Ecological Applications, 24(7), 2014, pp. 1748–1768

Radiocarbon dating of American pika fecal pellets provides insights into population extirpations and climate refugia

Constance I. Millar,[1,5] Katherine Heckman,[2] Christopher Swanston,[3] Karena Schmidt,[4] Robert D. Westfall,[1] and Diane L. Delany[1]

[1]*USDA Forest Service, Pacific Southwest Research Station, Albany, California 94710 USA*
[2]*USDA Forest Service, Northern Research Station, Lawrence Livermore National Lab, Livermore, California 94550 USA*
[3]*USDA Forest Service, Northern Research Station, Northern Institute of Applied Climate Science, Houghton, Michigan 49931 USA*
[4]*Michigan Technological University, School of Forest Resources and Environmental Science, Houghton, Michigan 49931 USA*

Abstract. The American pika (*Ochotona princeps*) has become a species of concern for its sensitivity to warm temperatures and potential vulnerability to global warming. We explored the value of radiocarbon dating of fecal pellets to address questions of population persistence and timing of site extirpation. Carbon was extracted from pellets collected at 43 locations in the western Great Basin, USA, including three known occupied sites and 40 sites of uncertain status at range margins or where previous studies indicated the species is vulnerable. We resolved calibrated dates with high precision (within several years), most of which fell in the period of the mid-late 20th century bomb curve. The two-sided nature of the bomb curve renders far- and near-side dates of equal probability, which are separated by one to four decades. We document methods for narrowing resolution to one age range, including stratigraphic analysis of vegetation collected from pika haypiles. No evidence was found for biases in atmospheric ^{14}C levels due to fossil-derived or industrial CO_2 contamination. Radiocarbon dating indicated that pellets can persist for >59 years; known occupied sites resolved contemporary dates. Using combined evidence from field observations and radiocarbon dating, and the Bodie Mountains as an example, we propose a historical biogeographic scenario for pikas in minor Great Basin mountain ranges adjacent to major cordillera, wherein historical climate variability led to cycles of extirpation and recolonization during alternating cool and warm centuries. Using this model to inform future dynamics for small ranges in biogeographic settings similar to the Bodie Mountains in California, extirpation of pikas appears highly likely under directional warming trends projected for the next century, even while populations in extensive cordillera (e.g., Sierra Nevada, Rocky Mountains, Cascade Range) are likely to remain viable due to extensive, diverse habitat and high connectivity.

Key words: American pika; climate refugia; habitat occupancy; historical ecology; isotopes; Ochotona princeps; *radiocarbon dating; Sierra Nevada.*

Introduction

American pikas (*Ochotona princeps*, Richardson) are small, generalist herbivores that inhabit patchily distributed rocky slopes in mountains of 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 (MacArthur and Wang 1973, Smith 1974*a*). This sensitivity, coupled with their low reproductive rate, poor dispersal capability, low population density, and occupancy of scattered mountain habitat, has raised concern for the persistence of pikas in the face of warming temperatures (Grayson 2005, Beever et al. 2011).

Manuscript received 20 March 2013; revised 21 February 2014; accepted 25 February 2014. Corresponding Editor (ad hoc): R. Guralnick.
[5] E-mail: cmillar@fs.fed.us

The spotlight on American pikas as potentially at risk has catalyzed research to investigate their current status, particularly through the resurvey of historical populations and assessments of the resilience of pikas when confronted with warming temperatures. The resulting studies have yielded varying results and raised new questions. One body of studies suggests that the species remains distributed across a wide range of elevations in the major western cordilleras, including the Rocky Mountains (Hafner 1994, Erb et al. 2011), Cascade Range (Simpson 2009, Manning and Hagar 2011), and Sierra Nevada (Millar and Westfall 2010, Stewart and Wright 2012). Behavioral adaptations, abundant habitat, and unique thermal regimes of talus habitat are offered as evidence that pikas might have capacity to adjust to contemporary climate dynamics in these parts of the species range (MacArthur and Wang 1974, Smith 1974*a*, Millar and Westfall 2008, 2010, Millar et al. 2013, Erb et al. 2011).

Studies in other parts of pikas' distribution range highlight a different prognosis. Trends in Great Basin ranges appear to follow Quaternary-long patterns, wherein populations in low-elevation warm locations became extirpated during warmer periods of the Holocene, and these sites were not recolonized (Grayson 2005). Resurvey studies of sites where pikas were reported in the early 20th century have revealed population extirpations, primarily at low-elevation warm margins of their range, in a trend that has accelerated over the past two decades. These losses appear to have occurred not only due to acute warm temperatures in summer but also to winter cold exposure, which results from thinner snowpacks and loss of thermal insulation (Beever et al. 2003, 2010, 2011).

Regional differences in response to climate change are being documented for other species, as well as for pikas. Elucidation of factors contributing to these differences can be important for understanding both species biology and conservation approaches. We demonstrate the application of radiocarbon dating to current topics of neo-ecology and conservation interest. Using evidence provided by dating pika pellets and haypile vegetation, we evaluate the strengths and weaknesses of the method and explore questions about pika population status related to climate vulnerability and biogeography.

Background

Isotope dating

Dating organic material based on decay rates of radioactive isotopes is a fundamental and essential technology widely employed in many fields of science (Tuniz et al. 2011). In paleoecology, analysis of radioactive carbon (^{14}C) has been routinely used to date historical material on late Quaternary timescales, for instance, subfossils from Holocene or Pleistocene sediment cores, pack rat middens, or anthropologic sites. Application of this technique to problems of the recent century, however, has been relegated mostly to forensic analysis, and ecological insights afforded by the method have not been widely exploited. Because ecologists might be unfamiliar with the precision, accuracy, and opportunities this method offers, we briefly summarize background information.

For terrestrial organisms, dating is based on the fact that tissues remain in equilibrium with atmospheric levels of ^{14}C while individuals are alive. Upon death, ^{14}C in tissues decays over time based on a rate determined by its half-life (5730 years). Under theoretical assumptions of constant atmospheric ^{14}C levels over time and a lack of geographic variability in those levels, the concentration of ^{14}C in dead organic tissue would decline steadily over time and directly correspond to its age. Calibration of the radiocarbon curve, however, using tree rings and other natural archives, has clarified that many forces cause atmospheric ^{14}C concentrations to fluctuate over time, including natural changes in cosmic ray activity in the upper atmosphere and a suite of natural and anthropogenic influences at and near the earth's surface. Natural effects prior to 1951 caused the atmospheric ^{14}C production rate to vary significantly during certain periods, in turn causing atmospheric ^{14}C concentration to fluctuate over time. The plot of atmospheric ^{14}C concentration vs. calendar year, thus, is riddled with deviations from the average concentration, a complication that can render calendar-year calibrations impractical for some time periods, and thus, certain lines of inquiry.

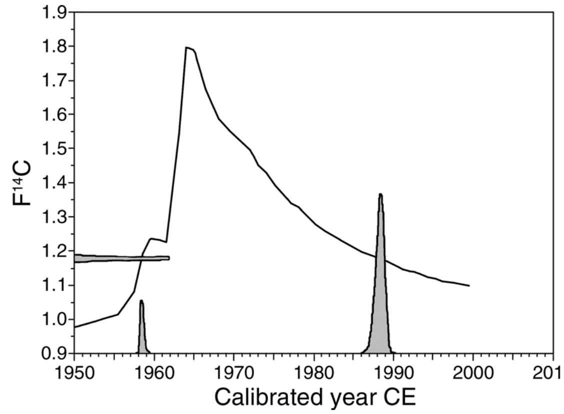

FIG. 1. Northern hemisphere zone 2 radiocarbon curve (black line) from 1950–2010 showing the effect of nuclear testing on atmospheric ^{14}C levels. Note the steep rise between 1954 and 1964 (the period of most active testing) and the slower decay after 1964. Standardized calibrations at hemispheric scale are not yet available after 2000 CE, although regional curves are available in some areas. The gray-filled curves along the *x*- and *y*-axes illustrate the radiocarbon dating results for a pellet sample in this study, Queen Bee Hill, a native pika habitat in the Bodie Mountains (BOD-2, Table 1). The $F^{14}C$ notation indicates that the radiocarbon values have been corrected for isotopic fractionation effects ($\delta^{13}C$-normalized).

Starting in 1951, however, the atmospheric situation became very different. The most significant known effect on global atmospheric levels of ^{14}C resulted from aboveground nuclear testing that took place between 1951 and 1980. As a result, ^{14}C concentration in the atmosphere nearly doubled, rising rapidly from background natural levels in 1951 to a peak in the early 1960s and declining at a slower rate thereafter (Taylor 1987; Fig. 1). For several reasons, this spike of bomb radiocarbon affords highly accurate dating of records that occur after about 1950. First, levels of ^{14}C in the atmosphere are higher than values in the known prior historical period, so the range of dates for an unknown sample can be narrowed with high confidence to the second half of the 20th century. Second, the steep slopes of the bomb curve mean that intersection of the ^{14}C value of a sample corresponds to a small, calibrated date range, greatly improving precision. A significant drawback of the spike, however, is that most ^{14}C values from this period will yield calibrated date estimates on both sides of the bomb curve. Without ancillary information,

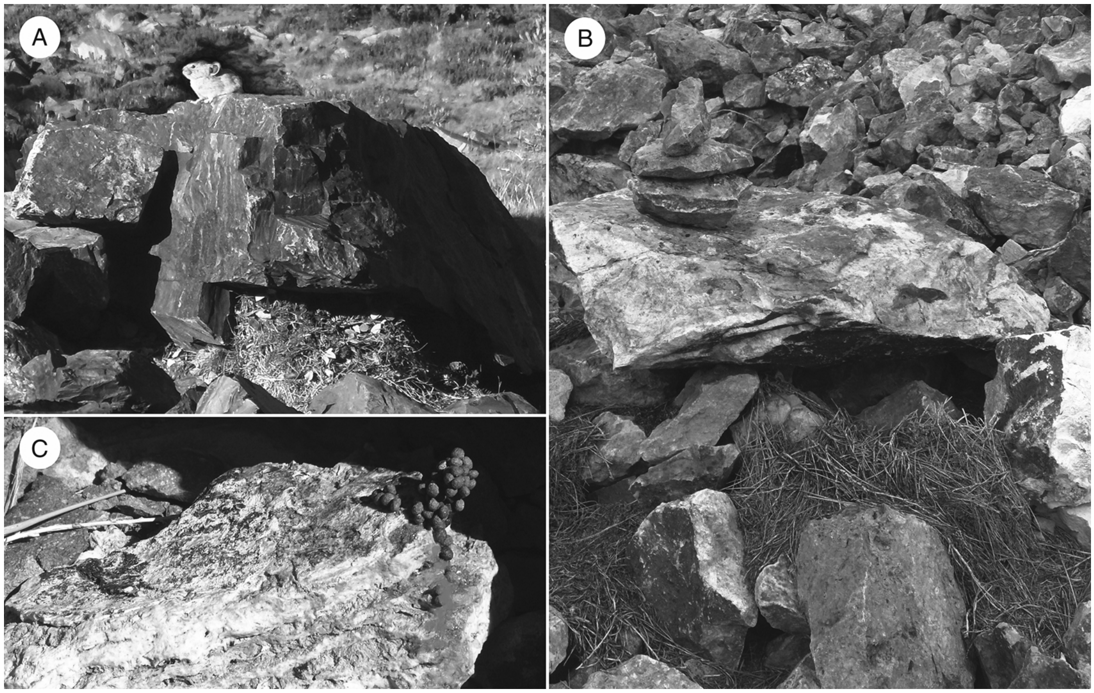

FIG. 2. (A) An American pika (*Ochotona princeps*) defending its winter cache of forage (haypile), which comprises a mix of herbaceous plant species. (B) Dry haypile; not all vegetation is consumed over winter. (C) Pika fecal pellets. Fresh pellets often are found adhered together by urine and mucus and balanced in a stack.

such near-side and far-side calibrations are equally likely.

While the bomb curve affords highly precise dating after 1950, regionalized and local effects can confound atmospheric ^{14}C concentrations. The enhanced production of ^{14}C in the atmosphere during bomb testing and the subsequent diffusion of this bomb radiocarbon into the broader global atmosphere caused significant geographical differences in atmospheric ^{14}C concentrations. Consequently, several hemispheric regions were mapped based on the global distribution of bomb radiocarbon, each with unique calibrated age curves. Another regional influence on atmospheric ^{14}C concentrations is the Suess- or industrial-effect, wherein burning of industrial and fossil fuels results in large amounts of ^{14}C-depleted CO_2 being emitted into the atmosphere (Hsueh et al. 2007). The infinite age of the sources (e.g., coal, petroleum) dilutes natural atmospheric ^{14}C levels in areas significantly affected by plumes of polluted air. Similar localized but natural effects can occur where active volcanic emissions (fumaroles, hot springs) of radiocarbon-depleted CO_2 can affect ^{14}C values in their zone of influence (Bruns et al. 1980). Further uncertainty can derive from biotic sources. For instance, cells from plant species with persistent tissue (e.g., long-lived trees) can yield wider ranges of dates than material from annual plants. Similarly, tissue from animals that eat dead forage could yield a wide range of calibrated dates.

Limitations notwithstanding, radiocarbon dating during the bomb era is a powerful and, as yet, underexploited tool with the potential to illuminate diverse questions in ecology and conservation. The capacity of modern accelerator mass spectrometry to assess small amounts of sample material adds to the scope of potential applications.

American pika

A central challenge in many conservation applications, including that for the American pika, is to assess population trends and ascribe causal factors. To do this requires accurate determination of times when sites were occupied and, more importantly, when populations at these sites might have become extirpated. Pika habitat, as well as the animals themselves, are easily recognized (Fig. 2). Pikas are highly restricted to talus and other rocky landforms and to adjacent vegetated forefields from which they forage. Indirect sign of pikas is diagnostic of the species as well (Rodhouse et al. 2010, Jeffress et al. 2013; Fig. 2). Typical of lagomorphs, fecal pellets of pikas are spherical, not readily confused with rodent sign, and are often deposited in piles within talus. Pikas do not hibernate in winter, and during the warm, season they collect herbaceous vegetation from a variety of plant species growing near talus margins. Foliage is carried into talus matrices where it is stacked into so-called haypiles from which pikas forage during winter. Haypiles are not entirely consumed, sites are often (but not always) reused, and old haypiles comprising short, thin-diametered woody stems, pellets, and decomposing litter persist for an unknown number of years (Smith and Weston 1990). During late summer and fall, green haypiles are considered diagnostic of pika occupancy, whereas dried haypiles suggest occupancy at an uncertain time in the past.

These indirect signs are widely accepted evidence that pikas have been present at a site sometime in the past. What has become increasingly unclear, however, is what indirect sign, other than green haypiles, indicates about current occupancy, and observations suggest that pellets can persist for many years in dry sites (Nichols 2011). Determination of occupancy or time since extirpation is critical for evaluating conservation status of pikas and their potential risk from climate change. The need for time-series information is especially important for a species such as the pika that exhibits metapopulation behavior, because small patches of habitat can naturally alternate between empty and occupied, even in the absence of long-term driving forces, as has been shown in longitudinal studies (Smith and Gilpin 1997; Smith and Nagy, *unpublished manuscript*). To date, no reliable method for estimating age of sign has been developed for situations where occupancy is inconclusive during the course of a survey.

Methods

Field

As part of an ongoing survey of pika distribution in California, Nevada, and Oregon, we have been collecting fecal pellets since 2007 to document observed sites (Millar and Westfall 2010). At the time of collection, we meant only to voucher the sites, thus no effort was made to select pellets of a particular type or from a specific context. In general, however, each sample represented a group of pellets from ~1-m^2 area. We subsampled this archive, choosing 43 sites for analysis (Table 1; Fig. 3). Three samples collected between 2007 and 2010 were from distinct and known occupied sites containing abundant fresh-appearing pellets. With these samples, we developed quantifiable lab methods, validated radiocarbon dating, and assessed sites from typical pika environments in the middle of the species' elevation range for these states.

The remaining 40 samples represented sites of uncertain occupancy at the time of collection. Many were in regions of prior published surveys; some were at locations of early 20th century records or where long-term studies had been conducted. We chose these sites to represent marginal pika environments at low elevations or with warm exposures, sites that had only relict-appearing sign, and/or sites that represented small, isolated, or suboptimal habitats. A few of these sites appeared from indirect sign to be have been modern (sensu Millar and Westfall [2010], haypiles with foliage intact although dry; pellets large and deep brown, not decomposing; and potentially currently occupied or in the past ~5 years), although no animals were seen or heard during the original surveys. During revisits in 2011–2012, at several of these sites animals and fresh haypiles were seen, and those sites were considered occupied, at least in that year.

Laboratory and analysis

Pika fecal pellets were sent to the Carbon, Water, and Soils Research Lab in Houghton, Michigan for pretreatment and graphitization. Samples were oven dried at 50°C for 24 h, then weighed into borosilicate culture tubes. The culture tubes were inserted into a heating block set to 95°C. Samples were treated first with 1 mol/L HCl for 20 min, then with successive washes of 1 mol/L NaOH for 25-minute periods until only undigested plant fibers remained. The samples were then treated with 1 mol/L HCl once more and washed twice with deionized water before drying. Water rinses were done at room temperature for 1–2 minutes each. When dried, the organics were weighed and transferred to quartz combustion tubes. Mineral grains were often found in the pretreated samples, but were removed from the sample with forceps prior to weighing. To obtain adequate material for subsequent analyses (~85 mg), we needed to homogenize 8–10 pellets from each 1-m^2 sample site, thus potentially mixing pellets from multiple defecation events that would have different ^{14}C abundances. Dates reported for each sample thus represent a composite of multiple pellets or an average date from one territory.

Pikas are known to consume a variety of plant species, including monocots and dicots (Huntly et al. 1986), which potentially includes taxa that use C_3 and C_4 photosynthetic pathways. Although evidence from a genus-wide survey suggests that pikas preferentially consume C_3 plants (Ge et al. 2012), many of the plant genera foraged by pikas in western North America include C_4 taxa, and information about pathways is not available for all species eaten by the American pika. Because of the large difference in δ^{13}C signatures of C_3 and C_4 plants (approximately −25‰ and −13‰ respectively), we chose in our initial analyses to include δ^{13}C measurements on each sample to improve precision of calculated radiocarbon activities in the event that some C_4 plants were included in the sampled pellets. After pretreatment and weighing, approximately half (~2 mg) of the remaining material for each sample was sent to Michigan Technological University Forest Ecology Stable Isotope Lab where δ^{13}C values were determined using a Costech Elemental Combustion System 4010 (Costech, Valencia, California, USA) connected to a continuous flow isotope ratio mass spectrometer (Delta Plus, Thermo-Finnigan, Bremen, Germany). δ^{13}C values are reported in reference to the international Pee Dee belemnite standard.

The remaining portion of each sample (~2 mg) was graphitized in preparation for ^{14}C measurement. Samples were combusted with CuO and Ag in sealed glass

TABLE 1. Collection information for American pika pellet sites.

Collection ID	Map code	Mountain range	Location	State	County
Known occupied sites					
VIR-1	A	Sierra Nevada	Virginia Lakes Canyon	CA	Mono
WAR-1	B	Sierra Nevada	Lee Vining Canyon	CA	Mono
SAD-1	C	Sierra Nevada	Saddlebag Lake	CA	Mono
Sites of uncertain occupancy					
SLI-1	1	Fremont Mtns	Slide Mtn	OR	Lake
SLI-2	2	Fremont Mtns	Slide Mtn	OR	Lake
COU-1	3	Fremont Mtns	Cougar Peak	OR	Lake
BAR-1	4	Mosquito Mtns	Barrel Springs	NV	Washoe
BAR-2	5	Mosquito Mtns	Barrel Springs	NV	Washoe
BAR-3	6	Mosquito Mtns	Barrel Springs	CA	Washoe
SUM-1	7	Idaho Canyon Range	Summit Lake	NV	Humboldt
SUM-2	8	Idaho Canyon Range	Summit Lake	NV	Humboldt
SUM-3	9	Idaho Canyon Range	Summit Lake	NV	Humboldt
MAD-1	10	Madeline Plain	Termo	CA	Lassen
MAD-2	11	Madeline Plain	Termo	CA	Lassen
SHO-1	12	Shoshone Mtns	Bald Mtn	NV	Nye
TOI-1	13	Toiyabe Mtns	Ophir Canyon	NV	Nye
WAS-1	14	Wassuk Mtns	Big Indian Mtn	NV	Mineral
WAS-2	15	Wassuk Mtns	Corey Peak	NV	Mineral
SON-1	16	Sierra Nevada	Sonora Bridge	CA	Mono
MAS-1	17	Bodie Mtns	Serita Mine, New York Hill	CA	Mono
MAS-2	18	Bodie Mtns	Serita Mine, New York Hill	CA	Mono
MAS-3	19	Bodie Mtns	Serita Mine, New York Hill	CA	Mono
MAS-4	20	Bodie Mtns	Masonic Mtn N	CA	Mono
MAS-5	21	Bodie Mtns	Chemung Mine	CA	Mono
MAS-6	22	Bodie Mtns	Chemung Mine	CA	Mono
SWE-1	23	Sweetwater Mtns	Devils Gate	CA	Mono
MAS-7	24	Bodie Mtns	Chemung Mine	CA	Mono
MAS-8	25	Bodie Mtns	Masonic Mtn NW	CA	Mono
POT-1	26	Bodie Mtns	Potato Peak/Aurora Canyon	CA	Mono
AUR-1	27	Bodie Mtns	Aurora Mine	NV	Mineral
AUR-2	28	Bodie Mtns	Aurora Mine	NV	Mineral
AUR-3	29	Bodie Mtns	Aurora Mine	NV	Mineral
AUR-4	30	Bodie Mtns	Brawley Peak	NV	Mineral
BOD-1	31	Bodie Mtns	Noonday Mine	CA	Mono
BOD-2	32	Bodie Mtns	Queenbee Hill	CA	Mono
BOD-3	33	Bodie Mtns	Sugarloaf Butte	CA	Mono
ROB-1	34	Sierra Nevada	Robinson Canyon	CA	Mono
CLE-1	35	Bodie Mtns	Clearwater Creek	CA	Mono
BRI-1	36	Bodie Mtns	Bridgeport Canyon	CA	Mono
BRI-2	37	Bodie Mtns	Bridgeport Canyon	CA	Mono
PAR-1	38	Sierra Nevada	Parker Canyon	CA	Mono
KEL-1	39	Glass Mtns	Kelty Ridge	CA	Mono
ROC-1	40	Sierra Nevada	Lower Rock Creel	CA	Mono

Notes: Sites are listed from north to south within known occupied sites and sites with uncertain occupancy, as evaluated in the field at the time of collection and prior to isotope dating. Sites ordered latitudinally within sections, from north (top) to south. Aspect is N, north; NE, northeast; E, east; SE, southeast; S, south; SW, southwest; W, west, and NW, northwest. Abbreviations are CA, California; OR, Oregon; NV, Nevada; Mtns, Mountains.

test tubes to form CO_2 gas. The CO_2 was then reduced to graphite through heating in the presence of H_2 gas and a Fe catalyst (Vogel et al. 1987). Radiocarbon content of each graphitized sample was measured by accelerator mass spectrometry in January 2012 at the Center for Accelerator Mass Spectrometry (CAMS), Lawrence Livermore National Lab, Livermore, California, USA (Davis et al. 1990). Sample measurements were normalized to the absolute activity of the international radiocarbon standard, oxalic acid I. Secondary radiocarbon standards of well-defined ^{14}C activity (oxalic acid II, ANU sucrose, and Tiriwood) were measured along with all unknowns as quality checks.

Radiocarbon data are reported as $F^{14}C$ following the recommendations of Reimer et al. (2004). The $F^{14}C$ term is more explicit than the more often reported Fm (Fraction modern) in that the $F^{14}C$ notation indicates that the radiocarbon values have been corrected for isotopic fractionation effects ($\delta^{13}C$-normalized), whereas the term Fm has been used to refer to ^{14}C data both with and without $\delta^{13}C$ normalization of the sample activity. In many cases, radiocarbon activities are calculated using a standard $\delta^{13}C$ ratio of −25‰ (per mil or parts per thousand) with respect to Pee Dee belemnite. However, calculations of sample radiocarbon activity can be skewed from their true value if the actual $\delta^{13}C$ ratio of the sample varies significantly from −25‰.

TABLE 1. Extended.

Aspect	Landform	Latitude (°N)	Longitude (°W)	Elevation (m)	Date collected
S	talus slope	38.06	119.28	3220	June 2009
SW	talus slope	37.98	119.24	3231	August 2010
E	talus slope	37.96	119.28	3050	August 2007
NE	talus slope	42.69	120.74	1967	June 2010
ENE	talus slope	42.69	120.74	1961	June 2010
SW	talus slope	42.29	120.64	1932	June 2010
SW	lava flow	41.91	119.96	1667	June 2010
SSW	lava flow	41.91	119.96	1666	June 2010
SSW	lava flow	41.90	119.96	1709	June 2010
W	talus slope	41.60	119.08	1853	June 2010
W	talus slope	41.60	119.08	1850	June 2010
W	talus slope	41.60	119.08	1849	June 2010
S	lava flow	40.93	120.47	1825	May 2011
SW	lava flow	40.92	120.47	1837	May 2011
NW	talus slope	39.01	117.56	2861	May 2008
SW	talus slope	38.95	117.35	2652	May 2008
S	inselberg	38.49	118.80	3048	August 2008
SE	talus slope	38.44	118.76	2680	August 2007
NW	talus slope	38.37	119.48	2038	October 2011
NW	ore dump	38.36	119.13	2556	October 2011
NW	eroded slope	38.36	119.13	2594	June 2011
NE	ore dump	38.36	119.13	2581	October 2010
N	talus slope	38.36	119.14	2463	June 2011
N	ore dump	38.35	119.15	2566	October 2010
SW	talus slope	38.35	119.15	2526	June 2011
N	talus slope	38.34	119.37	2310	August 2008
W	ore dump	38.33	119.15	2496	November 2008
W	talus slope	38.32	119.14	2612	January 2009
W	talus slope	38.28	119.12	2590	May 2010
SE	ore dump	38.28	118.90	2338	June 2011
NE	ore dump	38.28	118.90	2403	September 2010
E	ore dump	38.27	118.90	2455	September 2010
SE	talus slope	38.26	118.91	2853	November 2007
S	ore dump	38.20	119.01	2600	October 2007
E	eroded slope	38.20	119.01	2632	October 2007
NE	talus slope	38.19	119.01	2594	November 2007
S	talus slope	38.17	119.34	2287	July 2009
S	talus slope	38.16	119.15	2202	May 2010
S	talus slope	38.14	119.08	2519	May 2011
N	talus slope	38.13	119.08	2513	May 2011
N	talus slope	37.84	119.15	2520	October 2008
SW	talus slope	37.75	118.65	3031	November 2007
NE	talus slope	37.52	118.71	2555	September 2008

When $^{14}C/^{13}C$ values are used for calculations of radiocarbon activity, as is the case at CAMS, a deviation of 1‰ in $\delta^{13}C$ value of the sample from the assumed −25‰ results in a difference of approximately 0.001 $F^{14}C$ in the calculated radiocarbon activity (Reimer et al. 2004). Reported $F^{14}C$ values include a background subtraction determined from ^{14}C-free coal and the aforementioned $\delta^{13}C$ correction to account for isotopic fractionation (Stuiver and Polach 1977). Analytical precision, on average, was mean $\pm$ 0.0034 $F^{14}C$.

Calibrated dates and/or date ranges for each sample were determined from $F^{14}C$ values. Calibrated dates for older samples ($F^{14}C < 1.0$) were determined using the IntCal calibration curve (Reimer et al. 2009) with the software program OxCal 4.1.7 (Bronk Ramsey 2009). Reported date ranges are 95% confidence intervals and take into account the analytical error associated with each measurement. Modern samples ($F^{14}C > 1.0$) were calibrated using CALIBomb (Reimer et al. 2004) and the NH_zone2 (northern hemisphere zone 2) calibration curve of Hua and Barbetti (2004). Reported date ranges are 95% confidence intervals (listed as 2σ range in CALIbomb) and take into account the analytical error associated with each measurement. Calibrated dates reported are year CE (Common Era).

Due to geographical differences in the distribution of ^{14}C produced during nuclear weapons testing in the mid-20th century (bomb radiocarbon), different calibration curves are recommended for different regions of the globe (Hua and Barbetti 2004). The samples collected for the current study came from a region that lies on the demarcation between the NH_zone1 (northern hemisphere zone 1) and NH_zone2 calibration regions (40° N latitude). For this reason, calibrations for the samples

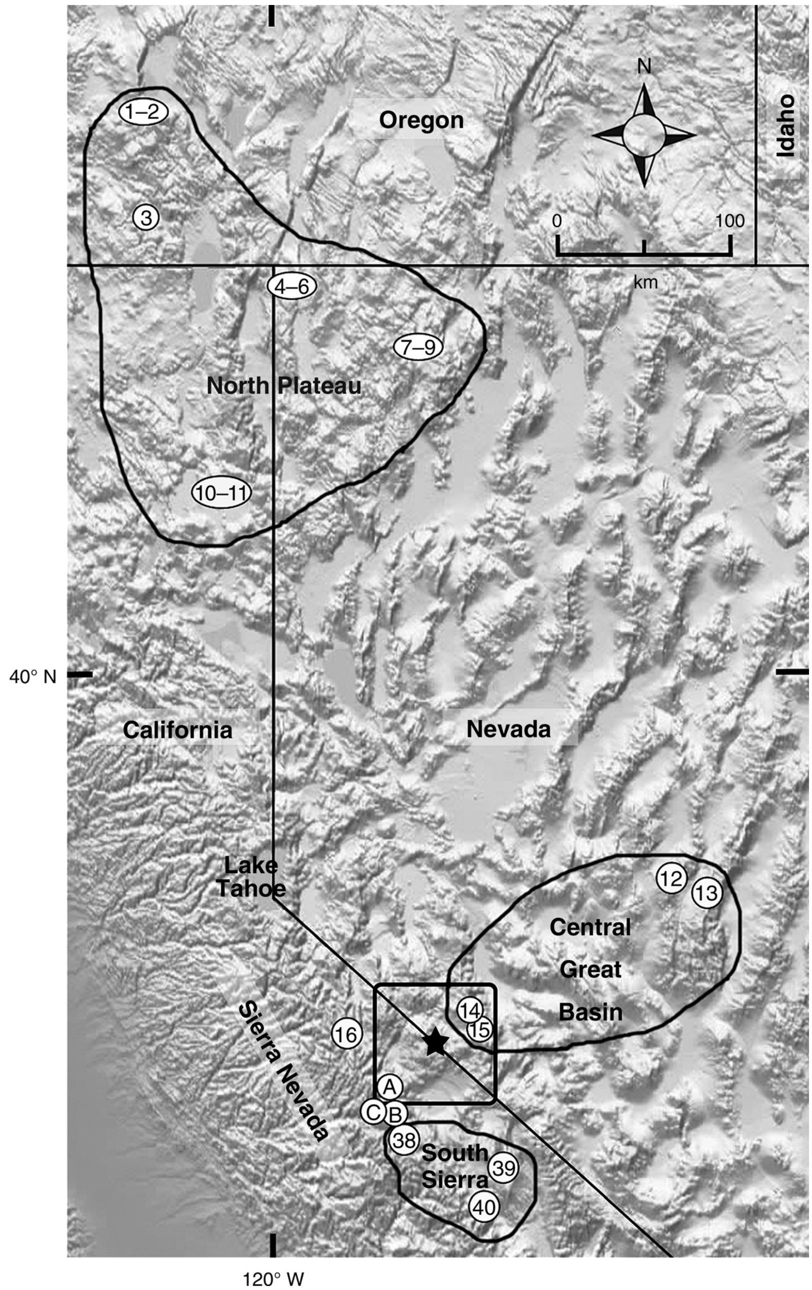

FIG. 3. Site locations and subregional groups for radiocarbon dating of pika pellets, haypile vegetation, and one *Artemesia tridentata* foliar sample. Labels correspond to sites given in Table 1 (letters are known modern samples; numbers are uncertain-age samples). Site locations within the starred inset box are shown in Fig. 7 (sites 14–15 and 17–37).

collected at sites north of 40° N latitude were carried out using both NH_zone1 and NH_zone2 calibration data sets. In all cases, the choice of calibration curve had only minor influence on the calibrated date ranges. Therefore, for simplicity and consistency within the data set, we report only the results of calibrations using the NH_zone2 curve for all samples.

As noted previously, the spike in the bomb curve means that for samples collected after 1955, one $F^{14}C$ value can correspond to two date ranges (i.e., one on each side of the ^{14}C spike). Where two calibrated date ranges were equally likely, both ranges are reported. Furthermore, the NH_zone2 calibration curve employed by CALIBomb extends only to the year 2000, making determination of calibrated dates more recent than 2000 contingent on availability of regional carbon monitoring data (until new standardized hemispheric curves are published). The reported $F^{14}C$ value for the northern hemisphere zone 2 atmosphere is 1.098 ± 0.02 (mean ± SD) for the year 2000, while contemporary northern hemisphere atmospheric $F^{14}C$ values are approaching ~1.04 (Graven et al. 2012), indicating that the atmospheric radiocarbon signature has continued to decrease over the past 13 years. Several of the dated samples have $F^{14}C$ values in the range of 1.098 to 1.04, indicating that they have calibrated ages that fall between the years of 2000 and 2012 (Graven et al. 2012).

Smoothing and resolution values in CALIbomb were both set to one year to reflect the dietary habits of American pikas. Pikas feed on a variety of plants, including vegetation of both annual and perennial plants. The plant tissues consumed, however, are generally annual growth, although older foliage from woody shrubs might also be eaten (Huntly et al. 1986). Though pikas are known to practice coprophagy, the majority of feces consumed is fresh and would therefore bear a similar ^{14}C signature to the rest of the animal's diet. Increasing the smoothing factor to three years to account for a broader range of ^{14}C signatures in the animals' diets had little to no effect on the calibrated ages calculated for the fecal samples.

After preliminary dates were determined, we attempted to resolve dates of samples where calibrated ages were equally likely on both the near side and far side of the bomb curve. At each of four sites in the Bodie Mountains, we collected vegetative material in 2012 from a single large haypile, two sites of which were identical to sites where pellets had been sampled (MAS-4, CLE-1; see Table 1 for site descriptions) and two that were from slightly different sites but within the same region as prior pellet sampling (MAS-1, MAS-6). Samples per haypile were collected stratigraphically for dating, that is, material was selected from the top, middle, and at the bottom of haypiles. The goal was to use the assumed chronological sequence of samples to determine dates as pre- or postbomb spike, thus providing evidence to narrow the date range to one side of the bomb curve. The haypile stratigraphic samples comprised embedded pellets and dry leaves and small stems from diverse, native herbaceous and shrub species that grow in the vicinity of the haypiles. From this material, annual plant tissues were sorted out and only vegetation was used for radiocarbon analysis. Pellets were not assessed because of their potential to fall through the vegetation matrix, thus disrupting the stratigraphic sequence. Haypile samples were pretreated and measured as described above. We report bottom and top sample dates.

To assess regional or local biases in contemporary atmospheric ^{14}C abundance, in 2012 we sampled current-year foliage from a single sagebrush (*Artemisia tridentata*) shrub growing on Kelty Ridge in the Glass Mountains at the site of one of our pellet sample locations (KEL-1). This site lies directly east of a long, low gap in the Sierra Nevada crest (Minaret Summit) that is well-known for passage of Pacific-dominated storms across the divide and thus, potentially transports fossil-derived CO_2 from urban areas in western California. The Kelty location is also the closest of our sample sites to natural contaminating sources (volcanic vents and hot springs) in the Mammoth Mountain area, 40-km distant. Live foliar tissues were pretreated and measured as described above.

Results

Radiocarbon calibrations and age of pellets and vegetation

Calibrated dates were resolved for all 43 pika pellet sample-sites representing 30 locations in California, Oregon, and Nevada. Sample ages ranged from contemporary (younger than the standard calibration curve, >2000 CE and dating to 2010 on the regional curves) to 1666 (Table 2; Fig. 4). All samples from the three known occupied sites had $F^{14}C$ values that yielded calibrated ages >2000, with interpolated dates from the regional curves in the mid-to-late 2000–2010 decade. Of the 40 uncertain occupancy samples, five had age ranges that extended before 1952, all of which extended before 1900 as well. Four of these (SLI-2, BAR-2, BRI-2, KEL-1) had $F^{14}C$ values that fell in a region of the radiocarbon atmospheric calibration curve where multiple date ranges during three centuries should be treated as equally likely because of poor resolution, and thus wide outer boundaries were rendered (e.g., 1666 and 1953). One of the five samples (MAD-2) that extended prior to 1900 had $F^{14}C$ values that resolved high precision but crossed variation in the radiocarbon curve that yielded two time ranges (1896–1902 and 1952–1956), again treated as equally likely without ancillary information. All five samples had their most recent dates in the 1950s.

The remaining 35 samples dated entirely within the second half of the 20th century (Table 2; Fig. 4). Five samples had dates exclusively in the 1950s (far side of the bomb curve), while 30 samples resolved date ranges for both the near side and the far side of the bomb curve. Given the steep slope of the radiocarbon curve during the major period of the bomb spike (~1955–1990), precision for each range was especially high in that period. All samples had near-side or far-side 2σ ranges of 2–4 yr, narrowing the cumulative dates (95% confidence interval) to 6 yr, notwithstanding 1–4 decades that separated the intervals. Six of the 35 samples had $F^{14}C$ values that resolved equally likely dates on the far side of the bomb curve and in the range of values likely >2000 CE. Each of these corresponded to $F^{14}C$ values on regional monitoring curves (Lehman et al. 2011, Graven et al. 2012). Further, four of the uncertain occupancy sites that were evaluated in the field as likely occupied or recent (indirect signs of current occupancy or recent use) also rendered near-side dates >2000 (MAD-1, WAS-1, MAS-3, BOD-1).

A gap in calibrated dates occurred in the mid-20th century, from 1963 to 1976 (Table 2; Fig. 4). Only two of the 40 samples (CLE-1, BRI-4) fell into this period, despite that the radiocarbon calibration curve provides

TABLE 2. Delta13C ($\delta^{13}C$), fraction modern radiocarbon ($F^{14}C$), calibrated ages of 43 American pika pellet samples, one contemporary sagebrush sample, and four haypile sites sampled stratigraphically.

CollectionID	Mapcode	Mountainrange	Location	State
Known occupied sites				
VIR-1	A	Sierra Nevada	Virginia Lakes Canyon	CA
WAR-1	B	Sierra Nevada	Lee Vining Canyon	CA
LVC-1	C	Sierra Nevada	Saddlebag Lake	CA
Sites of uncertain occupancy				
SLI-1	1	Fremont Mtns	Slide Mtn	OR
SLI-2	2	Fremont Mtns	Slide Mtn	OR
COU-1	3	Fremont Mtns	Cougar Peak	OR
BAR-1	4	Idaho Canyon Mtns	Barrel Springs, Fort Bidwell	NV
BAR-2	5	Idaho Canyon Mtns	Barrel Springs, Fort Bidwell	NV
BAR-3	6	Idaho Canyon Mtns	Barrel Springs, Fort Bidwell	CA
SUM-1	7	Mosquito Mtns	Summit Lake	NV
SUM-2	8	Mosquito Mtns	Summit Lake	NV
SUM-3	9	Mosquito Mtns	Summit Lake	NV
MAD-1	10	Lassen Plateau	Three Peaks, Termo	CA
MAD-2	11	Lassen Plateau	Three Peaks, Termo	CA
SHO-1	12	Shoshone Mtns	Bald Mtn	NV
TOI-1	13	Toiyabe Mtns	Ophir Canyon	NV
WAS-1	14	Wassuk Mtns	Big Indian Mtn	NV
WAS-2	15	Wassuk Mtns	Corey Peak	NV
SON-1	16	Sierra Nevada	Sonora Bridge	CA
MAS-1	17	Bodie Mtns	Serita Mine, New York Hill	CA
MAS-2	18	Bodie Mtns	Serita Mine, New York Hill	CA
MAS-3	19	Bodie Mtns	Serita Mine, New York Hill	CA
MAS-4	20	Bodie Mtns	Masonic Mtn North	CA
MAS-5	21	Bodie Mtns	Chemung Mine	CA
MAS-6	22	Bodie Mtns	Chemung Mine	CA
SWE-1	23	Sweetwater Mtns	Devils Gate	CA
MAS-7	24	Bodie Mtns	Chemung Mine	CA
MAS-8	25	Bodie Mtns	Masonic Mtn North	CA
POT-1	26	Bodie Mtns	Aurora Canyon	CA
AUR-1	27	Bodie Mtns	Aurora Mine	NV
AUR-2	28	Bodie Mtns	Aurora Mine	NV
AUR-3	29	Bodie Mtns	Aurora Mine	NV
AUR-4	30	Bodie Mtns	Brawley Peak	NV
BOD-1	31	Bodie Mtns	Noonday Mine	CA
BOD-2	32	Bodie Mtns	Queenbee Hill	CA
BOD-3	33	Bodie Mtns	Sugarloaf Butte	CA
ROB-1	34	Sierra Nevada	Twin Lakes	CA
CLE-1	35	Bodie Mtns	Clearwater Creel	CA
BRI-1	36	Bodie Mtns	Bridgeport Canyon	CA
BRI-2	37	Bodie Mtns	Bridgeport Canyon	CA
PAR-1	38	Sierra Nevada	Parker Creek Canyon	CA
KEL-1	39	Glass Mtns	Kelty Ridge	CA
ROC-1	40	Sierra Nevada	Lower Rock Creek Canyon	CA
Sagebrush foliage site				
KEL-1	39	Glass Mtns	Kelty Ridge	CA
Haypile vegetation sites				
MAS-1 top	17	Bodie Mtns	Serita Mine, New York Hill	CA
MAS-1 bottom	17	Bodie Mtns	Serita Mine, New York Hill	CA
MAS-4 top	20	Bodie Mtns	Masonic Mtn North	CA
MAS-4 bottom	20	Bodie Mtns	Masonic Mtn North	CA
MAS-6 top	22	Bodie Mtns	Chemung, native talus	CA
MAS-6 bottom	22	Bodie Mtns	Chemung, native talus	CA
CLE-1 top	35	Bodie Mtns	Clearwater Creek	CA
CLE-1 bottom	35	Bodie Mtns	Clearwater Creek	CA

Notes: Sites are ordered latitudinally from north to south within sections. Boldface type indicates dates corroborated by stratigraphic order. State abbreviations are defined in Table 1. Far and Near refer to the far side and near side of the bomb curve, respectively; $\pm 2\sigma$ is plus and minus the variance.

† Standardized hemispheric calibration curve not available after 2000 CE; $F^{14}C$ values and La Jolla, CA curve (Graven et al. 2012) indicate recent dates.

TABLE 2. Extended.

$\delta^{13}C$	$F^{14}C$	$\pm 2\sigma$	Calibrated ages of samples (yr CE)	
			Far	Near
−26.9	1.0635	0.0032	1956–1957	>2000†
−25.0	1.0474	0.0040	1955–1957	>2000†
−26.7	1.0096	0.0030	1892–1905	>2000†
−26.5	1.0042	0.0029	1952–1955	
−27.2	0.9808	0.0031	1666–1953	
−28.2	1.3246	0.0037	1962	1977–1978
−25.7	1.0300	0.0031	1954–1956	
−25.0	0.9868	0.0037	1681–1954	
−26.6	1.0052	0.0032	1952–1953	
−28.1	1.1652	0.0033	1958	1988–1990
−28.9	1.1648	0.0033	1958	1988–1990
−29.3	1.1294	0.0029	1957–1958	1992–1995
−28.7	1.0924	0.0031	1956–1957	>2000†
−25.5	1.0002	0.0028	1896–1902 or 1952–1956	
−27.3	1.1040	0.0033	1957	1995–1996
−29.0	1.1668	0.0033	1958	1988–1990
−27.7	1.0686	0.0030	1956–1957	>2000†
−25.3	1.1011	0.0042	1957	1995–>2000†
−30.0	1.1327	0.0034	1957–1958	1991–1994
−26.3	1.1320	0.0032	1957–1958	1991–1994
−26.9	1.1504	0.0028	1957–1958	1990–1992
−27.9	1.0760	0.0031	1956–1957	>2000†
−27.6	1.1683	0.0034	1958	1988–1990
−27.5	1.2235	0.0035	1958–1961	1983–1984
−25.9	1.2541	0.0044	1959–1961	1980–1982
−28.5	1.2918	0.0037	1961–1962	1979–1980
−25.8	1.2033	0.0032	1958–1959	1984–1986
−28.5	1.1577	0.0037	1957–1958	1989–1991
−27.3	1.3274	0.0038	1961–1962	1977–1978
−25.9	1.3225	0.0047	1961–1962	1977–1979
−27.0	1.2261	0.0035	1958–1961	1983–1984
−27.0	1.2521	0.0035	1959–1961	1981–1982
−28.2	1.1928	0.0034	1958–1959	1985–1987
−28.2	1.0825	0.0030	1956–1957	>2000†
−28.0	1.1772	0.0033	1958	1987–1989
−27.4	1.0170	0.0027	1953–1956	
−29.6	1.2381	0.0039	1959–1961	1982–1983
−26.4	1.5016	0.0042	1962–1963	1970–1972
−27.2	1.4909	0.0044	1962–1963	1971–1972
−26.3	0.9771	0.0028	1659–1952	
−27.5	1.1996	0.0034	1958–1959	1984–1987
−26.4	0.9907	0.0029	1694–1954	
−27.7	1.3489	0.0039	1961–1962	1976–1977
−25.7	1.0446	0.0035	1955–1957	>2000†
−28.0	1.0870	0.0036	1956–1957	**>2000**†
−27.5	1.1298	0.0033	1957–1958	**1992–1995**
−25.4	1.1351	0.0042	**1957–1958**	1991–1994
−26.1	1.1008	0.0033	**1956–1957**	1995–1996
−25.2	1.1108	0.0032	1957	**1995–1996**
−24.7	1.1927	0.0041	1958–1959	**1985–1987**
−28.7	1.2680	0.0037	**1959–1961**	**1980–1981**
−27.0	0.9881	0.0032	**<1953**	

opportunity for high resolution. Another pattern was the abrupt reduction in dates before 1952. All 40 samples of uncertain occupancy had potential dates in the 1950s and 1960s, but, as noted above, only five dated older than 1952. The pattern of these dates suggests that most dates are near side of the curve and post ~1976.

Regarding potential recent contamination from local or distant sources, none of the contemporary samples (2007–2012), including pika pellets and current-year

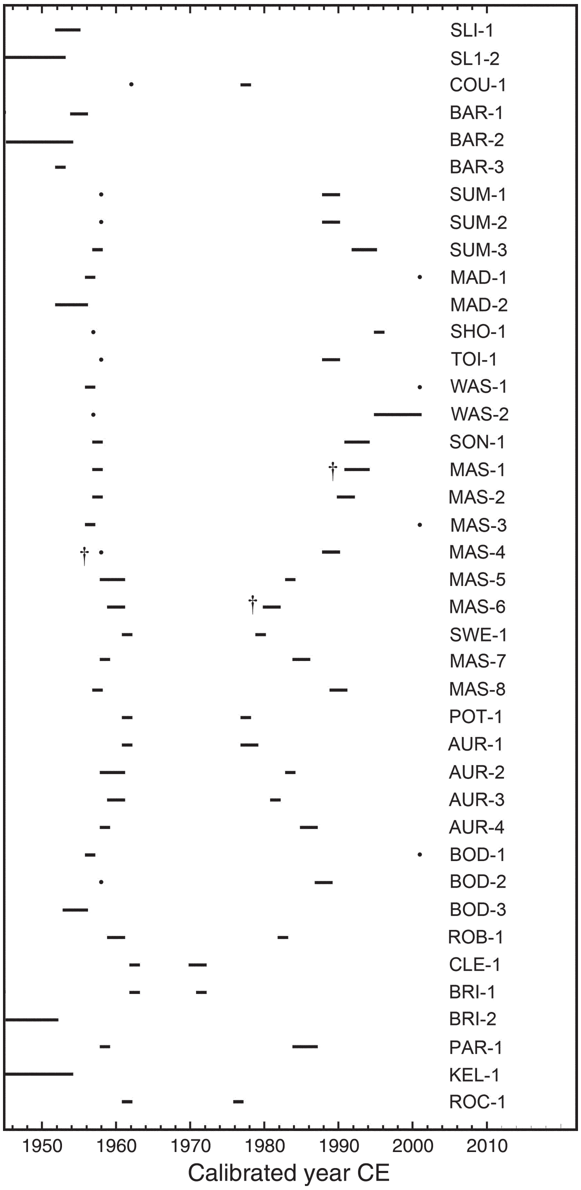

FIG. 4. Calibrated radiocarbon date ranges of pika pellets from 40 sites of uncertain occupancy at the time of field collection. Daggers (†) indicate sites where further calibration by haypile stratigraphy corroborated likelihood of dates. Site abbreviations are defined in Table 1.

sagebrush foliage, had $F^{14}C$ values that deviated from the extrapolated modern radiocarbon curve (Table 2).

At two locations where pellet dates could not be resolved for near and far sides of the bomb curve (CLE-1, MAS-4) and at two additional locations in the north Bodie Mountains, we attempted to improve dating by stratigraphic sampling of haypile vegetation. In each case, we were able to improve the date uncertainty with the strategy of placing calibrated dates of vegetation in order of their $F^{14}C$ values (Table 2; Fig. 5). The assumption made in reporting calibrated dates was that the material recovered from lower in haypiles was sequentially older than material at higher positions. In three of the four cases, trends of young to old samples within a haypile corresponded to sequences on the near side of the bomb curve (i.e., increasing ^{14}C abundance with depth in the haypile) and to years younger than 1978. One sample (CLE-1) resolved a sequence that spanned both sides of the curve, from <1953 to 1981; samples resolved in chronologic order in that case as well.

Regarding laboratory assessments, $\delta^{13}C$ values for all samples were very close to −25‰, the standard value for C_3 plants. The date estimation for the sample with the greatest deviation from that standard ($\delta^{13}C$ of −29.6‰) was improved by only one year with the use of the $\delta^{13}C$ correction.

Pellet age in relation to elevation

We could not test relationships of elevation to pellet age directly due to the two-tailed nature of the bomb curve resolving two possible date intervals for each sample. Reviewing the order of elevations of samples qualitatively within geographic groups, however, suggested two situations. One showed no obvious relationship of age with elevation. For example, in the northernmost group of samples (North Plateau; Fig. 3), the lowest (BAR 1–2) and highest elevation (SLI 1–2) samples had the oldest dates, whereas the range of dates for other sites included both modern and <1956. In the central Great Basin group, all samples had near- and far-side dates; without further evidence for which dates are correct, these cannot be ordered by age. Recent field observations, however, suggest that WAS-1 and WAS-2 (Wassuk Range sites) are occupied, which corroborates

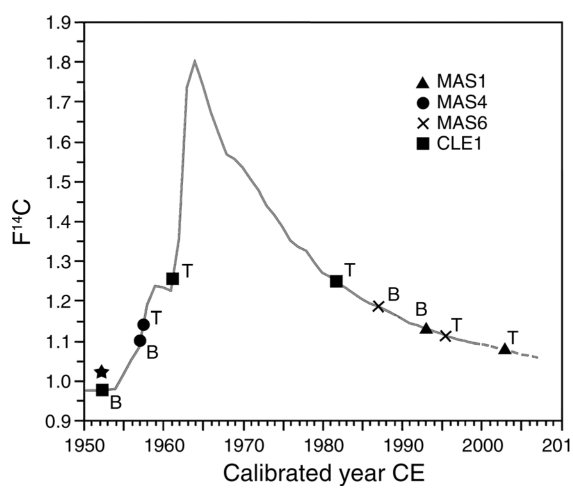

FIG. 5. Calibrated dates of vegetation sampled stratigraphically from four pika haypiles at different sites. Site abbreviations are defined in Table 1. T is top, and B is bottom. The date range for the bottom sample marked with a star from CLE1 extends beyond the graph (1666–1952 CE). The $F^{14}C$ notation indicates that the radiocarbon values have been corrected for isotopic fractionation effects ($\delta^{13}C$-normalized).

the >2000 estimates from radiocarbon dating. These, however, are the highest and second lowest elevation samples for the group (Table 1). At the northern subgroup in the Bodie Mountains (Masonic District, sites 17–22, 24–25; Table 1), estimated ages from radiocarbon measurements were also not obviously related to elevation. One high elevation site (MAS-8) had the oldest pellet ages, while another high site dated potentially as the youngest (>2000), and in recent field visits this site was confirmed as occupied. Finally, the southernmost group (South Sierra Nevada; Fig. 3) suggested no relationship of age and elevation. The highest elevation site (KEL-1) had the oldest date estimate, but the other two sites were inconsistent.

By contrast, the subgroups from Aurora/Brawley Peak (sites 27–30) and the Bodie District (sites 31–33) in the Bodie Mountains, including native habitats and mine-ore–dump-sites, showed a relationship of age with elevation. Older pellets occurred at lower elevation, and progressively younger ages occurred at sites with increasingly higher elevations (Table 2).

Discussion

Biases in calibrated ages

Although we expected $\delta^{13}C$ assessment to improve date estimations, in fact $\delta^{13}C$ values for all samples were very close to $-25‰$, the standard value for C_3 plants. Thus it appears that, despite a highly varied diet, pikas in our region had consumed mostly C_3 plants. This corroborates the recent review of the proportion of C_3 and C_4 plants in diets of Ochotonidae worldwide that found prominent preference for the former (Ge et al. 2012).

Geographic variation in atmospheric concentration of radiocarbon since the mid-1950s is well-known to occur at hemispheric scales. Our site locations dictated use of the northern hemisphere zone 2 (NHZ2) calibration curve, although some sites lay near the transition to northern hemisphere zone 1. Beyond this, local to regional effects can influence radiocarbon levels of plants in pikas' diet, in turn affecting the estimated age of pellets. $F^{14}C$ values, however, from live sagebrush foliage collected in 2012 and from pellets of occupied pika sites collected during 2007–2010 matched values based on extrapolated atmospheric isotopic decay after 2000 from the NHZ2 calibration curve and regional monitoring (Lehman et al. 2011, Graven et al. 2012). The finding of no detectable local contamination corroborates other results from our region. Whereas ^{14}C levels assessed from trees and shrubs within 1 km of actively degassing CO_2 volcanic vents near Mammoth Mountain, 40 km from our nearest site, showed detectable depletion of ^{14}C; trees at 6 km distance recorded background levels extrapolated from the NHZ2 calibration curve (Cooke et al. 2001, Bergfeld and Evans 2011). Thus, natural or anthropogenic influences appear unlikely to be contaminating the atmosphere near our sites. For our interpretations, we assumed radiocarbon-estimated dates to be accurate within the precision of the calibration curves used.

A possible limitation of the method as applied to pika fecal pellets was the need to combine pellets to obtain adequate carbon for analysis. This was further confounded by our use of pellets that had been collected in a prior study where sampling was not conducted in a way to maximize sampling a single defecation event. Thus, a range of ages of pellets could have been introduced to samples, and dates estimated represent averages of these. In that analytical error in calculated $F^{14}C$ values, however, were very small and consistent among samples, this doesn't appear to have introduced a major source of variability (Table 2). Further, within-location replicates yielded overlapping dates despite being separated by distances larger than the diameter of a single animal's territory and likely representing different animals. In future radiocarbon studies where youngest dates are desired, pellets could be collected from a single pile of fresh pellets (e.g., perched pile; Fig. 2C). As our results indicate that $\delta^{13}C$ analysis is not necessary, only half as much material is needed for radiocarbon analysis. Thus, as few as three to four large pellets (~42 g) should be adequate. On the other hand, use of multiple pellets as in our study, by potentially including more than one defecation event, might afford estimation of a better date of occupation than would be estimated from only one pellet or perched pile.

Value of radiocarbon dating to understanding species ecology

We were able to resolve dates for all material collected, including fresh and old pika fecal pellets, vegetative material from pika haypiles, and live foliage from a perennial shrub. The bomb spike in the second half of the 20th century enabled dating to one or two 2–3 yr ranges (including $\pm 2\sigma$, plus and minus the variance), with greatest precision between 1955 and 1990. By contrast, the nature of the radiocarbon calibration curve for 300 years before 1950 has such high variation that utility of dating within this interval is extremely limited.

Despite precision, the two-sided nature of the bomb curve means that dates rendered to near side and far side of the curve cannot be resolved without ancillary data, posing significant limitations to resolution. Two patterns in the calibrated dates provide indirect support that most samples that resolved two intervals are likely near-side dates and post-1976. First, if correct dates had included sites with pellets older than 1963 and some with pellets younger than 1976, an environmental reason would be needed to explain the 13-year gap between 1963 and 1976. Nothing obvious suggests pika population decline in this period, especially in that climates in our region were relatively cool and stable during the mid-20th century decades (Abatzoglou et al. 2009). By contrast, if near-side dates are correct, an explanation is needed for extirpations after the late-1970s. In California, as in many parts of the northern hemisphere,

TABLE 3. Climatic data interpolated from the PRISM (parameter-elevation regressions on independent slopes model) climate model (Daly et al. 1994) at a subset of sites used for radiocarbon dating.

Site	Annual PPT (mm)				JanPPT (mm)‡	JulPPT (mm)‡
	1900–1930†	1940–1970†	1971–2000†	1971–2000†		
Known occupied sites						
VIR-1	1099	1009	1035	1102	206	27
WAR-1	1001	899	932	960	177	26
SAD-1	1047	956	980	1065	195	25
Mean	1049	955	983	1042	192	26
Sites of uncertain occupancy						
SLI-1, SLI-2	758	849	905	708	89	16
BAR-1, BAR-2, BAR-3	264	304	336	394	51	5
SUM-1, SUM-2, SUM-3	262	285	311	288	30	10
MAD-1, MAD-2	330	367	368	363	40	25
SHO-1	251	283	233	480	49	19
TOI-1	446	486	531	585	62	22
WAS-1	539	536	544	532	72	20
Bodie Hills, Masonic District§	538	487	526	561	90	17
Bodie Hills, Aurora/Brawley¶	331	308	325	329	46	17
Bodie Hills, BodieDistrict#	379	359	364	321	43	19
CLE-1	396	354	384	389	58	16
BRI-1, BRI-2	374	336	364	395	59	19
PAR-1	946	893	875	729	126	21
KEL-1	926	882	887	512	77	15
ROC-1	520	498	516	452	69	13
Mean	484	482	498	469	64	17
Bodie COOP Weather Station				328	43	22

Notes: All values are means. Three 30-yr time periods are compared from PRISM 4-km grids; the 1971–2000 PRISM data are resolved to 800-m grid and shown for comparison. Bodie, California Coop Weather Station (2551 m) data averaged for 1971–2000. Abbreviations are PPT, precipitation; Tmax, maximum temperature; Tmin, minimum temperature.

† 4-km grid.
‡ 800-m grid.
§ Sites 17–22 and 24–25.
¶ Sites 27–30.
# Sites 31–33.

temperatures rose steeply after 1976 from the mid-20th century plateau or even cooling (Mann et al. 1999, Abatzoglou et al. 2009). Given that pikas appear sensitive to acute summer warmth in the interior Great Basin (Beever et al. 2010), that rates of extirpation increased by more than 10 fold, and that minimum elevations of occupancy rose by 145 m in the late 20th and early 21st centuries (Beever et al. 2011), many pika population locations may have crossed critical thresholds during this period. Thus, environmental evidence exists to support a hypothesis that the near-side dates are correct for many sites having intervals on both sides of the radiocarbon curve.

Near-side dates are further supported by the abrupt lack of two-interval samples dating older than 1952. No environmental explanation is apparent for abrupt pika population declines prior to 1952. To the contrary, this is the time period for documentation of extensive distribution of pika populations across the Great Basin (Howell 1924, Hall 1946, Verts and Carraway 1998). If, however, pika samples were from the near sides of the curve and very recent, lack of dates prior to 1952 would be due to the absence of samples having $F^{14}C$ levels lower than 2012 values (which, on the far side of the curve, corresponds to before about 1952), which was the youngest date possible given our collection dates.

In addition to these inferences, we tested a method to resolve the correct interval by dating stratigraphic samples from haypiles. Results from four pika haypiles suggest the method can be useful. This approach could be used in the future for pika studies and other species where stratigraphic collections are possible (e.g., pack rat middens, nests and dens, archaeological sites).

In addition to the challenges posed by the two-sided nature of the bomb curve, standardized calibration curves for the northern hemisphere are not yet available after 2000, making the recent years limited in value for radiocarbon dating if regional data are not available. Regional monitoring in parts of North America, including California, shows that radiocarbon levels have continued to decline in the atmosphere at expected rates (Lehman et al. 2011, Graven et al. 2012) slowly approaching the prebomb, 1955 $F^{14}C$ value (1.0). Given that the value in 1999 for NHZ2 was 1.098 $\pm$ 0.02 (Hua and Barbetti 2004), values smaller than this indicate more recent dates, especially where there is evidence to exclude the early 1950s. Our known occupied sites and 2012 sagebrush foliage sample resolved $F^{14}C$ values that

TABLE 3. Extended.

Annual Tmin (°C)						Annual Tmax (°C)					
1900–1930†	1940–1970†	1971–2000†	1971–2000†	Jan Tmin (°C) ‡	Jul Tmin (°C) ‡	1900–1930†	1940–1970†	1971–2000†	1971–2000†	Jan Tmax (°C) ‡	Jul Tmax (°C) ‡
−5.2	−4.4	−4.3	−4.2	−10.5	4.5	7.8	9.8	8.7	7.5	0.3	17.4
−5.5	−5.1	−4.8	−3.2	−9.5	5.4	7.8	9.0	8.4	8.2	1.5	18.0
−5.8	−5.7	−5.2	−4.1	−10.6	4.8	7.7	8.1	7.7	8.2	0.9	18.2
−5.5	−5.0	−4.7	−3.8	−10.2	4.9	7.7	9.0	8.3	8.0	0.9	17.9
−4.7	−4.7	−2.7	−1.4	−7.7	7.2	12.8	13.7	13.4	10.2	0.2	22.6
1.1	1.2	1.7	0.6	−6.9	9.8	14.4	14.9	14.6	14.3	3.7	22.1
0.6	1.6	1.6	−0.6	−7.5	8.8	13.9	14.2	14.4	12.9	2.0	26.8
−1.1	−0.6	−0.6	−1.1	−7.9	7.3	14.4	14.7	14.6	13.7	3.4	26.8
−2.8	−2.2	−1.9	0.1	−7.0	10.4	13.5	14.2	14.3	10.2	0.4	22.7
−4.2	−3.7	−3.2	0.2	−6.7	10.4	11.6	12.2	12.3	10.2	0.5	22.7
−4.1	−3.3	−3.6	−4.6	−10.8	4.2	11.8	12.5	12.3	9.5	0.8	20.5
−3.9	−3.2	−3.3	−3.0	−9.3	5.8	12.6	13.3	13.1	11.6	2.6	22.8
−1.0	−0.4	−0.6	−2.0	−9.2	7.2	13.6	14.0	13.9	13.3	4.1	24.9
−6.0	−5.4	−5.8	−3.5	−10.3	5.6	12.6	13.3	13.2	12.0	3.3	23.2
−3.5	−3.0	−2.9	−3.5	−10.5	5.4	13.1	13.6	13.6	14.8	5.9	26.0
−3.9	−3.2	−3.3	−3.6	−10.9	5.6	13.4	13.7	13.8	13.3	4.4	24.5
−4.4	−4.0	−3.8	−3.4	−10.5	5.1	9.8	10.1	10.0	12.8	4.5	23.2
−4.0	−3.6	−3.4	−1.4	−7.6	7.7	11.7	12.0	12.7	11.2	4.0	21.1
−3.6	−3.2	−3.4	−0.7	−6.7	8.1	12.4	12.1	12.1	12.9	5.0	23.4
−3.0	−2.5	−2.3	−1.9	−8.6	7.2	12.8	13.2	13.2	12.2	3.0	23.6
			−7.0	−14.6	1.6				13.6	4.4	24.6

correspond to recent years (>2000) from the La Jolla, California monitoring data (Graven et al. 2012). As regional monitoring data are published and standardized curves become available, modern dates can be detected at greater resolution. In future decades, when $F^{14}C$ values decline below 1.0 as expected, dating will continue to be assessed with accuracy, especially if there is evidence to exclude dates prior to ~1950.

A caveat when interpreting radiocarbon dates from indirect animal sign is that dates indicate only the years in which the pellets were eliminated by the animal; i.e., they are temporal snapshots. With additional information, however, the dates can provide evidence for hypotheses about prior or subsequent occupancy of a site. For example, in a species such as the American pika that exhibits metapopulation behavior, point-source dates can confirm, negate, and add value to time-series studies of extirpation–recolonization events, such as those done by the pioneering long-term censuses of pikas at Bodie (Smith and Gilpin 1997; Smith and Nagy, *unpublished manuscript*) and can be used to interpret pika trends in ongoing field observations. Dated pellets can fill in time-series gaps of field observations and are most useful when combined with results from such studies.

Interpreting pika population status

An important result for interpreting population occupancy is our finding that pika pellets can persist in exposed contexts for more than 59 years. Nine samples representing six widely separated regions had pellets older than 54 years. Previously the persistence time of pellets, and thus implications for population occupancy, has been unknown, although Nichols (*unpublished manuscript*) made indirect assumptions based on size that pellets from talus in the Bodie Mountains could persist 39 years.

An assumption that pellets persist longer under warmer and drier climates than cooler and wetter environments has not been previously investigated. We used the PRISM (parameter-elevation regressions on independent slopes model) climate model (Daly et al. 1994) to estimate historical (1900–2000) climate data divided into three time intervals for a subset of our sites (1900–1930, 1931–1970, 1971–2000; Table 3). The estimated range in annual precipitation for the 1971–2000 interval (800-m grid PRISM model, all sites) was 321–1102 mm, for minimum annual temperature −4.6–0.6°C, and for maximum annual temperature 7.5°–14.8°C. ANOVA results indicated significant differences ($P < 0.01$) for all climate indicators between occupied and recent sites (radiocarbon dates on the near side, younger than 1980) and assumed extirpated sites (radiocarbon dates older than 1971). Sites having pellets with the older radiocarbon dates had climates in the high-resolution PRISM model that were significantly warmer ($P < 0.01$) for maximum temperature and drier ($P = 0.049$) than environments of the group of younger sites in the region. This relationship did not hold for all regions consistently. For instance, in the recent 30-year period, sites in the central and southern Sierra Nevada were wetter and colder (minimum and maximum temperatures) than those in the North Plateau, Central Great Basin, and Bodie Mountains subgroups regardless of pellet age or site occupancy. Furthermore, for the entire set of sites, PRISM-derived changes in precipitation and temperature from 1900 to 2000 did not show consistent trends related to age of pellets (Table 3).

Comparing our radiocarbon-derived dates with field observations of occupancy/extirpation enables further evaluation of the usefulness and limitations of radiocarbon dating for interpreting population trends and processes. Pellets from sites of known or suspected current occupancy regularly returned dates younger than 2000, corroborating that fresh pellets are likely more abundant (more likely to be sampled) in occupied sites, even if older pellets remain. This is likely due to the abundance of modern pellets relative to older pellets, which, despite their potential for long-term persistence, are likely to wash away, gradually decompose, and occur in relatively lesser numbers than modern pellets from occupied sites. In contrast, no sites determined to be extirpated from field observations had pellets with radiocarbon-derived ages younger than 2000. By corollary, finding only old pellets at a site provided supporting evidence that a site is extirpated, although age of pellets could predate time of last occupancy. In the Bodie District, for example, Andrew Smith monitored patch occupancy ~annually from 1972 to 2010, and several of our sites overlap his network (A. Smith, *personal communication*). Smith observed pikas at Sugarloaf Butte, a natural habitat, from 1969 to 1977 and estimated that the population became extirpated between 1977–1989. Our pellets from this site dated 1953–1956, which predate Smith's extirpation estimate by 21–36 yr. Smith estimated extirpation at another native habitat, Queen Bee Hill, to be 2005; our near-side dates for this site were 1987–1989, which again predate Smith's estimate by 18–20 yr. Finally, our 2007 field observations for an ore dump at the Noonday Mine suggested that the site had been recently occupied. Radiocarbon ages for the pellets were potentially recent, and Smith's records indicate extirpation since 2006. Thus, in the case of a recent extirpation, radiocarbon analysis returned dates in the range of field-observed dates, whereas for older extirpations, pellet ages predate these events by decades.

Several other locations in the Bodie Mountains afforded comparison of field observations and radiocarbon interpretations and insight into persistence patterns. In 1970, Smith thoroughly inspected pika habitat in mine-ore dumps of the Aurora District, ~13 km northeast of the Bodie District (A. Smith, *personal communication*). At the lowest available habitat, 2270 m, Smith found abundant pikas calling and haypiling, as well as active in ore dumps on the low slopes above Aurora. During visits in 2007 and 2010, we found no direct or indirect evidence of pikas at the low-elevation site, increasing abundance of degraded, old sign upslope in ore dumps, which continue to 2500 m, and intact but dry sign in the very limited native talus on the summit of Brawley Peak, 2857 m, at elevations above Smith's survey. Accepting the near-side radiocarbon dates as correct, based on Smith's 1970 evidence, the ages of our four sites follow elevation, with the lowest site (2338 m) dated 1977–1979 and becoming progressively younger upslope, with the Brawley Peak summit site pellets dated the youngest, 1985–1987. In this example, dated pellets extended the value of field observations, which were based on low sites and one time period.

Elsewhere in the Bodie Mountains, Nichols (*unpublished manuscript;* L. Nichols, *personal communication*) inferred late 20th century extirpations for many previously inhabited native and anthropogenic sites. These include most of our remaining sites in the Bodie Mountains. Our near-side dates for all but one of these locations are in the range of 1980–1994, which is consistent with Nichols' field observations and demonstrate the value of pellet dating to extend locations and times of field studies. Finally, in the Masonic District at the north end of the Bodie Mountains are numerous small and isolated native talus patches, as well as clusters of ore-dump habitat, similar in nature but smaller in area than the Bodie District. Most of these contain signs of prior pika presence. Smith observed pikas in one area, the Serita Mine ore dumps, in 1972 (A. Smith, *personal communication*), and we observed animals active there in 2012. Our near-side radiocarbon dates of pellets ranged from 1978 to 1991 at the extirpated sites of the northern Bodie Mountains and younger than 2000 for the Serita Mine dumps, where we also have haypile stratigraphic dates that confirm the younger estimates. These comparisons of field and radiocarbon dates suggest that the latter corroborate field studies, and thus can be used to complement studies and extend inferences where direct observations are missing or incomplete.

Biogeographic-climatic effects on population dynamics: example of the Bodie Mountains

Combined results from the present study with prior field observations provide new evidence for evaluating biogeographic and climatic processes relating to pika population dynamics over time. Contrasting environments of major mainland cordillera, such as the Sierra Nevada and Rocky Mountains, versus isolated island ranges, as in the Great Basin, have been assumed to present different biogeographic conditions for pika persistence, extirpation, and recolonization (Smith 1974*a*, *b*, McDonald and Brown 1992, Hafner 1993, 1994, Beever et al. 2003, Grayson 2005, Lanier and Olson 2009). On the one hand, large areas of high-quality habitat with high connectivity, wide elevation gradients, diverse microclimates, and broad geomorphic diversity of the major cordillera provide abundant opportunities for range adjustments driven by natural climatic variability (e.g., Moritz and Agudo 2013) and supply ample source–sink conditions for local recolonizations following patch or metapopulation extirpations. The major north–south cordillera are likely to have been the historical corridors by which pikas first migrated into North America from boreal origins (Hafner and Sullivan 1995, Galbreath et al. 2009). Similarly, although fossil evidence prior to the last glacial interval is lacking, genetic diversity suggests that these ranges had adequate habitat in uplands or adjacent lowlands to sustain pikas through Quaternary climatic fluctuations (Hafner and Sullivan 1995, Galbreath et al. 2009).

At present, published and unpublished surveys corroborate that pikas in the Rocky Mountains, Cascade Range, and Sierra Nevada are abundant and broadly distributed across wide elevation ranges and habitat conditions (USFWS 2010). In the case of the Sierra Nevada and White Mountains, for example, occupancy of sites spans wide elevation ranges from basin bottom to mountain crest, as much as 1700 m in the Sierra Nevada and 1500 m in the White Mountains (Millar and Westfall 2010). As expected with warming, low-elevation and other warm-margin populations are at risk of extirpation, and in some cases appear to have been extirpated (e.g., the low-elevation White Mountains site of Beever et al. [2010]; in our study, ROB-1, PAR-1, ROC-1, AUR-1). Elsewhere in these ranges, however, sites lower than those potential extirpations and in similar climatic regimes remain occupied (Millar and Westfall 2010; Millar, *unpublished data*). Dispersal and successful recolonization following patch extirpation appears to be supported by favorable environmental conditions that derive from extensive Pleistocene glaciation in major mainland ranges. These include large and connected talus areas (Curry and Morris 2004), deep canyons that promote cold-air pooling (Pepin et al. 2011), and periglacial processes that enhance optimal thermal regimes within talus patches (Hafner 1994, Millar et al. 2013; Millar et al., *in press*). Talus area and distance between talus patches were key factors determining persistence vs. extirpation in northern Sierra Nevada sites (Stewart and Wright 2012). In the Rocky Mountains, Hafner (1994) found occupied but geographically marginal pika sites to have greater connectivity with higher talus and larger talus area than sites that had become extirpated.

Contrasting with the cordillera, Great Basin insular ranges contain less favorable environments for long-term persistence of pikas under variable climates (although, see Collins and Bauman 2012). Although no assessment of overall talus area has been conducted, relatively drier climates, coupled with limited Pleistocene or Holocene glacial activity (Osborn and Bevis 2001, Grayson 2011) and virtual absence of permafrost (Péwé 1983), mean that geomorphic processes promoting favorable talus environments have been less pervasive in the Great Basin than in the major cordillera. Further, with permafrost lacking and annual snowpacks comparatively smaller in the Great Basin ranges, talus that does exist is less likely to be underlain by persistent groundwater or internal ice as are periglacial taluses elsewhere (e.g., Clow et al. 2003, Roy and Hayashi 2009). Thus, thermal buffering capacities are likely more limited in the interior Great Basin, reflecting surface air temperature more directly than periglacial taluses (Millar and Westfall 2008, 2010, Millar et al. 2013; Millar et al., *in press*). Smaller elevation spans relative to the major cordillera further limit habitat availability. Combined, these factors result in insular Great Basin mountains having smaller talus areas within ranges, less connectivity of habitat within ranges, and poorer quality habitat where it does exist than the main cordillera. Confounding persistence is isolation among mountain ranges. Extensive low-elevation basin terrain surrounding these sky-island ranges is inhospitable for pikas, making dispersal among ranges during the present climatic regime highly improbable (Brown 1971, Grayson 2005). Extirpation of pikas since late-glacial time has been a one-way path without recolonization (Hafner 1994, Grayson 2005), a trend which appears to be continuing in modern times (Beever et al. 2003, 2011).

Intermediate to the situations of insular ranges vs. extensive cordillera is a geographic scenario that includes environmental contexts of our study. This pertains to mountain ranges that are adjacent to but disconnected or partially disjunct from the major cordillera at times during the Quaternary. Beever et al. (2011, 2013) refer to these as Great Basin spur ranges and suggest they have different biogeographic histories and likely exhibit markedly different population trends than ranges of the interior Great Basin. Of particular interest are ranges where upland connectivity to the cordillera exists, but corridors connecting the mainland are transiently available depending on climate, and upland areas have low relief (i.e., plateau-like). The Bodie Mountains are an example. This small range covers 2020 km^2 and has limited topographic diversity in the uplands (Figs. 6, 7), with 34% of land area at elevations between 2300–2600 m, 9% between 2600–2900 m, and 1% above 2900 m, corresponding generally to zones of pikas' recent decline, stability, and lack of habitat, respectively. The Bodie Mountains lie east of the Sierra Nevada escarpment and are connected to the latter by a narrow upland bridge that is ~10 km wide and has an average elevation ~2500 m, with low gaps of 2350 m.

Low topographic diversity and minimal, scattered native talus habitat suggest low refugial capacity throughout the Bodie Mountains, especially in periods when the corridor to major source areas was climatically unavailable. The current average minimum elevation of occupied sites in the Bodie Mountains and the adjacent eastern Sierra Nevada is estimated at 2590 m (Millar and Westfall 2010; Nichols, *unpublished manuscript*). This compares to Beever et al.'s (2011) average minimum elevation (calculated for the year 2008) for

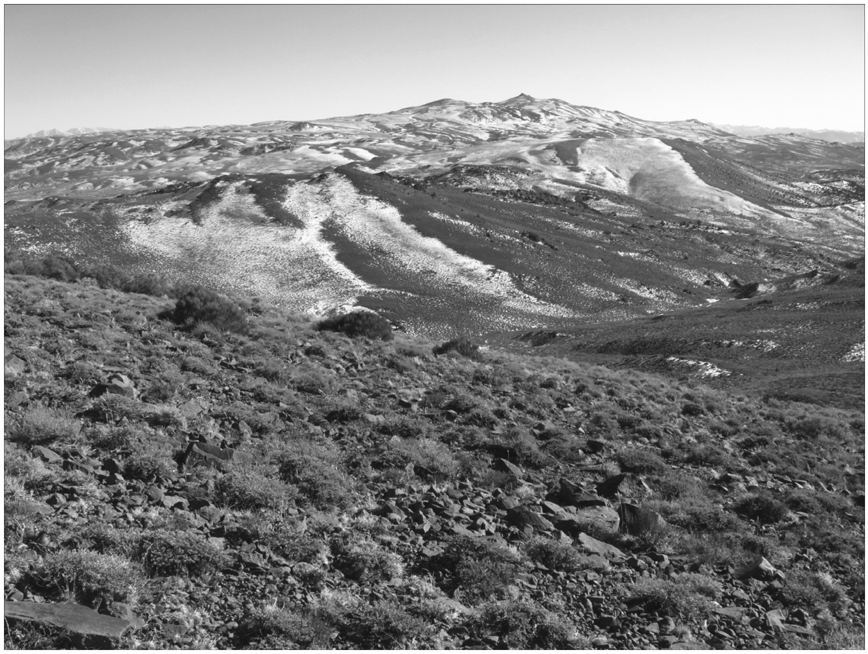

FIG. 6. Bodie Mountains, California. View southeast illustrating the low summit plateau that characterizes this range and similar mountain systems adjacent to the main cordillera.

occupied Great Basin sites of 2550 m. Assuming 2600-m elevation as a current low-elevation baseline for pika persistence allows comparison of historical dynamics. Several proxies document multicentennial periods of climatic variability over the past 7500 years in the western Great Basin region. From these, conservative estimates of change in average warm-season temperature relative to the late 20th century indicate +2°C for warm periods and −2°C for cold periods (i.e., a change of 4°C cumulative; Table 4). Similarly, although lapse rates vary in mountainous regions (Minder et al. 2011), the standard value of −6.5°C/1000 km translates to ∼300-m shift for a 2°C change.

Given these values, alternating historical cold and warm intervals for plateau-like ranges such as the Bodie Mountains render significant differences in area present within an elevation range and thus differences in amount of pika habitat (Fig. 7). During cold periods, both the corridor with the Sierra Nevada and the large area within the Bodie Mountains above 2300 m would be available for pika migration and colonization. Relatively long duration of these intervals (multiple centuries) would afford opportunity for stepping-stone dispersal into the limited and low-quality habitat of the Bodie Mountains. Hafner (1993) commented on a similar process in the Rocky Mountains (citing also Smith [1974*b*] and Tapper [1973]) noting that, "I have observed that virtually all suitable rocky areas, even tiny patches, are inhabited by pikas in cool climates, and dispersal distances of at least 3 km have been observed."

As historical cold intervals transitioned to warm periods, climatically available habitat for pikas to move across the corridor with the Sierra Nevada would disappear, cutting off colonization from those source environments, and increasingly eliminating from habitat use large areas of the Bodie Mountains plateau as well. At the peak of warm periods, only a very few scattered and small areas on the highest peaks of the Bodie Mountains would remain climatically adequate (Fig. 7). Within those locations, only minimal- and low-quality talus exists, leading to the likelihood that pikas were extirpated from the Bodie Mountains during historical warm periods. Whether pikas were extirpated entirely from the Bodie Mountains or persisted in refugial environments, as suggested by field observations and radiocarbon dating evidence, is unknown. Either way, a major recolonization would be unlikely until a subsequent cold period reopened the Sierra Nevada corridor, enabling migration back into the Bodie Mountains, and again making available stepping-stone habitats for dispersal and colonization within the range.

Similar dynamics have been proposed as recurring mechanisms for pika colonization–extinction at glacial–interglacial scales in the Great Basin (Mead 1987, Hafner 1993, Hafner and Sullivan 1995, Grayson 2005). During glacial periods, depression of the minimum elevation has been interpreted to be 900–1200 m below modern levels (Péwé 1983, Hafner 1993), corresponding to ∼5–7°C cooling, which enabled pikas to disperse across low basins that became too hot and dry for dispersal during interglacials such as the Holocene. Lack of these dispersal corridors during interglacials led to the relentless extirpation of pikas from warm ranges

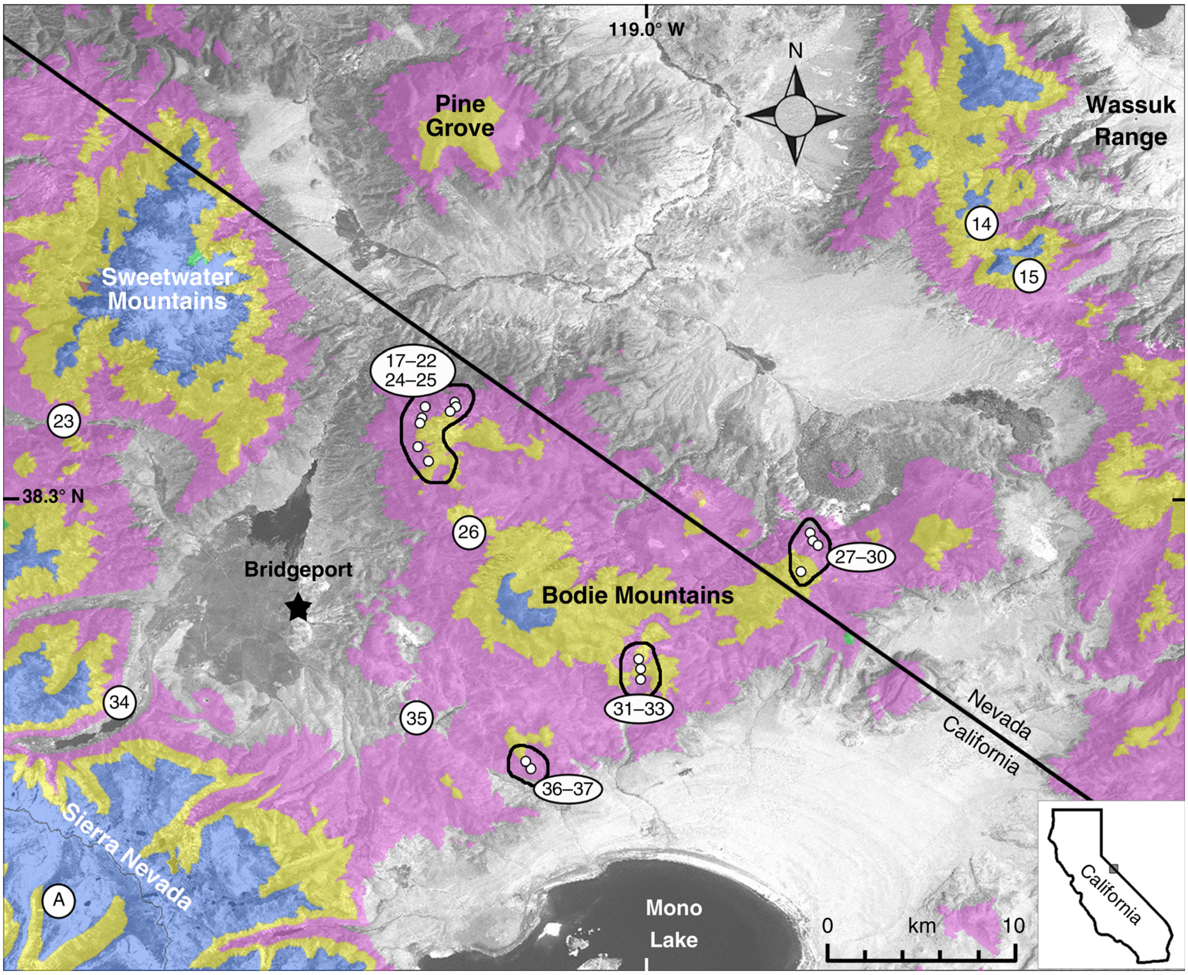

FIG. 7. Topographic relationships of American pika and population persistence. Map of Great Basin ranges adjacent to the central eastern Sierra Nevada having similar topography, including Bodie Mountains in California and Nevada, Sweetwater Mountains in California and Nevada, Pine Grove Hills in Nevada (no pikas known in the range), and Wassuk Range in Nevada. Blue is elevations over 2900 m; yellow is elevations between 2900 m and 2600 m; pink is elevations between 2600 m and 2300 m; gray is elevations below 2300 m. Sites 17–22 and 24–25 are the Masonic subgroup; 27–30 are the Aurora-Brawley subgroup; and 31–33 the Bodie District subgroup. Star marks location of city of Bridgeport.

and warm margins within ranges that Grayson (2005) described.

How common might the historical situation exemplified by the Bodie Mountains be? For our study, similar conditions could explain observed dynamics in the Fremont Mountains, Mosquito Mountains, Idaho Canyon Range, Lassen Plateau, and Glass Mountains (e.g., sites in Table 2). Beyond this, other environmental contexts throughout the range of pikas where small, plateau-like ranges are connected to major cordillera (spur ranges of Beever et al. 2011, 2013) might be explained by these processes. By contrast, larger Great Basin ranges adjacent to cordillera, such as the Sweetwater and Wassuk Mountains that have large upland areas above 2895 m (Fig. 7) and significant upland corridors to source areas, are more likely to have retained pikas during warm periods, explaining the continued persistence and abundance of pikas in these areas today. Unlike the mountains of central Nevada, these ranges also have adequate corridors to the main cordillera for replenishment during cool intervals of the Holocene.

CONCLUSIONS

Whereas radiocarbon dating of ecological material commonly is applied to problems at paleohistoric time scales, the capacity for precise dating due to the bomb curve in the modern period has been little exploited. We effectively extracted carbon from fecal pellets of American pikas collected in native sites and rendered dates post-1950 CE with high accuracy into narrow time ranges. The two-sided nature of the bomb curve, however, means that date estimates on the far and near sides of the bomb curve cannot be resolved without ancillary evidence. One to four decades can separate equally likely dates, posing significant limitations to the

TABLE 4. Historic climate changes over five periods in the western Great Basin.

Temperature deviation (°C)	Elevation shift (m)	Source	Comments
Mid Holocene, ca. 7.5–5.5 ka			
NA	+100–300	Hafner (1993), Porter (1989)	
NA	+300	Richmond (1962)	
+2.0	+120–150	LaMarche (1973)	summer temperatures only
Neoglacial, ca. 5.3–2.5 ka			
−2–3	NA	Feng and Epstein (1994)	
−1	NA	Potito et al. (2006)	for 5–4 ka period
NA	∼−50	Konrad and Clark (1998)	inferred from LIA relative locations
Medieval Climate Anomaly, ca. 900–1300 CE			
+3.2	+400	Millar et al. (2006)	
+1.3–2.4	NA	Graumlich (1993)	average temperature for period
+2.9–3.2	NA	Scuderi (1993)	June to January temperatures
Little Ice Age, ca. 1400–1925 CE			
−0.2–2.0	−90	Bowerman and Clark (2011)	
−0.4–2.4	NA	Graumlich (1993)	
−2.8–3.0	NA	Scuderi (1993)	June to January temperatures
NA	−135	Porter (1989)	
NA	−125	Hafner (1993)	
20th century, 1900–2000 CE			
+3.7	NA	Millar et al. (2004)	minimum annual temperature
+1.0	NA	Millar et al. (2007, 2008)	minimum annual temperature
+3.7	NA	Moritz et al. (2008)	January temperature
+5.3	NA	Moritz et al. (2008)	July temperature

Notes: Average temperature deviations or inferred ecosystems elevation shifts (+, increase; −, decrease) inferred from mid-20th century for historic cold and warm periods, except for period of 20th century, 1900–2000 CE, which shows temperature changes over the 20th century. NA indicates that values are not available.

method if other information is not available. In the case of pikas, we document strategies that help to resolve the date intervals. Under appropriate conditions, thus, radiocarbon dating can provide an opportunity to attain information on modern species population dynamics useful for conservation. Radiocarbon analysis returned ages of pika pellets more than 59 years old, implying that herbivore feces can persist for more than half a century and that pellets of multiple ages can co-occur in pika habitat. As a consequence, pellet age does not accurately indicate time of last occupation for extirpated sites, although for those situations where extirpations were documented in the field, pellet ages predated those dates by a few to 20 years. By contrast, modern pellet ages were found in all currently occupied sites, suggesting that in occupied or recently occupied sites, radiocarbon dates correspond to presence or absence.

Applying combined insights from field studies with information from radiocarbon dating on occupancy and extirpation of 40 pika sites in eastern California, western Nevada, and southern Oregon allowed us to evaluate relationships of environmental context to population dynamics. In particular, we propose that whereas the major cordillera appear to provide long-term stable habitats throughout Holocene climate variability (4°C amplitude), many ranges adjacent to these cordillera have topographic conditions that subject them to multiple fluctuations across the range of historical climate variability. Where only minor altitudinal relief occurs in uplands and where corridors to the cordillera become unavailable for dispersal during warm centuries (e.g., the mid-Holocene and Medieval Climate Anomaly), pika persistence would have been at risk. Pikas in those ranges likely were gradually extirpated during extended historical warm periods. Conversely, during cold centuries (e.g., the Little Ice Age), corridors became cool enough to be used by pikas, enabling recolonization into the ranges from adjacent source cordillera and dispersal via stepping-stone modes across talus habitat in the uplands. Recolonization and expansion of pikas throughout the Bodie Mountains during the cool Little Ice Age centuries appears to have been augmented near the end of that interval (late 19th century) by effects of the mining era, when the proliferation of anthropogenic ore-dump habitats were accessible to pikas, who readily colonized them from the saturated adjacent native habitats. Subsequent warming of the 20th century reduced availability of native and anthropogenic habitat and triggered extirpation at many warm and low sites in the range. Continued future warming, as in historical warm periods, appears likely to further reduce colonization into anthropogenic habitats or extirpated native habitats, and continued declines and extirpations are expected. Projections for future warming without relaxation to cool periods portend a pattern that differs from the climate variability of historical millennia and suggest that insular ranges adjacent to large cordillera will lose pikas. Scattered refugial habitats could sustain a few remaining populations in these contexts, but these too are likely only temporary holdouts unless significant cool periods intervene.

Acknowledgments

Radiocarbon analysis was graciously supported by the Radiocarbon Collaborative, which is jointly sponsored by the USDA Forest Service, Lawrence Livermore National Laboratory, and Michigan Technological University. We thank Dr. Andrew Smith (Arizona State University) and Dr. Donald Grayson (University of Washington) for critical comments on the draft manuscripts and three anonymous reviewers for comprehensive edits and thoughtful comments on the submitted manuscript.

Literature Cited

Abatzoglou, J. T., K. T. Redmond, and L. M. Edwards. 2009. Classification of regional climate variability in the state of California. Journal of Applied Meteorology and Climatology 48:1527–1541.

Beever, E. A., P. E. Brussard, and J. Berger. 2003. Patterns of extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. Journal of Mammalogy 84:37–54.

Beever, E. A., C. Ray, P. W. Mote, and J. L. Wilkening. 2010. Testing alternative models of climate-mediated extirpations. Ecological Applications 20:164–178.

Beever, E. A., C. Ray, J. L. Wilkening, P. F. Brussard, and P. W. Mote. 2011. Contemporary climate change alters the pace and drivers of extinction. Global Change Biology 17:2054–2070.

Bergfeld, D., and W. C. Evans. 2011. Monitoring CO_2 emissions in tree kill areas near the resurgent dome at Long Valley Caldera, California. U.S. Geological Survey Scientific Investigations Report 2011-5038. U.S. Geological Survey, Menlo Park, California, USA.

Bowerman, N. D., and D. H. Clark. 2011. Holocene glaciation of the central Sierra Nevada, California. Quaternary Science Reviews 30:1067–1085.

Bronk Ramsey, C. 2009. Bayesian analysis of radiocarbon dates. Radiocarbon 51:337–360.

Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. American Naturalist 105:467–478.

Bruns, M., M. I. Levin, K. O. Munnich, H. W. Hubberten, and S. Fillipakis. 1980. Regional sources of volcanic carbon dioxide and their influence on ^{14}C content of present-day plant material. Radiocarbon 22:532–536.

Clow, D. W., L. Schrott, R. Webb, D. H. Campbell, A. Torizzo, and M. Dornblaser. 2003. Ground water occurrence and contributions to stream flow in an alpine catchment, Colorado Front Range. Groundwater 41:937–950.

Collins, G. H., and B. T. Bauman. 2012. Distribution of low-elevation America pika populations in the northern Great Basin. Journal of Fish and Wildlife Management 3:311–318.

Cooke, A. C., L. J. Hainsworth, M. L. Sorey, W. C. Evans, and J. R. Southon. 2001. Radiocarbon studies of plant leaves and tree rings from Mammoth Mountain, CA: a long-term record of magmatic CO_2 release. Chemical Geology 177:117–131.

Curry, A. M., and C. J. Morris. 2004. Lateglacial and Holocene talus development and rockwall retreat on Mynydd Du, UK. Geomorphology 58:85–106.

Daly, C. R., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33:140–158.

Davis, J. C., et al. 1990. LLNL/US AMS facility and research program. Nuclear Instruments and Methods in Physics Research Section B 52:269–272.

Erb, L. P., C. Ray, and R. Guralnick. 2011. On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*). Ecology 92:1730–1735.

Feng, X., and S. Epstein. 1994. Climatic implications of an 8000-year hydrogen isotope time series from Bristlecone pine trees. Science 265:1079–1081.

Galbreath, K. E., D. J. Hafner, K. R. Zamudio, and K. Agnew. 2009. Isolation and introgression in the Intermountain West: contrasting gene genealogies reveal the complex biogeographic history of the American pika (*Ochotona princeps*). Journal of Biogeography 37:344–362.

Ge, D., Z. Zhang, L. Xia, Q. Zhang, Y. Ma, and Q. Yang. 2012. Did the expansion of C_4 plants drive extinction and massive range contraction of micromammals? Inferences from food preference and historical biogeography of pikas. Palaeogeography, Paleaeoclimatology, Palaeoecology 326–328:160–171.

Graumlich, L. 1993. A 1000 year history of temperature and precipitation in the Sierra Nevada. Quaternary Research 39:249–255.

Graven, H. D., T. P. Guilderson, and R. F. Keeling. 2012. Observations of radiocarbon in CO_2 at La Jolla, California, USA 1992–2007: analysis of the long-term trend. Journal of Geophysical Research 117:D02302.

Grayson, D. K. 2005. A brief history of Great Basin pikas. Journal of Biogeography 32:2103–2111.

Grayson, D. K. 2011. The Great Basin. A Natural Prehistory. University of California Press, Berkeley, California.

Hafner, D. J. 1993. North American pika (*Ochotona princeps*) as a Late Quaternary biogeographic indicator species. Quaternary Research 39:373–380.

Hafner, D. J. 1994. Pikas and permafrost: post-Wisconsin historical zoogeography of *Ochotona* in the southern Rocky Mountains, USA. Arctic and Alpine Research 26:375–382.

Hafner, D. J., and R. M. Sullivan. 1995. Historical and ecological biogeography of Nearctic pikas (Lagomorpha: Ochotonidae). Journal of Mammalogy 76:302–321.

Hall, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley.

Howell, A. H. 1924. Revision of the American pikas. North American Fauna 47:1–57.

Hsueh, D. Y., N. Y. Krakauer, J. T. Randerson, X. Xu, S. E. Trumbore, and J. R. Southon. 2007. Regional patterns of radiocarbon and fossil fuel-derived CO_2 in surface air across North America. Geophysical Research Letters 34:L02816.

Hua, Q., and M. Barbetti. 2004. Review of tropospheric bomb ^{14}C data for carbon cycle modeling and age calibration purposes. Radiocarbon 46:1273–1298.

Huntly, N. J., A. T. Smith, and B. L. Ivins. 1986. Foraging behavior of the pika (*Ochotona princeps*), with comparisons of grazing versus haying. Journal of Mammalogy 67:139–148.

Jeffress, M. R., T. J. Rodhouse, C. Ray, S. Wolff, and C. W. Epps. 2013. The idiosyncrasies of place: geographic variation in the climate–distribution relationships of the American pika. Ecological Applications 23:864–878.

Konrad, S. K., and D. H. Clark. 1998. Evidence for an early Neoglacial glacier advance from rock glaciers and lake sediments in the Sierra Nevada, California, U.S.A. Arctic and Alpine Research 30:272–284.

LaDochy, S., R. Medina, and W. Patzert. 2007. Recent California climate variability: spatial and temporal patterns in temperature trends. Climate Research 33:159–169.

LaMarche, V. C., Jr. 1973. Holocene climatic variations inferred from treeline fluctuations in the White Mountains, California. Quaternary Research 3:632–660.

Lanier, H. C., and L. E. Olson. 2009. Inferring divergence times within pikas (*Ochotona* spp.) using mtDNA and relaxed molecular dating techniques. Molecular Phylogenetics and Evolution 53:1–12.

Lehman, S. J., J. B. Miller, C. Sweeney, and A. Karion. 2011. University of Colorado, Institute of Alpine and Arctic Research (INSTAAR), Radiocarbon composition of atmospheric carbon dioxide ($^{14}CO_2$) from the NOAA ESRL

Carbon Cycle Cooperative Global Air Sampling Network, 2003–2009, version 2012-04-26. ftp://aftp.cmdl.noaa.gov/data/trace_gases/co2c14/flask/README_flask_co2c14.html

MacArthur, R. A., and L. C. H. Wang. 1973. Physiology of thermoregulation in the pika, *Ochotona princeps*. Canadian Journal of Zoology 51:11–16.

MacArthur, R. A., and L. C. H. Wang. 1974. Behavioral thermoregulation in the pika *Ochotona princeps*: a field study using radiotelemetry. Canadian Journal of Zoology 52:353–358.

Mann, M. E., R. S. Bradley, and M. K. Hughes. 1999. Northern Hemisphere temperatures during the past millennium: inferences, uncertainties, and limitations. Geophysical Research Letters 26.6:759–762.

Manning, T., and J. C. Hagar. 2011. Use of nonalpine anthropogenic habitats by American pikas (*Ochotona princeps*) in western Oregon. Western North American Naturalist 71:106–112.

McDonald, K. A., and J. H. Brown. 1992. Using montane mammals to model extinctions due to global change. Conservation Biology 6:409–415.

Mead, J. I. 1987. Quaternary records of pika, *Ochotona*, in North America. Boreas 16:165–171.

Millar, C. I., L. J. Graumlich, D. L. Delany, R. D. Westfall, and J. K. King. 2004. Response of subalpine conifers in the Sierra Nevada, California, U.S.A., to 20th-century warming and decadal climate variability. Arctic, Antarctic, and Alpine Research 36:181–200.

Millar, C. I., J. C. King, R. D. Westfall, H. A. Alden, and D. L. Delany. 2006. Late Holocene forest dynamics, volcanism, and climate change at Whitewing Mountain and San Joaquin Ridge, Mono County, Sierra Nevada, USA. Quaternary Research 66:273–287.

Millar, C. I., and R. D. Westfall. 2008. Rock glaciers and periglacial rock-ice features in the Sierra Nevada; classification, distribution, and climate relationships. Quaternary International 188:90–104.

Millar, C. I., and R. D. Westfall. 2010. Distribution and climate relationships of American pika (*Ochotona princeps*) in the Sierra Nevada and western Great Basin, USA; periglacial landforms as refugia in warming climates. Arctic, Antarctic, and Alpine Research 42:76–88.

Millar, C. I., R. D. Westfall, and D. L. Delany. 2007. Response of high-elevation limber pine (*Pinus flexilis*) to multi-year droughts and 20th-century warming: Sierra Nevada, California, USA. Canadian Journal of Forest Research 37:2508–2520.

Millar, C. I., R. D. Westfall, and D. Delany. 2013. Thermal and hydrologic attributes of rock glaciers and periglacial talus landforms: Sierra Nevada, California, USA. Quaternary International 310:169–180.

Millar, C. I., R. D. Westfall, and D. Delany. *In press*. Thermal regimes and snowpack relations of periglacial talus slopes, Sierra Nevada, California, USA. Arctic, Antarctic, and Alpine Research.

Minder, J. R., D. R. Durran, and G. H. Roe. 2011. Mesoscale controls on the mountainside snow line. Journal of Atmospheric Science 68:2107–2127.

Moritz, C., and R. Agudo. 2013. The future of species under climate change: resilience or decline? Science 341:504–508.

Nichols, L. 2011. Fecal pellets of American pikas provide a crude chronometer for dating patch occupancy. Western North American Naturalist 70:500–507.

Osborn, G., and K. Bevis. 2001. Glaciation in the Great Basin of the western United States. Quaternary Science Reviews 20:1377–1410.

Pepin, N., C. Daly, and J. D. Lundquist. 2011. The influence of surface versus free-air decoupling on temperature trend patterns in the western U.S. Journal of Geophysical Research—Atmospheres 116(D10):D10109.

Péwé, T. L. 1983. Alpine permafrost in the contiguous United States: a review. Arctic and Alpine Research 15:145–156.

Porter, S. C. 1989. Some geological implications of average Quaternary glacial conditions. Quaternary Research 32:245–261.

Potito, A. P., D. F. Porinchu, G. M. MacDonald, and K. A. Moser. 2006. A late Quaternary chironomid-inferred temperature record from the Sierra Nevada, California, with connections to northeast Pacific sea surface temperatures. Quaternary Research 66:356–363.

Reimer, P. J., T. A. Brown, and R. W. Reimer. 2004. Discussion: reporting and calibration of post-bomb ^{14}C data. Radiocarbon 46:1299–1304.

Reimer, P. S., et al. 2009. IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. Radiocarbon 51:1111–1150.

Richmond, G. M. 1962. Quaternary stratigraphy of the La Sal Mountains, Utah. USGS Professional Paper 324:1–135.

Rodhouse, T. J., E. A. Beever, L. K. Garrett, K. M. Irvine, M. R. Jeffress, M. Munts, and C. Ray. 2010. Distribution of American pikas in a low-elevation lava landscape: conservation implications from the range periphery. Journal of Mammalogy 91:1287–1299.

Roy, J. W., and M. Hayashi. 2009. Multiple, distinct groundwater flow systems of a single moraine-talus feature in an alpine watershed. Journal of Hydrology 373:139–150.

Scuderi, L. A. 1993. A 2000-year tree ring record of annual temperatures in the Sierra Nevada Mountains. Science 259:1433–1436.

Simpson, W. G. 2009. American pikas inhabit low-elevation sites outside the species' previously described bioclimatic envelope. Western North American Naturalist 69:243–250.

Smith, A. T. 1974*a*. The distribution and dispersal of pikas: influences of behavior and climate. Ecology 55:1368–1376.

Smith, A. T. 1974*b*. Distribution and dispersal of pikas: consequences of insular population structure. Ecology 55:1112–1119.

Smith, A. T., and M. E. Gilpin. 1997. Spatially correlated dynamics in a pika metapopulation. Pages 407–428 *in* I. A. Hanski and M. E. Gilpin, editors. Metapopulation dynamics: ecology genetics and evolution. Academic Press, San Diego, California, USA.

Smith, A. T., and M. L. Weston. 1990. Ochotona princeps. Mammalian Species 352:1–8.

Stewart, S. A. E., and D. H. Wright. 2012. Assessing persistence of the American pika at historic localities in California's northern Sierra Nevada. Wildlife Society Bulletin 36:759–764.

Stuiver, M., and H. A. Polach. 1977. Discussion: reporting of ^{14}C data. Radiocarbon 19:355–363.

Tapper, S. C. 1973. The spatial organisation of pikas (*Ochotona*) and its effect on population recruitment. Dissertation. University of Alberta, Edmonton, Alberta, Canada.

Taylor, R. E. 1987. Radiocarbon dating: an archaeological perspective. Academic Press, Orlando, Florida, USA.

Tuniz, C., J. R. Bird, D. Fink, and G. F. Herzog. 2011. Accelerator mass spectrometry: ultrasensitive analysis for global science. Second edition. CRC Press, Boca Raton, Florida, USA.

USFWS (US Fish and Wildlife Service). 2010. 12-month finding on a petition to list the American pika as threatened or endangered. Federal Register 50 CFR Part 17.

Verts, B. J., and L. N. Carraway. 1998. Land mammals of Oregon. University of California Press, Berkeley, California, USA.

Vogel, J. S., J. R. Southon, and D. E. Nelson. 1987. Catalyst and binder effects in the use of filamentous graphite for AMS. Nuclear Instruments and Methods in Physics Research Section B 29:1–56.