

# Isotopic niche of the American pika (*Ochotona princeps*) through space and time

M.L. Westover, K.A. Lizewski, K.B. Klingler, and F.A. Smith

**Abstract:** Anthropogenic climate change is influencing the ecology and distribution of animals. The American pika (*Ochotona princeps* (Richardson, 1828)) is considered a model species for studying the effects of climate on small alpine mammals and has experienced local extirpation across its range. Using stable isotope analysis of two seasonal molts and bone collagen, we characterize the isotopic carbon and nitrogen niche of pika populations across their range and through time. We find pika isotopic diet to be stable across both time and space compared with other animals and considering the geographic and environmental extent of their range. We find that climatic, not geographic, factors explain part of the isotopic variation across their range. Both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from the fall-onset molt decrease with relative humidity of the environment and  $\delta^{15}\text{N}$  values from bone collagen increase with temperature and precipitation. We find a small but significant seasonal difference in  $\delta^{13}\text{C}$ , which could be explained by microbial enrichment of cached haypiles. We establish a baseline of pika isotopic diet and patterns related to climate across their range. We conclude that differences in isotopic signature between pika populations likely reflect the physiology of their forage plants in different environmental conditions.

**Key words:** alpine ecosystems, biogeography, climate, dietary ecology, American pika, *Ochotona princeps*, stable isotope analysis.

**Résumé :** Les changements climatiques d'origine humaine influencent l'écologie et la répartition des animaux. Le pika d'Amérique (*Ochotona princeps* (Richardson, 1828)), considéré comme une espèce modèle pour l'étude des effets du climat sur les petits mammifères alpins, a connu de la disparition locale en différente région de son aire de répartition. En utilisant l'analyse des isotopes stables de deux mues saisonnières et de collagène des os, nous caractérisons les niches isotopiques du carbone et de l'azote de populations de picas à la grandeur de leur aire de répartition et dans le temps. Nous constatons que le régime alimentaire isotopique des picas est stable dans le temps et dans l'espace comparativement à celui d'autres animaux et étant donné l'étendue géographique et environnementale de leur aire de répartition. Nous constatons aussi que des facteurs climatiques, et non géographiques, expliquent une partie des variations isotopiques dans leur aire de répartition. Les valeurs de  $\delta^{13}\text{C}$  et  $\delta^{15}\text{N}$  de la mue du début de l'automne diminuent parallèlement à l'humidité relative du milieu et les valeurs de  $\delta^{15}\text{N}$  du collagène des os augmentent parallèlement à la température et aux précipitations. Nous relevons une différence faible, mais significative du  $\delta^{13}\text{C}$ , qui pourrait s'expliquer par l'enrichissement microbien de piles de foin cachées. Nous établissons des conditions de référence pour le régime alimentaire et les motifs isotopiques des picas associés au climat à la grandeur de leur aire de répartition. Nous concluons que les différences de signatures isotopiques entre populations de picas reflètent vraisemblablement la physiologie des plantes dont ils se nourrissent dans différentes conditions ambiantes. [Traduit par la Rédaction]

**Mots-clés :** écosystèmes alpins, biogéographie, climat, écologie alimentaire, pika d'Amérique, *Ochotona princeps*, analyse des isotopes stables.

## Introduction

Climate change is disrupting species and communities worldwide through range shifts, local extirpation, and population declines (Beever et al. 2003; Parmesan and Yohe 2003; Pearce-Higgins et al. 2010). While there are now multiple studies documenting latitudinal and elevational shifts in response to climate change (e.g., Moritz et al. 2008; Lenoir and Svenning 2015), the mechanisms underlying these distributional changes are not as well understood (Chen et al. 2011). The specific mechanisms are likely to be diverse and may include factors such as physiological limits, drought stress, and reductions in food sources (Cahill et al. 2012). In this contemporary era of climate change, a synoptic understanding of the mechanisms influencing species distributions is more pressing than ever (Cahill et al. 2012; Wisz et al. 2013; Rapacciuolo et al. 2014).

Anthropogenic climate change has altered geographic ranges for many species (Parmesan and Yohe 2003; Moritz et al. 2008; Thomas 2010; Chen et al. 2011; McCain and King 2014). A wide variety of taxa have expanded their ranges poleward and (or) upslope in elevation, consistent with expected responses to warming temperatures (e.g., Parmesan and Yohe 2003; Tingley et al. 2009, 2012; Chen et al. 2011; Lenoir and Svenning 2015). Low latitude and low elevation or “trailing edge” extirpations are also common, impacting nearly half of plant and animal species surveyed (Wiens 2016). While some species are following their climatic niche through distributional shifts, many populations appear unable to keep pace with climate change and succumb to local extinction (Thomas 2010; Beever et al. 2011; Wiens 2016; Panetta et al. 2018).

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Temperature and precipitation often determine species distributions (Grinnell 1929; Thomas 2010; Lesica and Crone 2017), but biotic interactions such as food availability, predation, competition, or mutualisms are also important contributors (Hutchinson 1957; Guisan and Thuiller 2005; Wisz et al. 2013; Louthan et al. 2015). Potential mechanisms behind climate-induced distributional shifts and local extinctions include temperature or drought stress, as well as alterations of biotic factors (Tylianakis et al. 2008; Blois et al. 2013; Cahill et al. 2014). Habitat specialists are limited by the availability of suitable habitats and vegetation communities, which may themselves be constrained by climate (Van der Putten et al. 2010). For example, populations of desert bighorn sheep (*Ovis canadensis* Shaw, 1804) have disappeared from lower elevation and lower precipitation areas presumably because of a lack of forage (Epps et al. 2004). The extent to which climate change is impacting animals directly or indirectly through exacerbating changes in biotic interactions deserves increased investigation (Guisan and Thuiller 2005; Sexton et al. 2009; Anderson 2013; Cahill et al. 2014).

One way that climate change can lead to distributional shifts and local extinction is by altering food webs and resource availability. Reduced food availability was identified as the most commonly implicated cause of climate-related extirpation and population declines in case studies of mammals, fish, birds, and insects (Cahill et al. 2012). Temperature changes can alter the availability and abundance of food species, thus initiating indirect impacts on the distribution and abundance of consumers (Pörtner and Farrell 2008; Graham et al. 2009; Stirling and Derocher 2012). Climate change can also rearrange food webs by causing the loss or decline of species in a community, which can lead to changes in ecosystem function (Petchev et al. 1999; Lurgi et al. 2012). Changes in food availability or quality may be an under-appreciated mechanism behind extirpations related to climate change and population declines.

American pikas (*Ochotona princeps* (Richardson, 1828); henceforth simply referred to as pikas) are small, cold-adapted lagomorphs that have experienced well-documented extirpations and range contractions due to contemporary climate change (Beever et al. 2003, 2011, 2016; Wilkening et al. 2011). Local extirpations across their range, including parts of the southern Rocky Mountains, Great Basin, and Sierra Nevada, are associated with warming temperatures or decreased precipitation in the past few decades (Erb et al. 2011; Beever et al. 2016; Stewart et al. 2017). Additional studies suggest forage availability and quality may be the primary factors influencing pika occupancy and persistence in more arid environments (e.g., Rodhouse et al. 2010; Ray et al. 2016). The availability of quality vegetation and diet may be important factors influencing pika populations across their range. Pikas select for two different types of diet: summer forage, which they consume immediately, and winter forage, which they collect during the summer months and cache in haypiles for use in the winter and early spring (Conner 1983; Dearing 1997a). Pikas may preferentially collect high-quality forbs (e.g., higher nitrogen and nutrient content, greater percent phenolic compounds, lower fiber) for haypile storing, which could lead to seasonal variation in diet between winter and summer months (Huntly et al. 1986; Dearing 1996, 1997a, 1997b; Smith and Erb 2013).

Pika diet and hay stockpiling may also be affected by warmer temperatures, through limiting the time spent foraging or reducing the quality of food available (Dearing et al. 2008; Bhattacharyya and Ray 2015; Hall and Chalfoun 2018). Exposure to ambient temperatures above 25.5 °C can cause hyperthermia in these animals, limiting their active surface time (MacArthur and Wang 1974; Smith 1974). In general, pikas tend to select proportionally more forbs compared with less nutritious grass (Hall and Chalfoun 2019). As daytime temperatures increase, pikas spend less time foraging and caching food as a way to avoid thermoregulatory stress (Hall and Chalfoun 2019). Pikas select higher quality

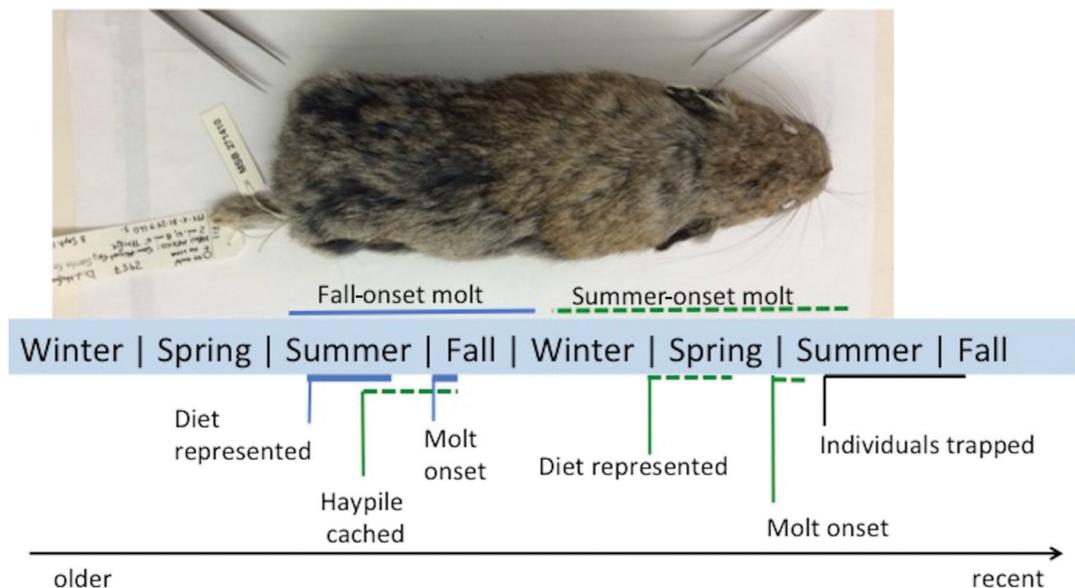
forage (high nitrogen and water content) particularly when their foraging time is limited by warmer summer temperatures (Smith and Erb 2013; Hall and Chalfoun 2018). Thus, the availability of a diverse and nutritious vegetation community may contribute to pika resilience in the face of challenging temperatures. However, climate change may precipitate nutritionally challenging environments for pikas, as increasing temperatures and drought stress can lead to lower nutrient content in plants and relative increases in less-nutritious graminoids (Barbehenn et al. 2004; Venn et al. 2014; Rosenblatt and Schmitz 2016). As vegetation communities shift due to climate change, pika diet may change with consequences that could potentially influence pika distribution.

Stable isotope analysis (SIA) of carbon and nitrogen is an accepted technique in animal ecology to determine approximate dietary composition (Crawford et al. 2008; Ben-David and Flaherty 2012). Different plant types differentially uptake carbon isotopes, which are then incorporated into an animal's tissues, providing a signature of what types of plants the individual ate (DeNiro and Epstein 1978, 1981; O'Leary 1988).  $\delta^{13}\text{C}$  values are typically used to distinguish the proportions of  $\text{C}_3$  and  $\text{C}_4$  plants in animal diets (Kohn 2010). Greater discrimination of  $^{13}\text{C}$  during photosynthesis in  $\text{C}_3$  plants leads to distinctive isotopic signatures in  $\text{C}_3$  ( $\delta^{13}\text{C} = -20\text{‰}$  to  $-37\text{‰}$ ) and  $\text{C}_4$  ( $\delta^{13}\text{C} = -12\text{‰}$  to  $-16\text{‰}$ ) plants (O'Leary 1988). In addition,  $\delta^{13}\text{C}$  signatures can also be used to distinguish categories within  $\text{C}_3$  plants, such as graminoids and forbs (O'Leary 1988; Farquhar et al. 1989). Graminoids tend to be less nutritious (lower nitrogen, higher fiber) and have higher  $\delta^{13}\text{C}$  isotope values compared with forbs, a trend that is particularly relevant to pika diets and our study (O'Leary 1988; Farquhar et al. 1989). Carbon isotopes are also considered indicators of past climatic patterns in that  $\text{C}_3$  plants demonstrate a negative relationship between both precipitation and humidity across varying spatial and temporal scales (Sternberg et al. 1984; Kohn 2010). Globally, plant  $\delta^{15}\text{N}$  are negatively correlated with precipitation and positively correlated with temperature (Amundson et al. 2003; Craine et al. 2015).

We investigate the isotopic dietary niche of the pika through space and time. By analyzing multiple tissue types and museum specimens sampled at different time scales across the last century, we document the range of their isotopic diet and the extent to which it is influenced by climate. Stable isotopes from bone collagen capture the long-term average of a mammal's diet (Koch et al. 2009). Analysis of fur can be used to study diet at the time when fur growth occurred and thus characterize seasonal variation (West et al. 2004; Cryan et al. 2004; Chambers and Doucett 2008). Seasonal molts progress in a nasocaudal direction and are easily distinguishable in pikas. The summer-onset molt typically begins in late June or July and is shorter and lighter in color than the fall-onset molt, which begins in September and remains through much of the year, although the timing of molts likely varies across the range (Howell 1924; Krear 1965) (Fig. 1). Rates of carbon isotope turnover in pika fur are not known but are probably  $\sim 48$  days (Tieszen et al. 1983). Using this estimation, we are able to investigate if pikas consume different isotopic diets for summer forage (via fall-onset molt) and haypiles and (or) spring forage (via summer-onset molt) (Fig. 1). Our study is the first to document the pika's isotopic dietary niche. It is unique in that we compare historical pika isotopic diet spanning the early 20th century with modern diets of extant populations, as well as comparing seasonal diets.

We hypothesize that climate may impact the isotopic diet niche of pika populations through space and time. If pikas preferentially cache or consume different proportions of plant functional types (e.g., more forbs cached for winter consumption; Dearing 1997a), then there should be isotopic differences in seasonal fur molts. Based on global isotope trends in plants, we predict that pika population  $\delta^{15}\text{N}$  values will be negatively correlated with moisture and positively correlated with temperature (e.g., Craine

**Fig. 1.** Timeline illustrating the influences of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures in American pika (*Ochotona princeps*) winter and summer molts. Fall-onset molt likely reflects summer forage from the year prior to pika specimen collection. Summer-onset molt may represent early spring forage or diet from haypiles cached the summer prior to collection. Color version online.



et al. 2015). We predict that populations in warmer and drier areas will have isotopic diets that are more enriched in  $^{13}\text{C}$  owing to increased water stress of plants and increased graminoid consumption relative to forbs (Ehleringer and Cooper 1988; O’Leary 1988; Farquhar et al. 1989; Tieszen 1991). More recent pika populations may have higher  $\delta^{13}\text{C}$  associated with higher temperatures and increased drought stress relative to historical populations since regional temperatures have increased  $1.5\text{ }^{\circ}\text{C}$  in the past century (IPCC 2014). Populations along the trailing edge of the species’ range (low elevation, low latitude) are likely to show the strongest initial responses to warming climate because they tend to sit on the boundary of a species’ ecological limits (Hampe and Petit 2005; Sexton et al. 2009). We therefore predict that populations at lower elevation and (or) lower latitudes will have higher  $\delta^{13}\text{C}$  values, indicating increased graminoid consumption or increased drought stress.

## Materials and methods

### Study design

We investigated isotopic dietary trends in pikas across their range and historical time using museum collections, in addition to modern field-collected pika fur. Our populations range in latitude from  $35.8^{\circ}\text{N}$  to  $45.4^{\circ}\text{N}$  and spanned the years 1912 to 2016, including five populations that were surveyed across multiple time periods (Fig. 2 and Supplementary Table S1<sup>1</sup>). We obtained both fur and bone from museum specimens for 13 populations and fur alone from 8 live-trapped populations (Supplementary Table S1).<sup>1</sup> Thus, in total, we analyzed 21 distinct spatiotemporal pika populations from 13 geographic locations across a century. All specimens were caught during the summer months of June to September. We grouped pikas into “populations”, defined as individuals ( $n = 8\text{--}26$ ) collected from the same locality (the same mountain massif with no valleys or major rivers separating individuals) within 3 years of each other. Typically, sample populations were collected in the same summer with the same location reported on specimen tags.

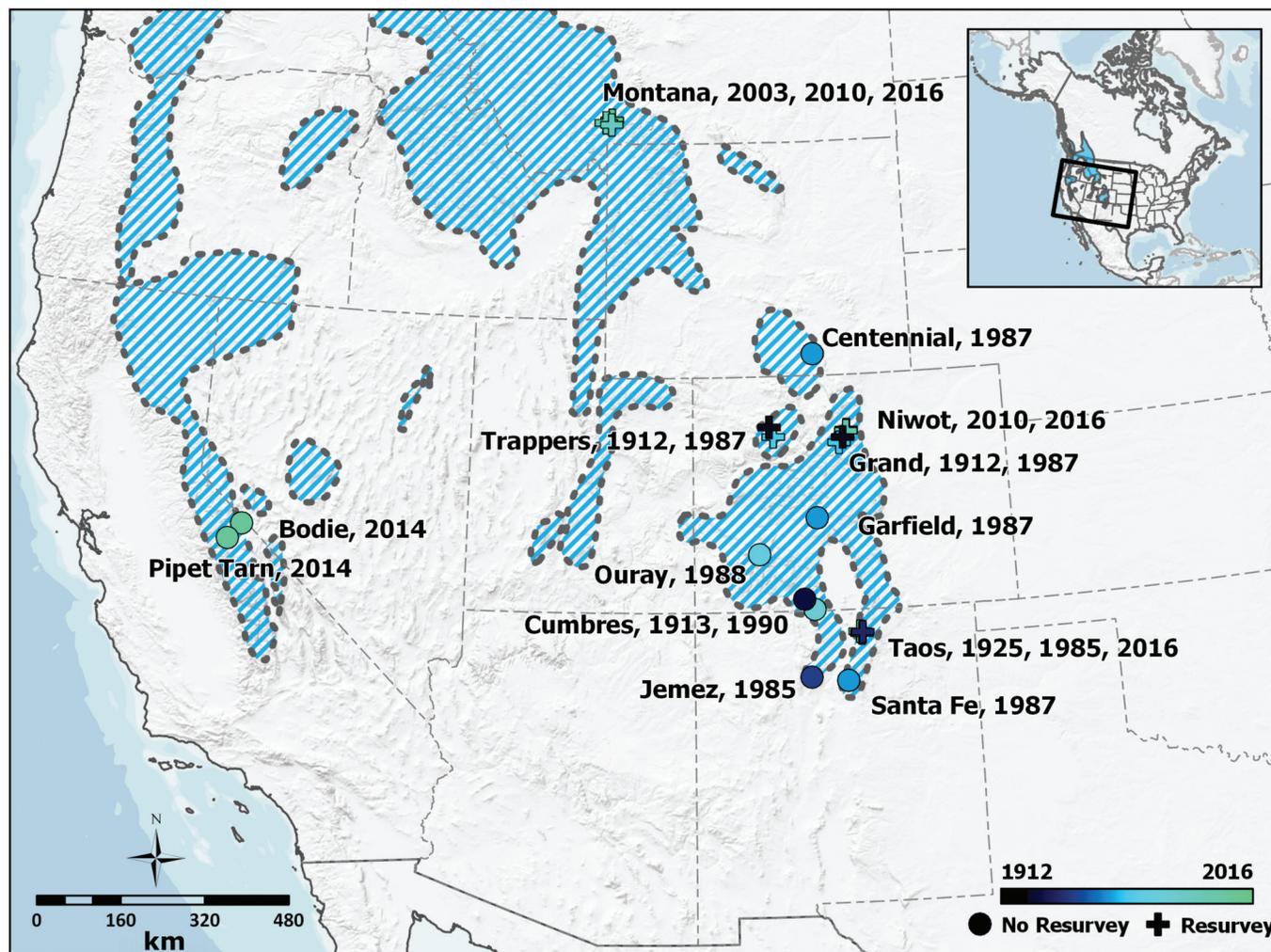
To compare trailing edge population isotopic diets to central populations, we included specimens from the southernmost pika populations, as well as from lower elevation and comparatively xeric sites. We analyzed bone samples ( $n = 195$ ) and summer-onset ( $n = 203$ ) and fall-onset ( $n = 278$ ) molts for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotope composition (Supplementary Table S2).<sup>1</sup> We used GeoLocate (<http://www.geo-locate.org/>) software and Google Earth (<https://www.google.com/earth/>) to determine latitude and longitude from recorded location data on specimen tags when GPS coordinates were not recorded. Permission and protocols for sampling via live capture and release of pikas were approved through Colorado Parks and Wildlife (license No. 10TR2014 and No. 16TR2014); Montana Fish, Wildlife and Parks (permit No. 2010-064 and No. 2016-002); the University of Colorado Institutional Animal Care and Use Committee (IACUC protocol No. 08-07-RAY-01 and No. 1405.3); the University of Nevada–Reno IACUC (protocol No. 00557); California Department of Parks and Recreation (No. 2014-03); California Department of Fish and Wildlife (SC-012184); US Department of Agriculture (USDA) Forest Service, Pacific Southwest Region, Harvey Monroe Hall RNA (No. PSW-4000-12, by letter); USDA Forest Service, Inyo National Forest (No. LVD14021 and No. RMT143); and the Department of the Interior. Collections in New Mexico were approved by IACUC (protocol No. 12-100764-MC) at the University of New Mexico and Museum of Southwestern Biology.

### Fur sampling

Since pika specimens were all collected in the summer (June–September), we were able to take advantage of molt lines to characterize seasonal diet variation. For museum specimens, we sampled small clumps of fur ( $\sim 1\text{--}2\text{ g}$ ) with tweezers and scissors from both sides of the molt line, near the shoulder for summer-onset fur and near the rump for fall-onset fur to analyze seasonal variation in isotope ratios (Fig. 1). We analyzed paired summer-onset and fall-onset molts for 14 populations. The summer-onset molt and previous year fall-onset molt were usually easily distinguished, but if not, then we sampled only fall-onset molt. For

<sup>1</sup>Supplementary tables and figures are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2019-0212>.

**Fig. 2.** Locations of American pika (*Ochotona princeps*) populations sampled for stable isotope analysis. The distribution of pikas is outlined and hatched in blue. Circles indicate locations of populations that were sampled from one time period and crosses indicate locations that were sampled for temporal comparison. Darker colors indicate older samples. Years of sampling are indicated next to the population names. Figure was created using ArcGIS Pro version 2.4 (esri, Inc., Redlands, California, USA) and assembled from a shapefile of the geographic range of pika (<https://www.iucnredlist.org; IUCN 2016>) and data from the current study. Color version online.



pikas from Pipet Tarn and Bodie, we collected a small hair sample (~2.0 cm × 1.0 cm square patch) using scissors on the dorsal side of the animal near the rump. Additional collaborators pulled a small amount of fur from the rump of pikas at Niwot Ridge (Colorado) and Montana using tweezers.

We rinsed fur samples in 2:1 chloroform–methanol mixture two times before drying for at least 24 h in a fume hood. We weighed fur samples to 0.5–0.6 or 0.9–1.0 mg, depending on the amount of available material, and wrapped samples in tin capsules for SIA. All isotope ratio analysis for fur, bone, and plant materials was completed at the Center for Stable Isotopes at the University of New Mexico. Isotope ratios were quantified using a Thermo Scientific Delta V Plus mass spectrometer with a dual inlet and ConFlo IV interface connected to a Costech 4010 elemental analyzer. Analytical precision was estimated via repeated measurements of reference materials calibrated to internationally accepted standards; within-run standard deviation for all reference materials was ≤0.2‰ for δ<sup>15</sup>N and ≤0.04 for δ<sup>13</sup>C‰.

#### Bone collagen sampling

We analyzed bone collagen from nine modern (years 1987–2016) and four historical (years 1909–1925) populations to study the lifetime-averaged pika isotopic diet (Supplementary Table S1).<sup>1</sup>

We collected 25–100 mg bone samples from a rib, or bone collagen samples from samples of ribs when available, or taken from the condylar process with a low speed Dremel® tool if the post-cranial skeleton was unavailable. We placed samples in glass vials with foil-lined caps and demineralized them in 0.25 mol/L HCL for 24–72 h. We rinsed samples in deionized water (3 times) and then bathed in a 2:1 chloroform–methanol mixture for 24 h (3 times), rinsing with deionized water 6–8 times in between each chloroform–methanol bath. After the final deionized water rinse, we moved the samples to microcentrifuge tubes with the caps secured closed with parafilm and two small holes created in the cap for moisture to escape. We freeze-dried samples for at least 6 h and then weighed out 0.9–1.0 mg samples for SIA as described above.

#### Plant sampling

We analyzed plants from seven localities to estimate modern pika diet composition (collected 2014–2016, *n* = 128; Supplementary Table S3<sup>1</sup>). Plant collection locations included the Sangre de Cristo Mountains in northern New Mexico, the Rocky Mountains near Niwot Ridge, Colorado, and Emerald Lake, Montana, as well as two localities in the Sierra Nevada Mountains in California (Pipet Tarn and Cabin Slope), which span from latitude 35.8018°N

**Table 1.** Models with substantial support that best describe variability in mean isotope values of American pika (*Ochotona princeps*) populations as ranked by Akaike's information criterion corrected for small sample size ( $AIC_c$ ) and  $\Delta AIC_c < 2$ .

Tissue	Model	Isotope	K	$AIC_c$	$\Delta AIC_c$	$AIC_c$ weight	Cumulative $AIC_c$ weight	Log likelihood	df
Fall-onset fur*	RH_prev	$\delta^{13}C$	3	38.8	0	0.34	0.34	-15.7	19
Fall-onset fur	MAP_prev + RH_prev	$\delta^{13}C$	4	38.93	0.13	0.32	0.66	-14.2	18
Fall-onset fur	RH_sm_prev	$\delta^{15}N$	3	65.74	0	0.54	0.54	-29.2	19
Summer-onset fur†	Tave_wt	$\delta^{13}C$	3	20.05	0	0.63	0.63	-5.82	12
Summer-onset fur	NullModel	$\delta^{15}N$	2	38.15	0	0.25	0.25	-16.5	13
Summer-onset fur	Tave_wt	$\delta^{15}N$	3	39.35	1.2	0.14	0.38	-15.5	12
Summer-onset fur	PPT_sm_prev	$\delta^{15}N$	3	39.85	1.7	0.11	0.49	-15.7	12
Fur seasonal difference‡	NullModel	$\delta^{13}C$	2	7.31	0	0.6	-0.6	1.11	13
Fur seasonal difference	NullModel	$\delta^{15}N$	2	-15.43	0	0.48	0.48	10.26	13
Fur seasonal difference	Temp seasonality	$\delta^{15}N$	4	-13.72	1.7	0.21	0.69	13.08	12
Fur	NullModel	SEA§	2	7.31	0	0.87	0.87	-1.11	13
Bone	NullModel	$\delta^{13}C$	2	24.88	0	0.38	0.38	-9.84	12
Bone	MAP_prev	$\delta^{13}C$	3	25.82	0.95	0.24	0.61	-8.58	11
Bone	MAT_prev + MAP_prev	$\delta^{15}N$	4	22.07	0	0.54	0.54	-4.53	10
Bone	MAP_prev	$\delta^{15}N$	3	23.05	0.98	0.33	0.88	-7.19	11
Bone	Temp seasonality	SEA	4	35.52	0	0.57	0.57	-11.3	11
Bone	NullModel	SEA	2	36.29	0.77	0.39	0.96	-15.6	12

**Note:**  $\Delta AIC_c$  is the difference between each model and the most parsimonious model;  $K$  is the number of free parameters; Akaike weight ( $AIC_c$  weight) indicates the level of support. Cumulative  $AIC_c$  weight and log likelihood of each model are provided. For a complete model suite see Supplementary Table S2.<sup>1</sup> Abbreviations in the model column are as follows: RH, relative humidity (%); prev, climate data from year prior to collection; MAP, mean annual precipitation (mm); sm, summer; Tave, seasonal mean temperature; wt, winter; PPT, precipitation (mm); Temp seasonality, Tave\_sm - Tave\_wt; MAT, mean annual temperature (°C).

\*We analyzed annual climate variables from the year prior to collection to reflect the climate of the year that the fur was grown, as well as summer, spring, and winter seasonal variables of relative humidity, precipitation, and mean temperature.

†For summer-onset molt, we investigated winter and spring seasonal climate variables from the year of collection, as well as summer from the year prior to collection, to include the weather when haypiles would have been cached.

‡Fur seasonal difference is the absolute difference between fall-onset fur and summer-onset fur.

§Standard ellipse area (SEA) is a measure of isotopic dietary niche breadth.

||Bone collagen reflects isotopic diet over the lifetime of individuals; we tested climate values from year prior to collection.

to 45.41100°N and elevations from 2609 to 3722 m. Plant collection sites align with contemporary fieldwork locations and dates to provide baseline stable isotope values of pika forage. Plant samples were opportunistically collected from within a ~12 m radius of a pika-inhabited talus slope or haypile, within the mean home-range size of pikas (Smith and Weston 1990; Bhattacharyya and Ray 2015). Many of the plant samples came from near the edge of the talus slope and were also found cached in active haypiles; thus, capturing a variety of plant types likely consumed by each pika population. We transferred plants from the Sangre de Cristo mountains of New Mexico to a plant press for drying and identification at the Museum of Southwestern Biology Herbarium. Dried plant samples from Colorado, Montana, and California were stored in envelopes until processing. For stable isotope analysis, we preferentially selected plant genera that were found across different sampling localities in an attempt to reduce confounding variables across localities. We analyzed plants from 18 different families and sorted identified plant species into one of three main functional groups of our study: forb ( $n = 55$ ), woody ( $n = 19$ ), or graminoid ( $n = 53$ ) (Supplementary Table S3).<sup>1</sup> We cleaned plant samples with deionized water and paper towels to remove dirt, dried them in an oven at 40 °C overnight, and weighed 3.5–3.6 mg samples (based on 2.9–3.0 mg test run not having enough nitrogen content for analysis) before isotope analysis as described above.

## Climate

We obtained climate data specific to the year and location of each population from ClimateWNA software, which interpolates climate values from PRISM data (Daly et al. 2008) and adjusts for elevation lapse rates (<http://www.climatewna.com/>; Wang et al. 2016). We analyzed the mean annual temperature (MAT), mean annual precipitation (MAP), and relative humidity (RH) of the year prior to collection to determine the effects of climate on pika bone isotope values (Supplementary Table S2).<sup>1</sup> We tested the relationships of fur isotope values to the annual and seasonal tem-

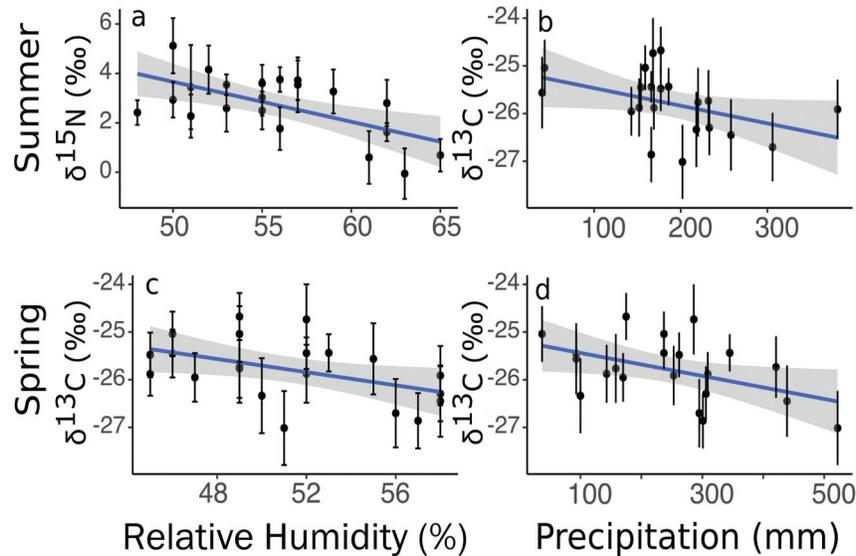
perature, precipitation, and RH of the year before collection since these variables are known to influence  $\delta^{13}C$  and  $\delta^{15}N$  of plants globally (e.g., Sternberg et al. 1984; Kohn 2010; Craine et al. 2015) (Supplementary Table S2).<sup>1</sup> RH (the amount of moisture in the air) physiologically impacts plant ecology from stomatal closure to species' distributions, and thus, could impact consumer's isotopic signatures (Daly et al. 2015; Konings et al. 2017). To study the relationships between climate seasonality and seasonal differences in fur, we calculated temperature seasonality as the difference between mean summer (June, July, and August) temperature and mean winter (December, January, and February) temperatures. We generated precipitation and RH seasonality variables by subtracting seasonal mean values from the annual total precipitation and RH annual mean values.

## Statistical analyses

We calculated the mean and standard deviations (SD) for  $\delta^{13}C$  and  $\delta^{15}N$  values of each population's winter fur, summer fur, and bone samples. We performed all statistical analyses in R version 3.3.2 (R Core Team 2016) and calculated standard ellipse areas (SEA) as a quantitative measure of isotopic niche size using the R package SIBER (Jackson et al. 2011). We corrected for the increase of  $\delta^{13}C$  in the atmosphere since nuclear testing (Suess effect) by applying the following equation: if younger than 1960, then  $(2016 - \text{year}) \times -0.022$ ; if between 1860 and 1960, then  $[(1960 - \text{year}) \times -0.005] - 1.21$ . Thus, we standardized all  $\delta^{13}C$  values to the year 2016 (Chamberlain et al. 2005).

To determine the relationships of climate and geography to pika isotopic dietary niche, we ran univariate linear regressions and multiple linear models between selected climate variables and population mean  $\delta^{13}C$  and  $\delta^{15}N$  values from fur and bone (Table 1; for a full list of models see Supplementary Table S2<sup>1</sup>). We selected the most likely models as determined by the highest  $AIC_c$  weight set (where  $AIC_c$  is Akaike's information criterion corrected for small sample size) and considered additional models with substantial support ( $\Delta AIC_c \leq 2$ ) from each model set (Table 1;

**Fig. 3.** Fall-onset American pika (*Ochotona princeps*) fur stable isotope values correlate with seasonal climate variables from the year prior to collection. Circles show the population mean isotope values, vertical lines indicate 1 SD, and shading indicates the 95% confidence region. (a) Pika population  $\delta^{15}\text{N}$  values are negatively correlated with mean summer relative humidity ( $R^2 = 0.35$ ,  $P < 0.001$ ; Supplementary Table 2<sup>1</sup>). (b) Summer precipitation is negatively correlated with mean  $\delta^{13}\text{C}$  values of pika populations ( $R^2 = 0.14$ ,  $P = 0.005$ ; Table 1). (c) Spring relative humidity ( $R^2 = 0.17$ ,  $P < 0.05$ ; Supplementary Table S2<sup>1</sup>) and (d) spring precipitation ( $R^2 = 0.17$ ,  $P < 0.05$ ; Supplementary Table S2<sup>1</sup>) are significantly related to  $\delta^{13}\text{C}$  values. Color version online.



Burnham and Anderson 2002). Since many climate variables are related to each other, we removed variables with correlations of  $R^2 > 0.5$  to other variables, keeping the variable with a higher  $R^2$  in a univariate model, before running multiple linear models. Since the range of temperature and precipitation may also influence the breadth of pika isotopic dietary niche, we examined if climate seasonality variables correlated with the SEA of pika population bone and fall-onset fur isotopes. To investigate isotopic trends in pika populations over historical time, we calculated the difference between historical and most recent population mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values. To test whether seasonal changes in weather contributed to seasonal differences in fur isotope values, we compared the magnitude of mean seasonal differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of populations ( $n = 21$ ) with temperature, precipitation, and RH seasonality. Mean population  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values for summer- and fall-onset fur and bone were normally distributed according to Shapiro–Wilk’s tests. We compared all linear models to null models and used  $\text{AIC}_c$  to select the most explanatory models for each isotope and pika tissue sample type. We studied shifts in isotopic composition over seasonal time by calculating the differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from summer-onset and fall-onset fur molts with Student’s  $t$  test assuming normal distribution and unequal variance.

We used ANOVA to determine if plant functional types (forb, graminoid, and woody) have distinct  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, which could then inform our ability to determine what proportions of plant types comprise the pika population diets. We determined that the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values for  $\text{C}_3$  plant ( $\delta^{13}\text{C} < -17\text{‰}$ ) samples were normally distributed according to Shapiro–Wilk’s tests. To explore how climate may directly impact plant isotopic values, we ran linear mixed-effects models using lme4 (Bates et al. 2015) with climate variables as fixed and plant functional type as random effects. We also compared isotope values between leaves and flowers of forbs and graminoids using two-sample Welch’s  $t$  tests assuming normal distribution and unequal variance. The range of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for pika populations did not fall between the values for plants sampled, and thus, violated assumptions of isotopic mixing models, so we were unable to estimate the propor-

tions of plant functional types that contributed to the diets of pika populations with mixing models (Stock et al. 2018).

## Results

Environmental variables, rather than geography, tended to be associated with pika stable isotope values. Individual pika fur  $\delta^{13}\text{C}$  values had a mean ( $\pm\text{SD}$ ) of  $-25.41\text{‰} \pm 0.90\text{‰}$  and ranged from  $-23.05\text{‰}$  to  $-28.73\text{‰}$ , which are completely within the values for  $\text{C}_3$  plants. Individual fur  $\delta^{15}\text{N}$  values ranged from  $-1.6\text{‰}$  to  $7.1\text{‰}$  with a mean ( $\pm\text{SD}$ ) of  $2.68\text{‰} \pm 1.28\text{‰}$  ( $n = 481$ ). Pika population  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotope values did not uniformly meet expectations set by global isotope trends. Moisture-related variables of RH and precipitation were consistently correlated with  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotope values at both annual and seasonal time scales for fall-onset molts and bone. The most predictive climate variable was RH of the year prior to collection, which demonstrates a negative relationship with  $\delta^{13}\text{C}$  mean population values, as expected (as determined by  $\text{AIC}_c$ ,  $n = 21$  populations; Table 1 and Figs. 3a–3d). Fall-onset fur, but not summer-onset fur or bone, conformed to our predictions that  $\delta^{15}\text{N}$  would correlate negatively with moisture (Table 1 and Supplementary Table S2<sup>1</sup>).

Precipitation and temperature annual variables strongly related to population mean bone collagen  $\delta^{15}\text{N}$ , but not  $\delta^{13}\text{C}$  ( $n = 13$ ; Supplementary Table S2<sup>1</sup>). Mean ( $\pm\text{SD}$ ) bone collagen values across populations sampled were  $-23.3\text{‰} \pm 0.7\text{‰}$  for  $\delta^{13}\text{C}$  and  $2.6\text{‰} \pm 1.1\text{‰}$  for  $\delta^{15}\text{N}$  ( $n = 195$ ). MAT and MAP from the year prior to collection together explained the majority of the variation in population mean  $\delta^{15}\text{N}$  values (Table 1 and Figs. 4a–4c). Bone  $\delta^{15}\text{N}$  was positively correlated with temperature, but contrary to our expectations, bone  $\delta^{15}\text{N}$  increased instead of decreased with precipitation (Supplementary Table S2<sup>1</sup>).

RH best predicted fall-onset pika fur  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. RH and precipitation both negatively correlated with fall-onset fur  $\delta^{13}\text{C}$  values (Supplementary Table S2<sup>1</sup>). Summer RH had a strong negative relationship to fall-onset fur  $\delta^{15}\text{N}$  values, as predicted based on global  $\delta^{15}\text{N}$  being negatively correlated with moisture (Table 1 and Fig. 3a). Summer-onset molt  $\delta^{15}\text{N}$  values did not correlate to any seasonal climate variables tested (Supplementary

**Fig. 4.** American pika (*Ochotona princeps*) bone collagen  $\delta^{15}\text{N}$  and standard ellipse areas (SEA) values relate positively to temperature and negatively with precipitation. Circles show population mean values, vertical lines indicate 1 SD, and shading indicates the 95% confidence region. (a) Population mean  $\delta^{15}\text{N}$  values exhibit a negative relationship with mean annual precipitation from the year prior to collection ( $R^2 = 0.59$ ,  $P = 0.001$ ). (b) Population mean  $\delta^{15}\text{N}$  values positively correlate with mean annual temperature from the year prior to collection ( $R^2 = 0.35$ ,  $P = 0.001$ ). (c) Population bone collagen  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  SEA values positively correlate with temperature seasonality, which we calculated as the difference in mean summer temperature and mean winter temperature ( $R^2 = 0.41$ ,  $P = 0.010$ ). Color version online.

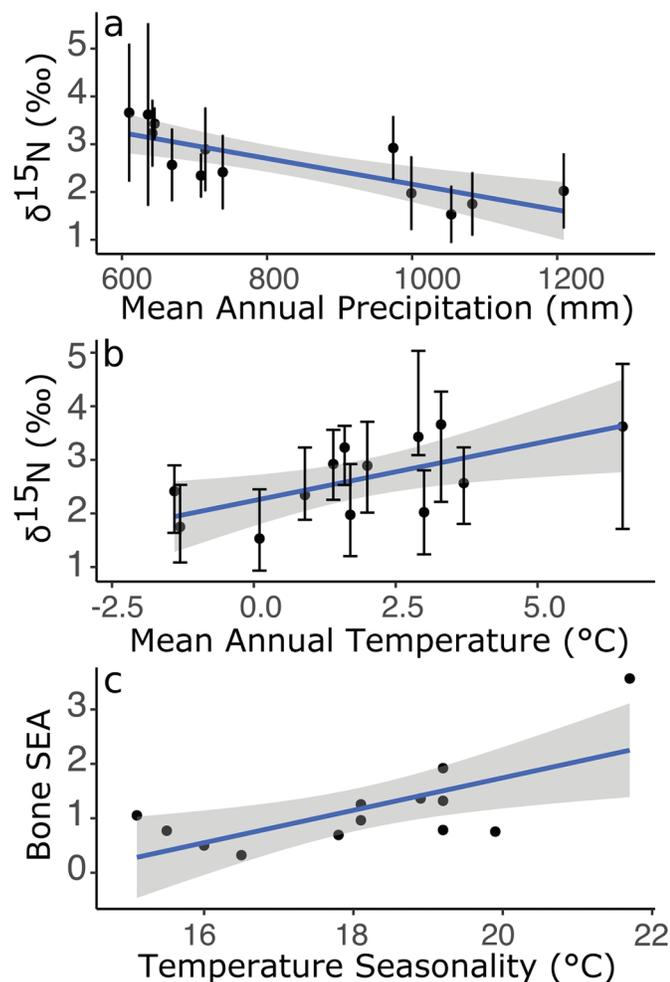


Table S2).<sup>1</sup> Although we expected larger SEAs to be associated with greater climate seasonality, seasonality in temperature, precipitation, and RH did not influence pika fur SEA (Supplementary Table S2).<sup>1</sup> We found no impact of elevation or latitude on pika  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  values, seasonal fur differences, or SEA (Supplementary Table S2).<sup>1</sup>

#### Over time

Pika populations exhibited small but consistent changes in isotope values over both seasonal time and historical time. Across the 21 populations that we sampled,  $\delta^{13}\text{C}$  mean fall-onset fur values ranged only 2.3‰ (Supplementary Table S4).<sup>1</sup> Seasonally, population mean  $\delta^{13}\text{C}$  values were, on average, 0.8‰  $\pm$  0.7‰ higher in the summer-onset molt ( $-24.9\text{‰} \pm 0.7\text{‰}$ ) than in the fall-onset molt ( $-25.7\text{‰} \pm 0.8\text{‰}$ ) (two-sample Welch's  $t$  test,  $t_{[24,83]} = 3.35$ ,  $P = 0.003$ ; Fig. 5c). Seasonal mean  $\delta^{15}\text{N}$  values were not significantly

different across summer and fall molts (mean ( $\pm$ SD)  $\delta^{15}\text{N} = 2.7\text{‰} \pm 1.3\text{‰}$ ; two-sample Welch's  $t$  test,  $t_{[24,99]} = -0.55$ ,  $P = 0.59$ ; Fig. 5d). Climate variables or seasonality in temperature or precipitation did no better to explain seasonal variation in fur isotopic values than the null model (Supplementary Table S2).<sup>1</sup> However, seasonality appeared to have an impact on pika bone isotopic niche space. Temperature seasonality was significantly correlated with the SEA of pika population bone (Table 1). Across the populations that were resampled over decades, mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values significantly decreased in fall-onset fur for four out of five resampled populations (Supplementary Table S5).<sup>1</sup> However, the direction of climate change among these resampled populations was not consistent. The population sites did not have significantly different MAT or MAP between historical and modern samples (ANOVA — MAP:  $F_{[2,11]} = 2.11$ ,  $P = 0.17$ ; MAT:  $F_{[2,11]} = 0.19$ ,  $P = 0.83$ ; RH:  $F_{[2,11]} = 2.15$ ,  $P = 0.16$ ). We found that RH increased at our study locations over time ( $\beta = 3.51$ , standard error (SE) = 1.52; Student's  $t$  test,  $t_{[12]} = 2.31$ ), but that year of collection did not significantly influence MAP or MAT in linear mixed-effects model where we fit the population location as a random effect (Satterthwaite's method — MAP:  $\beta = 0.006$ , SE = 0.005,  $t_{[12]} = 1.35$ ; MAT:  $\beta = -1.82$ , SE = 5.92,  $t_{[12]} = -0.31$ ).

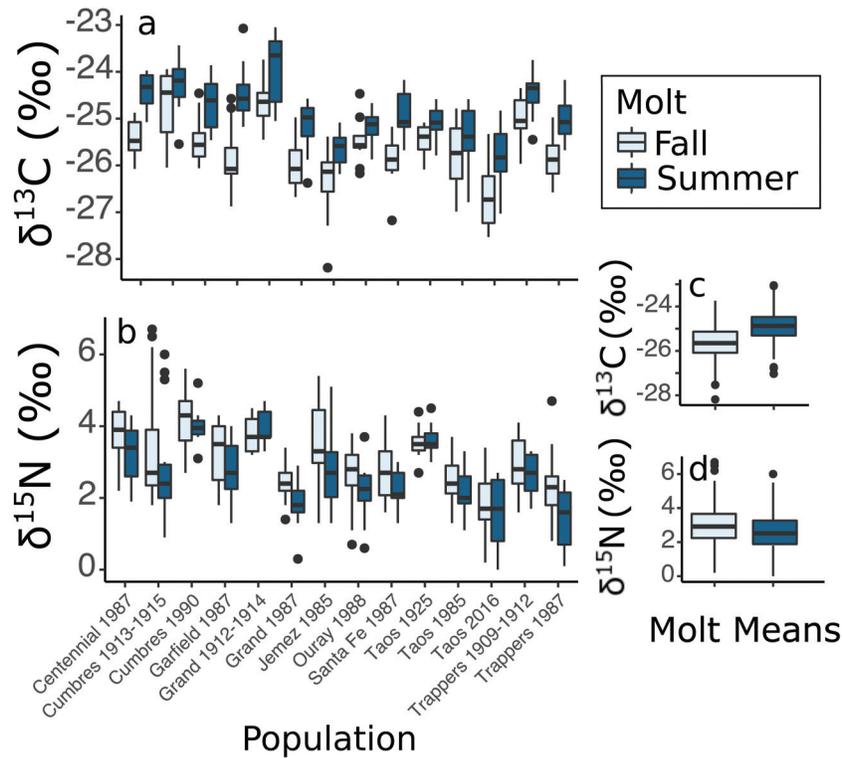
#### Plants

Forbs and graminoids had distinct isotope values. The mean  $\delta^{13}\text{C}$  value of  $\text{C}_3$  graminoids in our study were 2‰ higher than those of forbs and woody vegetation, which was a significant difference (mean ( $\pm$ SD)  $\delta^{13}\text{C}$  values of  $-25.8\text{‰} \pm 1.5\text{‰}$  (graminoid),  $-27.8\text{‰} \pm 1.7\text{‰}$  (forb), and  $-27.9\text{‰} \pm 1.3\text{‰}$  (woody); ANOVA,  $F_{[2,119]} = 11.3$ ,  $P < 0.001$ ; Tukey's honestly significant difference (HSD) test,  $P < 0.001$  (graminoid–forb),  $P = 0.45$  (woody–forb),  $P = 0.03$  (woody–graminoid); Supplementary Fig. S1<sup>1</sup>). Forbs had higher mean ( $\pm$ SD)  $\delta^{15}\text{N}$  values compared with graminoids ( $-1.8\text{‰} \pm 2.4\text{‰}$  (graminoid),  $-0.6\text{‰} \pm 1.8\text{‰}$  (forb),  $-2.2\text{‰} \pm 2.7\text{‰}$  (woody); ANOVA,  $F_{[2,122]} = 4.9$ ,  $P < 0.005$ ; Tukey's HSD test,  $P = 0.01$  (graminoid–forb),  $P = 0.06$  (woody–forb),  $P = 0.99$  (woody–graminoid); Supplementary Fig. S2<sup>1</sup>). Forb flowers averaged 1.8‰ higher in  $\delta^{13}\text{C}$  than forb leaves (Kruskal–Wallis  $\chi^2$  test,  $\chi^2_{[4]} = 17.32$ ,  $P = 0.002$ ; Tukey's HSD test,  $P = 0.02$ ; Supplementary Fig. S1<sup>1</sup>). The part of the plant (flower or leaf) sampled did not influence  $\delta^{15}\text{N}$  isotope values in forbs (mean ( $\pm$ SD)  $\delta^{15}\text{N}$  of  $-0.22\text{‰} \pm 1.64\text{‰}$  (forb flower) and  $-0.18\text{‰} \pm 1.54\text{‰}$  (forb leaf); two-sample Welch's  $t$  tests,  $t_{[26]} = -0.41$ ,  $P = 0.94$ ) or graminoids (mean ( $\pm$ SD)  $\delta^{15}\text{N}$  of  $-0.89\text{‰} \pm 1.75\text{‰}$  (graminoid flower) and  $-1.72\text{‰} \pm 1.54\text{‰}$  (graminoid leaf); two-sample Welch's  $t$  test,  $t_{[18]} = 1.07$ ,  $P = 0.30$ ). MAT slightly lowered  $\delta^{13}\text{C}$  values ( $\beta = -0.19$ , SE = 0.07; Satterthwaite's method,  $t_{[116]} = -2.68$ ;  $\chi^2_{[4]} = 7.02$ ,  $P = 0.008$ ) and summer RH slightly lowered  $\delta^{15}\text{N}$  values ( $\beta = -0.13$ , SE = 0.04; Satterthwaite's method,  $t_{[115]} = -3.11$ ;  $\chi^2_{[4]} = 9.46$ ,  $P = 0.002$ ) across plant types in linear mixed-effects models. Pika fur isotope values did not fall within the isotopic values of plants collected from the environment, as would be expected for generalist herbivores (e.g., Stock et al. 2018) (Supplementary Fig. S3).<sup>1</sup>

#### Discussion

Despite the broad latitudinal, elevational, and environmental gradients represented by our study, as well as over a century of climate change, we find that pika isotopic diets are surprisingly invariant. The lack of isotopic dietary diversity among pika populations from xeric Bodie to high elevations of central Colorado indicates that even as environments change, the isotopic signature of pika diet does not (Table 1). Contrary to our initial expectations, we find no evidence that trailing edge or marginal populations are consuming isotopically distinct and potentially nutritionally inferior diets. Pikas do appear to have a narrow isotopic niche that correlates with certain aspects of climate, including RH for fall-onset fur and temperature and precipitation for bone.

**Fig. 5.** Fall-onset molt and summer-onset molt isotopic differences in American pika (*Ochotona princeps*) populations.  $\delta^{13}\text{C}$  values are Suess-corrected to the year 2016. Color version online.



While few stable isotopic dietary studies have encompassed the geographic and temporal range of our research, other small-mammal isotopic diets are often broader than the isotopic variation found in pika diets from across their range and over a century of climate change. Other lagomorphs (hares (genus *Lepus* Linnaeus, 1758) and cottontails (genus *Sylvilagus* Gray, 1867)) exhibited greater isotopic niche breadth and higher values in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  than pikas (Somerville et al. 2018). Black-tailed jackrabbit (*Lepus californicus* Gray, 1837) populations show much greater population  $\delta^{15}\text{N}$  variability in bone collagen within the state of Utah than pikas do across their entire range (Ugan and Coltrain 2011). Voles (Arvicolinae) showed little intra-population variation in  $\delta^{13}\text{C}$  values, with similarly small standard variations to those of pikas from one sampling event at one locality (Gehler et al. 2012). Murid rodents had greater isotopic variability, and indicate a more generalist diet, from one sampled population than pikas exhibited across their range and over nearly a century (Gehler et al. 2012). In larger mammals, stable isotopes from caribou (*Rangifer tarandus* (Linnaeus, 1758)) and moose (*Alces alces* (Linnaeus, 1758)) spanned similar ranges in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  to pikas but at a much smaller geographic scale, limited to Denali National Park and over only 2 years of sampling (Ben-David et al. 2001). Thus, we conclude that pika inter-population isotopic variation is low compared with the intra-population isotopic dietary niche of many other mammals.

We do find a significant, but small, influence of season on pika isotopic values across all populations. Summer-onset molts are invariably higher in  $\delta^{13}\text{C}$  compared with fall-onset molts, with a mean ( $\pm$ SD) increase of  $0.8\text{‰} \pm 0.7\text{‰}$ . Animals may be expected to have seasonal changes in diet, particularly in environments with high seasonal variability. Similar to pikas, moose and caribou also exhibit a  $0.5\text{‰}$ – $0.6\text{‰}$  enrichment of  $\delta^{13}\text{C}$  in winter, attributed to seasonal shifts in diet (Ben-David et al. 2001). Alternatively, seasonal variation in pika isotopes could potentially be attributed to seasonal changes in water availability impacting isotope values of forage, not dietary changes (Zazzo et al. 2015). While we find

changes in  $\delta^{13}\text{C}$  over time, our results are consistent with previous findings that  $\delta^{15}\text{N}$  does not change seasonally in herbivorous mammals, suggesting that  $\delta^{15}\text{N}$  may not be a good indicator of seasonal diet (Ben-David et al. 1999, 2001) (Fig. 5b).

Pika diet is known to vary seasonally, with pikas selecting forbs with greater concentrations of secondary phenolic compounds for winter caching compared with less specific summer grazing (Dearing 1997a; Varner and Dearing 2014). Therefore, we expected the isotopic signature in summer-onset molt to reflect increased forb consumption from haypiles with lower  $\delta^{13}\text{C}$ , and relatively higher  $\delta^{13}\text{C}$  in fall-onset molt from less selective summer grazing (Dearing 1996; Varner and Dearing 2014). However, summer-onset molt is enriched in  $\delta^{13}\text{C}$  compared with fall-onset molt, which is the opposite trend that we would expect if the isotopes were reflecting increased forb consumption from winter haypiles (Figs. 5a and 5c). Our results indicate that seasonal differences in pika  $\delta^{13}\text{C}$  isotope ratios are not likely derived from isotopically distinct diets in summer forage and winter haypiles.

One potential explanation of seasonal shifts in pika  $\delta^{13}\text{C}$  is that microbial respiration of cached haypiles result in consistent  $\delta^{13}\text{C}$  enrichment of summer-onset fur in pikas. Experimental haypiles lose mass over winter, indicating significant microbial decomposition that could alter haypile isotopic values (Dearing 1997a). Pikas store plants with high, potentially toxic, phenolic compounds in haypiles and consume them when the plants have become more digestible through decomposition, indicating that pikas manipulate their diet through haypile decomposition (Dearing 1997b). More decomposed leaves tend to be moderately enriched in  $\delta^{13}\text{C}$ , with a mean (but variable) enrichment of  $\sim 0.5\text{‰}$  compared with fresh leaves (Wedin et al. 1995). However, microbial decomposition has a varied effect on  $\text{C}_3$  plant material ranging from  $-6\text{‰}$  to  $8\text{‰}$ . Microbes and fungi are enriched in  $\delta^{13}\text{C}$  by  $\sim 1.6\text{‰} \pm 0.3\text{‰}$  compared with soils, so microbes that occur on haypile vegetation may contribute to higher pika  $\delta^{13}\text{C}$  values in summer molt (Dijkstra et al. 2006; Bowling et al. 2008). Therefore,

we suggest that microbial decomposition of haypile vegetation is a likely factor leading to the consistent  $\delta^{13}\text{C}$  enrichment of summer-onset fur compared with fall-onset fur, rather than seasonal dietary differences as we originally predicted.

The mismatched position of pika isotopic values relative to dietary sources of forbs, graminoids, and woody vegetation suggests that the best estimate of pika's trophic discrimination factor (the difference in isotopic values sourced from rabbits (*Oryctolagus cuniculus* (Linnaeus, 1758)) on a diet of alfalfa (*Medicago sativa* L.); Sponheimer et al. 2003a, 2003b) is not suitable for pikas in the wild. It is also possible that we failed to collect one or more isotopically distinct food sources contributing to pika diet. However, we know from the literature that pikas consume a variety of forbs, grasses, and shrubs (Dearing 1997a; Bhattacharyya and Ray 2015; Hall and Chalfoun 2018). Possible missing dietary sources include mosses, lichens, and trees (Varner and Dearing 2014), but these were not present at all of our study sites and we did not observe these taxa cached in pika haypiles. Plant isotope values differ seasonally, which may also be a factor influencing the small but consistent seasonal variation in pika fur  $\delta^{13}\text{C}$  values. Plants seasonally discriminate less against  $\delta^{13}\text{C}$  as water becomes less available (Smedley et al. 1991; Ehleringer and Dawson 1992). Pika molt  $\delta^{13}\text{C}$  should mimic the seasonal variation in plants, but we observe the opposite trend expected if pikas were eating early-season forage before the summer-onset molt, which would coincide with increased moisture from snowmelt (Zazzo et al. 2015). However, if summer-onset molts are reflective of pikas relying more heavily on late-summer-procured haypiles than early-spring forage, then seasonality in alpine plant  $\delta^{13}\text{C}$  could also contribute to the observed summer enrichment in pika molts.

While there was limited variation in pika isotope values across both fur and bone tissues, the variation that exists appears to be related to climate. Moisture influences pika isotope values, particularly for  $\delta^{13}\text{C}$  in fall-onset fur and  $\delta^{15}\text{N}$  in bone. For fall-onset fur, RH and precipitation are important to  $\delta^{13}\text{C}$  values at both seasonal and annual time scales. MAP and RH have a negative effect on mean  $\delta^{13}\text{C}$  values, as does spring RH (Supplementary Table S2).<sup>1</sup> We attribute these trends to plants decreasing  $^{13}\text{C}$  uptake in environments with more moisture available (Ehleringer and Cooper 1988; O'Leary 1988; Farquhar et al. 1989; Tieszen 1991). We predict that under future climate change, pika populations in areas that experience decreased precipitation and RH will eventually have higher  $\delta^{13}\text{C}$  values in fur.

Herbivore  $\delta^{15}\text{N}$  isotope values can be challenging to interpret because plants have high  $\delta^{15}\text{N}$  variability and multiple mechanisms influence  $\delta^{15}\text{N}$  values (Kielland et al. 1998; Ben-David et al. 1998; Craine et al. 2015). In our study, precipitation and temperature correlate most strongly with bone collagen  $\delta^{15}\text{N}$ . Previous studies on leporids also found positive relationships of bone collagen  $\delta^{15}\text{N}$  with temperature (Ugan and Coltrain 2011; Somerville et al. 2018). We report, as other studies have, a negative relationship between precipitation and  $\delta^{15}\text{N}$  of pika bone collagen, suggesting that water stress may have an impact on pika bone collagen  $\delta^{15}\text{N}$  values (Cormie and Schwarcz 1996; Somerville et al. 2018) (Table 1).

While overall populations from low latitudes and low elevations are no different isotopically from more central populations, pika fur from our most arid site (Bodie) has significantly higher  $\delta^{15}\text{N}$  values than all other sites, suggesting possible water or nutritional stress (Supplementary Table S4).<sup>1</sup> In addition, mean bone  $\delta^{15}\text{N}$  values are negatively correlated with MAP across the species' range, indicating that precipitation has a significant impact on lifetime isotope values (Fig. 4a). Plants grown in arid environments tend to have lower nitrogen content, perhaps adding to nutritional stress of herbivores (Sealy et al. 1987; Cormie and Schwarcz 1996). While pikas still occupy the atypical and sagebrush-dominated habitat of Bodie Hills in eastern California, pikas from similar sites nearby have become extirpated within

the 20th century and as recently as 2015, providing further evidence that pikas in this habitat may be under stress (Stewart et al. 2015; Nichols et al. 2016). Our data offer support to the hypothesis that the isotopic fractionation of nitrogen in animal metabolism is larger in arid environments (Schoeninger and DeNiro 1984; Ambrose and DeNiro 1986, but see Cormie and Schwarcz 1996; Murphy and Bowman 2006). With this in mind, pikas from Bodie are likely under water stress compared with other populations. Analyzing  $\delta^{15}\text{N}$  may be a way to predict which pika populations are at greater risk of extirpation due to a combination of nutrient and water stress.

Throughout their range and across time, pikas appear to be strict  $\text{C}_3$  specialists, which may one day pose challenges for pika conservation.  $\text{C}_3$  plants, including  $\text{C}_3$  graminoids, have higher nutritional quality compared with  $\text{C}_4$  plants (Barbehenn et al. 2004). Multiple pika species appear to be averse to consuming  $\text{C}_4$  plants, even when they are available in the environment (Ge et al. 2012). Plateau pika (*Ochotona curzoniae* (Hodgson, 1858)), the only other pika species to have its isotopic niche documented, also consumes an overwhelmingly  $\text{C}_3$ -based diet that varies little across regions of the Tibetan Plateau (Yi and Yang 2006). The expansion of  $\text{C}_4$  grasses in the late Miocene coincided with mass extinction of the pika genera and a severe range contraction of the remaining pika taxa to the  $\text{C}_3$ -dominated refugia of alpine areas in Asia (Ge et al. 2012).  $\text{C}_4$  plants are well adapted to arid environments, and thus, may expand farther into alpine environments with increasing temperatures and aridity (Sage and Kubien 2003; Angelo and Daehler 2013). Climate-induced shifts in alpine vegetation communities may pose ecological consequences for pikas.

Our study documents the American pika's isotopic dietary niche for the first time. We illustrate a connection between fall-onset fur and bone isotopes with climate across their range, likely due to physiological changes in the plants that they consume. We establish a consistent difference in  $\delta^{13}\text{C}$  between the seasonal molts that might be related to microbial alteration of haypiles. Additional research on how decomposition and isotopic enrichment might contribute to nutritional value would benefit our understanding of pika winter diets. While SIA has the ability to provide insight into modern and historical animal diets, it is limited in that it cannot distinguish between species, or sometimes even functional groups of plants consumed. While we do not find a connection between climate change and alterations to pika diet over historical time, we establish a baseline of pika isotopic diet and isotopic patterns related to climate across their range. Being a small hindgut herbivore is energetically challenging and pikas may be increasingly restricted to a diet containing higher quality vegetation in thermally stressful environments (Geist 1974; Smith 1992, 1995; Hall and Chalfoun 2018, 2019; but see Varner and Dearing 2014). Climate change may precipitate nutritionally challenging environments for pikas, as increasing temperatures and drought stress can lead to lower nutrient content in plants and relative increases in less-nutritious graminoids (Barbehenn et al. 2004; Venn et al. 2014; Rosenblatt and Schmitz 2016). From the trends that we established, we can predict that pika populations in areas with decreased moisture will exhibit higher  $\delta^{13}\text{C}$  values in fur, as well as potentially higher  $\delta^{15}\text{N}$  in bone collagen. Studying shifts in isotopic niche, or lack thereof, can provide insights into how pikas and other animals respond to changes in the biotic and abiotic environment over space and time.

## Author contributions

M.L.W. and F.A.S. conceived and designed the study. M.L.W. and K.B.K. collected specimens. M.L.W. and K.A.L. prepared specimens. M.L.W. analyzed the data and wrote the manuscript. K.B.K., K.A.L., and F.A.S. provided comments and edited the manuscript.

## Data accessibility

Isotope data: population means are currently uploaded as Supplementary Tables S6<sup>1</sup> and S7<sup>1</sup> and individual specimen data will be uploaded to Digital Dryad and IsoBank ([isobank.org](http://isobank.org)) upon its launch.

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