103–11.

27. Garrett L, Jeffress M, Britten M, Epps C, Ray C, Wolff S. Pikas in peril: multiregional vulnerability assessment of a climate-sensitive sentinel species. Park Sci. 2011; 28(2):1–3.

28. Beever EA, Brussard PF, Berger J. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. J Mammal. 2003 Feb; 84(1):37–54.

29. Ray C, Beever EA, Loarie S. Retreat of the American Pika: Up the Mountain or into the Void? In: Wildlife Conservation in a Changing Climate. Chicago (IL): University of Chicago Press; 2012. p. 245–70.

30. Stewart JAE, Perrine JD, Nichols LB, Thorne JH, Millar CI, Goehring KE, et al. Revisiting the past to foretell the future: summer temperature and habitat area predict pika extirpations in California. Riddle B, editor. J Biogeogr. 2015 May; 42(5):880–90.

31. Stewart JAE, Wright DH, Heckman KA. Apparent climate-mediated loss and fragmentation of core habitat of the American pika in the Northern Sierra Nevada, California, USA. Guralnick R, editor. PLOS ONE. 2017 Aug 30; 12(8):e0181834. https://doi.org/10.1371/journal.pone.0181834 PMID: 28854268

32. MacArthur RA, Wang LCH. Behavioral thermoregulation in the pika *Ochotona princeps*: a field study using radiotelemetry. Can J Zool. 1974 Mar 1; 52(3):353–8. https://doi.org/10.1139/z74-042 PMID: 4819475

33. Smith AT. The Distribution and Dispersal of Pikas: Influences of Behavior and Climate. Ecology. 1974 Nov; 55(6):1368–76.

34. Smith AT, Weston ML. Ochotona princeps. Am Soc Mammal. 1990 Apr;(No. 352):1–8.

35. MacArthur RA, Wang LCH. Physiology of thermoregulation in the pika, *Ochotona princeps*. Can J Zool. 1973 Jan 1; 51(1):11–6. https://doi.org/10.1139/z73-002 PMID: 4696076

36. Fountain AG, Campbell JL, Schuur EAG, Stammerjohn SE, Williams MW, Ducklow HW. The Disappearing Cryosphere: Impacts and Ecosystem Responses to Rapid Cryosphere Loss. BioScience. 2012 Apr; 62(4):405–15.

37. Biskaborn BK, Smith SL, Noetzli J, Matthes H, Vieira G, Streletskiy DA, et al. Permafrost is warming at a global scale. Nat Commun. 2019 Dec; 10(1):264. https://doi.org/10.1038/s41467-018-08240-4 PMID: 30651568

38. Berthling I. Beyond confusion: Rock glaciers as cryo-conditioned landforms. Geomorphology. 2011 Aug; 131(3–4):98–106.

39. Knight J, Harrison S, Jones DB. Rock glaciers and the geomorphological evolution of deglacierizing mountains. Geomorphology. 2019 Jan; 324:14–24.

40. Kittel TGF, Williams MW, Chowanski K, Hartman M, Ackerman T, Losleben M, et al. Contrasting long-term alpine and subalpine precipitation trends in a mid-latitude North American mountain system, Colorado Front Range, USA. Plant Ecol Divers. 2015 Nov 2; 8(5–6):607–24.

41. Janke JR. Modeling past and future alpine permafrost distribution in the Colorado Front Range. Earth Surf Process Landf. 2005 Nov; 30(12):1495–508.

42. Janke JR. Colorado Front Range Rock Glaciers: Distribution and Topographic Characteristics. Arct Antarct Alp Res. 2007 Feb; 39(1):74–83.

43. Ives JD, Fahey BD. Permafrost Occurrence in the Front Range, Colorado Rocky Mountains, U.S.A. J Glaciol. 1971; 10(58):105–11.

44. Krear HR. An ecological and ethological study of pika (*Ochotona princeps saxatilis, bangs*) in the Front Range of Colorado. University of Colorado at Boulder; 1965.

45. Krear RH, Garrett T. Four seasons north: exploration and research in the Arctic and subarctic. 1st ed. New York: Vantage Press; 2006. 368 p.

46. Marr JW. Ecosystems of the east slope of the Front Range in Colorado. Boulder: University of Colorado Press; 1961. 134 p. (Series in Biology No. 8).

47. McGuire CR, Nufio CR, Bowers MD, Guralnick RP. Elevation-Dependent Temperature Trends in the Rocky Mountain Front Range: Changes over a 56- and 20-Year Record. Añel JA, editor. PLoS ONE. 2012 Sep 6; 7(9):e44370. https://doi.org/10.1371/journal.pone.0044370 PMID: 22970205

48. Bueno de Mesquita CP, White CT, Farrer EC, Hallett LM, Suding KN. Taking climate change into account: Non-stationarity in climate drivers of ecological response. Battipaglia G, editor. J Ecol. 2021 Mar; 109(3):1491–500.

49. Kittel T, White C, Hartman M, Chowanski K, Ackerman T, Williams M, et al. Infilled air temperature data for C1 chart recorder, 1952–2018, daily [Internet]. Environmental Data Initiative; 2019 [cited 2022 Feb 27]. Available from: https://doi.org/10.6073/pasta/6b8288f9498b00cf4f2156a3fefc1b72

50. Kittel T, White C, Hartman M, Chowanski K, Ackerman T, Williams M, et al. Infilled air temperature data for D1 chart recorder, 1952–2018, daily [Internet]. Environmental Data Initiative; 2019 [cited 2022 Feb 27]. Available from: https://doi.org/10.6073/pasta/1b62f2cda71579c4870ac5c1af71e6f3

51. Morse JF, Losleben M, Niwot Ridge LTER. Air temperature data for C1 chart recorder, 1952—ongoing. [Internet]. Environmental Data Initiative; 2022 [cited 2022 Feb 27]. Available from: https://doi.org/10.6073/pasta/edd9e457fd22a703a587cc8608d54bde

52. Morse JF, Losleben M, Niwot Ridge LTER. Air temperature data for D1 chart recorder, 1952—ongoing. [Internet]. Environmental Data Initiative; 2022 [cited 2022 Feb 27]. Available from: https://doi.org/10.6073/pasta/1e9f40409e69299b1a41f98ac767bcd7

53. Ray C, Niwot Ridge LTER. Pika demography data for west knoll and Indian Peaks wilderness, 2008—ongoing ver 4. Environ Data Initiat.

54. R Core Team. R: A language and environment for statistical computing [Internet]. Vienna, Austria: R Foundation for Statistical Computing; 2021. Available from: https://www.R-project.org/

55. Kahle D, Wickham H. ggmap: Spatial Visualization with ggplot2. R J. 2013; 5(1):144.

56. Wood SN. Generalized Additive Models: An Introduction with R. 2nd ed. Chapman and Hall/CRC; 2017.

57. Wickham H. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York; 2016.

58. Gergel DR, Nijssen B, Abatzoglou JT, Lettenmaier DP, Stumbaugh MR. Effects of climate change on snowpack and fire potential in the western USA. Clim Change. 2017 Mar; 141(2):287–99.

59. Mote PW, Li S, Lettenmaier DP, Xiao M, Engel R. Dramatic declines in snowpack in the western US. Npj Clim Atmospheric Sci. 2018 Dec; 1(1):2.

60. Runnalls KE, Oke TR. A Technique to Detect Microclimatic Inhomogeneities in Historical Records of Screen-Level Air Temperature. J Clim. 2006 Mar 15; 19(6):959–78.

61. Maclean IMD, Duffy JP, Haesen S, Govaert S, De Frenne P, Vanneste T, et al. On the measurement of microclimate. Methods Ecol Evol. 2021 Aug; 12(8):1397–410.

62. Inkley DB, Anderson MG, Blaustein AR, Burkett VR, Felzer B, Griffith B, et al. Global climate change and wildlife in North America. Wildl Soc. 2004;Wildlife Society Technical Review 04–2:26.

63. McCain CM, Colwell RK. Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate: Climate change risk for montane vertebrates. Ecol Lett. 2011 Dec; 14(12):1236–45. https://doi.org/10.1111/j.1461-0248.2011.01695.x PMID: 21981631

64. Beever EA, Perrine JD, Rickman T, Flores M, Clark JP, Waters C, et al. Pika (*Ochotona princeps*) losses from two isolated regions reflect temperature and water balance, but reflect habitat area in a mainland region. J Mammal. 2016 Dec 5; 97(6):1495–511.

65. Pendergrass AG, Knutti R, Lehner F, Deser C, Sanderson BM. Precipitation variability increases in a warmer climate. Sci Rep. 2017 Dec; 7(1):17966. https://doi.org/10.1038/s41598-017-17966-y PMID: 29269737

66. Nogués-Bravo D, Araújo MB, Errea MP, Martínez-Rica JP. Exposure of global mountain systems to climate warming during the 21st Century. Glob Environ Change. 2007 Aug; 17(3–4):420–8.

67. Henry P, Henry A, Russello MA. Variation in Habitat Characteristics of American Pikas along an Elevation Gradient at Their Northern Range Margin. Northwest Sci. 2012 Sep; 86(4):346–50.

68. Rodhouse TJ, Hovland M, Jeffress MR. Variation in subsurface thermal characteristics of microrefuges used by range core and peripheral populations of the American pika (*Ochotona princeps*). Ecol Evol. 2017 Mar; 7(5):1514–26. https://doi.org/10.1002/ece3.2763 PMID: 28261461

69. Moyer-Horner L, Mathewson PD, Jones GM, Kearney MR, Porter WP. Modeling behavioral thermoregulation in a climate change sentinel. Ecol Evol. 2015 Dec; 5(24):5810–22. https://doi.org/10.1002/ece3.1848 PMID: 26811756

70. Wright DH, Stewart JAE. Within-talus temperatures are not limiting for pikas in the northern Sierra Nevada, California, USA. Calif Fish Game. 2018; 104(4):180–95.

71. Benedict LM, Wiebe M, Plichta M, Batts H, Johnson J, Monk E, et al. Microclimate and Summer Surface Activity in the American Pika (Ochotona princeps). West North Am Nat. 2020 Oct 7; 80(3).

72. Varner J, Horns JJ, Lambert MS, Westberg E, Ruff JS, Wolfenberger K, et al. Plastic pikas: Behavioural flexibility in low-elevation pikas (*Ochotona princeps*). Behav Processes. 2016 Apr; 125:63–71. https://doi.org/10.1016/j.beproc.2016.01.009 PMID: 26851456

73. Millar CI D. Westfall R, Delany DL. Thermal Regimes and Snowpack Relations of Periglacial Talus Slopes, Sierra Nevada, California, U.S.A. Arct Antarct Alp Res. 2014 May; 46(2):483–504.