Journal of Mammalogy, 2024, **105**, 1418–1429
https://doi.org/10.1093/jmammal/gyae083
Advance access publication 26 August 2024
Research Article

Research Article

Fifty-year population trajectory in a marginal American Pika (*Ochotona princeps*) population

Andrew T. Smith[1,*], Constance I. Millar[2], Easton R. White[3]

[1]School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, United States
[2]Pacific Southwest Research Station, USDA Forest Service, Albany, CA 94710, United States
[3]Department of Biological Sciences, University of New Hampshire, Durham, NH 03824, United States

[*]Corresponding author: School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, United States. Email: a.smith@asu.edu
Associate Editor was Jennifer Frey

Abstract

The American Pika (*Ochotona princeps*) has been considered a species at risk due to warming temperatures associated with climate change. Many life-history attributes of pikas contribute to the sensitivity of pikas to warming temperatures. Repeated censuses of a marginal (warm, low-elevation) population of pikas at Bodie State Historic Park, California, conducted from 1972 to 2022, are presented to track the population trajectory of pikas for a time period predating recent awareness of global warming to the present day, thus giving a comprehensive portrayal of how American pikas may be responding to climate change. The northern constellation of anthropogenic habitat patches (mine ore dumps) showed no decline in percent of patches occupied or in total number of pika territories over time, suggesting that pikas in that area have not been at risk of extirpation resulting from climate change. In contrast, the pika population in the southern constellation of patches showed significant declines in percent of patches occupied and number of pika territories occupied. That area was unoccupied for about a decade beginning in 2006, but was recently recolonized from the northern constellation of patches. The most likely cause of the initial decline and transient extirpation in the south appears to result from fragmentation and stochastic population dynamics, independent of climatic factors that we investigated. Assessments of climatic impacts on American pikas should take into account the dynamics documented in the Bodie pika population and its resilience over time.

Key words: American Pika, Bodie State Historic Park, climate change, global warming, metapopulation, *Ochotona princeps*, population trends.

The American Pika (*Ochotona princeps*) was one of the first mammalian species identified as being at risk due to warming caused by climate change (Beever et al. 2003, 2011; Smith et al. 2004; Ray et al. 2012). The USDA Forest Service highlighted the pika as 1 of 3 species of mammal being negatively affected by climate change (McKelvey et al. 2013), and the pika was identified by the US Department of Interior (2015) as 1 of 9 species (5 of which were mammals) that had been negatively impacted by climate change.

Evidence exists to support the sensitivity of pikas to warming temperatures. The range of pikas across North America has contracted as global temperatures have increased over the course of the Late Pleistocene through the Holocene (Grayson 2005). Their elevational distribution today across the intermontane west is higher at low latitudes and lower at high latitudes, reflecting prevailing temperatures (Grinnell 1917). Experimental and behavioral studies have shown that pikas have a poor physiological capacity to tolerate warm environments (MacArthur and Wang 1973, 1974; Smith 1974a), although it has been shown that pikas adjust to this limitation by being active during cool hours of the day or at night (Smith 1974a; Otto et al. 2015; Smith et al. 2016; Millar and Hickman 2021).

Several other attributes of pikas may interact with thermal aspects of the environment to jeopardize the fitness of local pika populations. Pikas occupy a fixed and patchily distributed habitat type: talus, or piles of broken rock (Smith and Weston 1990). Because pikas are individually territorial (Smith and Ivins 1984), and thus are found at low density, local populations, particularly those living on small or isolated habitat patches, are vulnerable to stochastic extirpation (Smith 1974b; Smith and Gilpin 1997; Moilanen et al. 1998; White and Smith 2018). Pikas are poor dispersers, particularly in warm environments (Smith 1974a, 1974b, 1987; Smith and Ivins 1983a; Peacock and Smith 1997). Thus, increasing ambient temperatures, coupled with the low physiological tolerance of pikas to heat and the incumbent thermal stress of dispersal, could become a limiting factor leading to regional extirpation of pika populations (Smith 1974a, 1974b; Smith and Nagy 2015; Millar et al. 2016; Millar and Smith 2022).

Demographic characteristics may also come into play regarding the population persistence of pikas. Pikas have a very low reproductive rate for a small mammal; across their range most females successfully produce only 2 young per year (Millar 1973, 1974; Smith 1978; Smith and Ivins 1983b). Thus, when populations are negatively

Received: February 24, 2023; Editorial Decision: June 28, 2024; Accepted: July 15, 2024

impacted, their potential to respond is limited. One factor operating in favor of pika population persistence is that they are relatively long-lived; most populations are composed of animals as old as 3 to 4 years of age, and pikas have been known to live as long as 7 years (Millar and Zwickel 1972; Smith 1978).

How these pika life-history traits interact with increasing temperatures is sometimes contradictory (reviewed in Smith et al. 2019; Smith 2020). A range-wide survey determined that pikas have a low adaptive capacity when confronted with warming temperatures, and in particular that Great Basin pikas have a high susceptibility to anthropogenic climate change (Beever et al. 2023). In contrast, extensive surveys from across the Great Basin determined that pika populations may tolerate a broader set of habitat conditions than previously understood (Millar et al. 2018). Millar et al. (2018) compiled 2,387 records of extant pika sites, 89 records of recently extirpated sites, and 774 records where only old pika sign was found. The range of temperatures and precipitation values at these sites combined was greater than those that had previously been described. Extirpated and old sign sites were primarily located within the climatic space of extant sites, although often in warmer and drier portions (Millar et al. 2018).

Most local extirpations that have been documented have been on small, isolated, habitat patches which—independent from local warming—are at risk of stochastic extirpation (McCain et al. 2016; Smith 2020). Further complicating the pika story is that documented extirpations may be temporary (Millar and Smith 2022) or result from false negatives during the sampling period (McCain et al. 2016; Smith 2020). Finally, although pikas are widely considered to be an alpine species, extant pika populations occur at warm, low elevations, and many of these populations occupy habitats that are demonstrably marginal compared with core-range pika populations (e.g., Beever et al. 2008; Millar et al. 2013a; Shinderman 2015; Smith et al. 2016; Jeffress et al. 2017; Millar et al. 2018; Camp et al. 2020).

There are 2 prevailing field approaches to measuring and predicting the effects of climate change on species. The first is one-time (or "snapshot") resampling to document population differences between 2 points in time, where the baseline represents populations documented from an earlier period (frequently decades or even a century earlier). However, in-depth analyses of this approach have determined that conclusions drawn from this type of comparison are frequently inaccurate. Populations resampled at historically known sites are commonly found to shift in the opposite direction of known long-term trends (particularly to overestimate the magnitude of change) or fail to detect a lack of population change (McCain et al. 2016; Stuble et al. 2021). Many contemporary studies of American Pika populations adopt the snapshot approach (e.g., Beever et al. 2003, 2016; Stewart et al. 2015, 2017; Millar et al. 2018; Billman et al. 2021).

The second approach relies on continuous or semicontinuous monitoring of a population over a protracted period as the species responds to global change (i.e., longitudinal studies). Such data sets offer what snapshot sampling cannot—they provide an accurate portrayal of the changing environment in which the species occurs (White 2019; Stuble et al. 2021). Accurate population trend detection is not strictly contingent on annual sampling; even semi-regular monitoring helps us to better understand changes in a population in the context of its past history (Stuble et al. 2021). Data sets of this nature are rare and infrequently span more than 2 or 3 decades (Stuble et al. 2021), and this is particularly true for pikas. Prior to recent focus on the effect of climate change, there have been few long-term or ongoing investigations of pika populations.

Here we present population data from a marginal (warm, low-elevation) pika population at Bodie State Historic Park (BSHP), Mono County, California, that we have studied for over 50 years. Our 21 complete censuses between 1972 and 2022 have allowed us to track the resiliency of pikas, or lack thereof, over a time period predating recent awareness of global warming to the present day. These censuses provide an independent window of how American pikas may respond to climate change. If the warm temperatures, reflecting the onset of observable anthropogenic global warming, had negatively affected the BSHP pikas, we would expect a decline in both the occupancy rates of pikas on habitat patches and the numbers of surviving animals, particularly over the past decade (Beever et al. 2011). What we have observed, however, is a mixed response; the northern half of the study area has maintained a robust population, while the southern half has declined precipitously despite the same changes in environmental conditions. Our 50-year data set has given us a unique opportunity to investigate the trajectory of these 2 populations over time and has allowed us to investigate the likelihood that climate change (or other factors) has been responsible for the population dynamics we have observed.

Materials and methods.

Study area.

A population of American pikas was studied at BSHP, Mono County, California (38°11.5′ to 13.4′N; −118°59.7′ to −119°0.7′W; 2,530 to 2,650 m a.s.l.; Fig. 1). The rocky environment that pikas occupy at BSHP consists of anthropogenic ore dumps created by hard-rock mining operations conducted from the late 1800s into the early 1900s (Fig. 2). Native pika habitat in the region, discontinuously scattered across the Bodie Mountains, was presumably the source for their colonization of the BSHP ore dumps (Smith 1974b; Millar et al. 2013a; Nichols et al. 2016). The habitat separating ore dumps is dominated by Great Basin sage vegetation (*Purshia tridentata*, *Artemisia tridentata*, *Ericameria nauseosa*). The BSHP pikas were discovered by Severaid (1955), who studied them for several years in the late 1940s. Severaid (1955) interviewed long-time residents of Bodie who claimed that pikas occupied the ore dumps as early as the turn of the 19th century. At the time of his observations, Severaid (1955) found that pikas occupied or had occupied—as evidenced by characteristic sign (see below)—all of the available ore dump habitat throughout the mining district. He further noted that not all ore dumps were occupied by pikas at any one time. Inspection of historical records also has shown that these habitat patches are permanent and have not changed quantitatively in size or spacing from the mid-1940s to the present (Smith and Nagy 2015; McCain et al. 2016).

Temperature and climate.

A comprehensive profile of standard meteorological measurements (air temperature at 1.5 m) provided maximum summer temperatures at BSHP available from the Western Regional Climate Center (WRCC; https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca0943) beginning in 1895. Gaps in this record were adjusted by correcting for the lapse rate between the weather stations at BSHP and Bridgeport, California (1,972 m a.s.l.), 20 km away. Lapse rates by month were calculated based on a parallel 48-year record for BSHP and Bridgeport (see Smith and Nagy 2015). No climate data were recorded at these sites from 1904 to 1912, 1917 to 1931, 2019, and 2022. Comparative temperature data between BSHP and other environments across the range of American pikas are available from PRISM (https://prism.oregonstate.edu; Daly et al. 1994). The long-term difference between average summer (July, August) monthly maximum temperature data from PRISM and the WRCC for BSHP

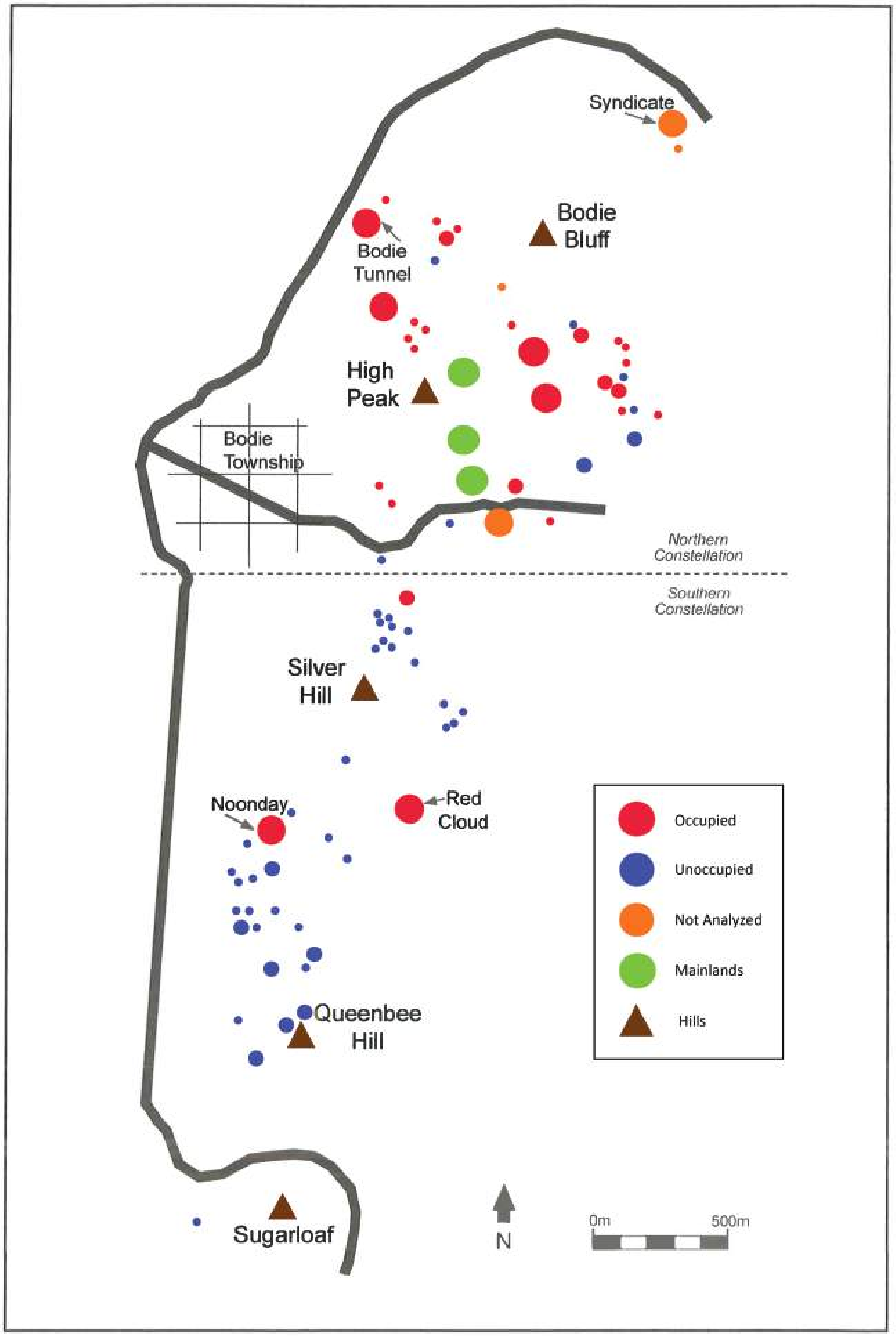

Fig. 1. Distribution of ore dump habitat occupied by American pikas (*Ochotona princeps*) at BSHP, California, showing the distinction between a northern versus southern constellation of ore dumps. Red circles = occupied patches in 2022; blue circles = unoccupied patches in 2022. Orange circles indicate 4 patches with several missing censuses over the 51-year period from 1972 to 2022, thus were not included in occupancy analyses (see text). Large, medium, and small circles portray the relative size of ore dumps. Green patches demarcate "mainland" samples of relatively continuous habitat that were not included in occupancy analyses.

varied by less than 0.1 °C, so we were able to backfill the summer temperatures for BSHP for 2019 and 2022 from PRISM data. Thus, after years with missing data were eliminated, we obtained a record of 104 years of daily temperature values for BSHP with only 4 missing days between 1895 and 2022. We used simple linear regression to assess changes in temperature over this time. We verified model assumptions by examining residual plots.

Pika occupancy.

The common determination of habitat occupancy by American pikas consists of observing the diurnally active animals, hearing their distinctive vocalizations, or observing fresh characteristic sign (e.g., Smith 1974b; Beever et al. 2003). Our censuses at BSHP were conducted in late summer after the reproductive season of pikas when the population level was likely to be at its largest (Smith

1974b). Pikas are infrequently seen or heard at this time; thus, our surveys primarily relied on visual signs of pika occupancy (Smith 1974a). Pikas are the smallest lagomorph in the region, and their small spherical fecal pellets are unlike those of sympatric small rodents, which have elongate feces (Smith and Weston 1990; Fig. 3A). Often pikas perch for long periods on or under the lips of favored rocks, most often near the center of their territory, where piles of their pellets are deposited (Fig. 3A). Pikas do not hibernate; thus, during early summer at BSHP they engage in harvesting vegetation that is stored into caches (haypiles) to serve as a source of food over winter (Smith and Weston 1990; Figs. 2 and 3C). Haypiles at BSHP are generally located close to the ore dump/vegetation interface and vary greatly in size—from huge domes to a small amount of vegetation tucked into the talus surface when most of the cache is stored deeply in the interstices of the rocks (Figs. 2 and 3C).

Fig. 2. Ore dump habitat for American pikas (*Ochotona princeps*) at BSHP, California, showing an active haypile characteristically positioned close to the talus–vegetation interface.

Fig. 3. Diagnostic sign of habitat occupancy by American pikas (*Ochotona princeps*) at BSHP, California. (A) A latrine with fresh fecal pellets; (B) an old latrine with desiccated fecal pellets; (C) a small haypile tucked into the ore dump talus; (D) a desiccated old haypile from a pika territory that is not currently occupied.

Pikas are individually territorial, and at BSHP the number of territories on an ore dump, thus the patch carrying capacity, is relatively fixed (Smith 1974a). Pika haypiles are most commonly situated near the rock/vegetation interface (patch perimeter; Fig. 2) and close to the center of the left-right reach along this perimeter. The average distance separating the main haypile of a pika with that of its neighbors is 21.8 m (n = 153; Smith 1974a). Our surveys primarily consisted of careful inspection for fresh pellets and haypiles. We used the nearest-neighbor distance between centrally placed haypiles in adjoining territories to guard against double-counting an animal on a patch.

Evidence of prior territory occupancy by pikas was determined by observation of old haypiles (dry sticks; no fresh leafy vegetation; Fig. 3D), which in the dry climate at BSHP can persist for years to decades (Millar et al. 2014a), and degraded fecal pellets (Fig. 3B). Old pellets are easily identified relative to fresh scat; they appeared desiccated, of smaller diameter, lighter in color, and generally scattered rather than concentrated in 1 spot (Fig. 3B; Nichols 2010; Millar et al. 2014a).

Population census.

ATS conducted the initial census of the full BSHP pika population in 1972 following 4 years of intensive fieldwork on site (Smith 1974b). Similar to the observations of Severaid 2 decades earlier, all ore dumps included in the survey showed signs of current or prior occupancy by pikas. In 1972, the size of each ore dump patch was determined and the entire census area was mapped. Seventy-six discrete ore dumps were identified and measured along with sample transects in 3 “mainland” sites where mining was most active and the tailings were continuous over a relatively large area (Fig. 1). Each ore dump was classified as being small (potential habitat for 1 to 3 pikas; perimeter ≤ 75 m; 52 patches), medium (potential habitat for 4 to 6 pikas; perimeter 76 to 150 m; 16 patches), or large (potential for 7 or more pikas; perimeter ≥ 151 m; 8 patches; Fig. 1); the largest patch had a perimeter of 335 m.

The first repeat survey was conducted by ATS in 1977 (Smith 1980). Following a hiatus of 12 years, the BSHP pika population was re-censused 18 times, beginning in 1989, by ATS and colleagues and/or former students of ATS. Results of the first 4 censuses appear in Smith and Gilpin (1997) and Moilanen et al. (1998). Additional investigations of the population structure of pikas at BSHP were made in 1988 to 1991 by Peacock and Smith (1997). A census in 2004 was not included in our analysis, as inexperienced volunteers noticeably inflated the number of pikas. The final 2 censuses in this series were made in 2009 and 2010, conducted by ATS, CIM, and colleagues. Census results through to 2010 were published in Smith and Nagy (2015). Additional results of censuses of pikas at BSHP following 2010 are reported in Stewart et al. (2015), Nichols et al. (2016), and Klingler (2017). In 2021, Millar and Smith (2022) investigated pika occupancy in the southern reaches of the study area. Herein, following a 12-year hiatus, we present the results of a complete census conducted in 2022.

For each annual census, we present data on the percentage of ore dump patches occupied and the sum of occupied pika territories on patches. Due to the geography at BSHP, the configuration of ore dump patches is mildly constricted in the middle (like a figure-8), and we present census data separately for the resulting northern and southern constellations of ore dumps, respectively (Fig. 1). While this distinction is arbitrary and only ~300 m separate the northernmost patch in the south from the southernmost patch in the north, data from the 1989 and 1991 censuses began to show distinctly different population trajectories in the northern and southern constellation of ore dump patches (Smith and Gilpin

1997; Smith and Nagy 2015). There are no physical barriers separating the northern and southern constellations other than distance, mean elevations are similar (north: 2,634 m; south: 2,604 m), and range of elevations is equivalent. The aspects and structure of ore dumps inhabited by pikas in the 2 areas are identical.

The southern constellation comprises 39 ore dumps (Fig. 1). Only 2 large ore dumps (from the Red Cloud and Noonday mines) occur in the south, and 15 patches, formerly occupied, were never occupied during our annual censuses. The northern constellation of ore dumps comprises 37 patches, 33 of which are included in our analysis (Fig. 1). Of the 33, 6 small patches are missing data from 1 census; in these instances the percent occupied was calculated based on 32 patches. The pika count for each of these 6 patches was back-filled based on the average number over the remaining census years, in each case a small addition (4 patches were increased by 1 pika; 2 patches were increased by 2). Two significant larger ore dumps were deleted from the sample because they were missing several censuses (Fig. 1). One patch was covered with a white dust that ATS believed was a poisonous substance, thus was not included in the first 3 censuses; it was occupied in all subsequent censuses with an average occupancy rate of 4.4 pikas. Another patch, the Syndicate, was missing 4 censuses between 1992 and 1996 because owners of the mine, before it became part of the BSHP, refused access; it was occupied in all 17 other censuses with an average occupancy of 6.9 pikas. One small patch close to the Syndicate was similarly off limits during that time, thus was not included in our analysis; it was, however, occupied in the first and last census, with an average occupancy of 0.7 pikas. One patch was not sampled 7 times between 1989 and 1996, and thus was not included in our analysis; it too was occupied in both the first and last census. Six of the 8 large ore dump patches were located in the northern constellation, and 5 ore dumps in the north were occupied in all 22 censuses from 1972 to 2022 (Smith and Nagy 2015; Fig. 1). The 3 mainland areas (Fig. 1) were each continuously occupied by a large number of pikas. These areas are not included in our analysis, as doing so would have artificially inflated our measures of percent occupancy of patches and number of pikas in the northern half of the study area.

Population trends in the 2 subregions were assessed using simple linear regression analyses of percent patch occupancy and number of pikas in each subregion as a function of time. The null hypothesis is that there has been no change over time in each subregion; a significant decline in each variable would suggest an effect due to climate change or some other linear factor. Similarly, we regressed pika patch occupancy and number of censused pikas with temperature variables (summer monthly maximums; number of days ≥ 28 °C) for each year (Table 1). Number of days ≥ 28 °C is a recognized metric for determining acute heat stress in pikas, whereas mean monthly maximum temperatures potentially represent a chronic stress to pikas (Beever et al. 2010, 2011). Further, in a longitudinal study, it is important to keep survey methods, including temperature analyses, as consistent as possible over time. The null hypothesis again is that there was no effect due to temperature on population variables; a significant observed decline would indicate a climate change effect.

Metapopulation dynamics.

The pika population at BSHP strictly meets the criterion of a metapopulation: (1) suitable habitat is found only in discrete patches; (2) all subpopulations have a risk of extirpation; (3) patches are close enough to allow for recolonization of extirpated patches; and (4) dynamics of local patch populations are not synchronized (Hanski 1998). Prior analyses of the BSHP pika metapopulation incorporated spatially explicit models assuming that connectivity between patches is distance-dependent and probability of extirpation on any given patch is related to patch size (Smith and Gilpin 1997; Moilanen et al. 1998; White and Smith 2018). Herein we include the 2022 census into the metapopulation model developed by White and Smith (2018) to further explore whether metapopulation models based on parameters of the local pika population are necessary and sufficient predictors of our observed occupancy patterns in both the northern and southern constellations, independent of climate change. The White and Smith (2018) model incorporates explicit spatial dynamics both within patches (with competition for territories) and between patches with juvenile dispersal. The model is also stochastic as it models relevant pika life-history patterns (natality, mortality, dispersal) as random variables on individual ore dump patches based on detailed studies conducted earlier at BSHP (Smith 1974a, 1974b, 1978). This approach allows examination of how these parameters may scale up to the entire population.

Table 1. Relationships (simple linear regression analysis) of the potential effects of ambient temperatures with the number of American pikas (*Ochotona princeps*) or percent of patches (ore dumps) occupied at BSHP 1972 to 2022 as determined in 21 censuses.

Model	R^2	F	P-value
Northern constellation			
Mean maximum temperature in July and August			
Number of pikas	0.0003	0.005	0.942
Percent patches occupied	0.0190	0.3490	0.562
Summer days ≥ 28 °C			
Number of pikas	0.0158	0.289	0.597
Percent patches occupied	0.0113	0.205	0.656
Southern constellation			
Mean maximum temperature in July and August			
Number of pikas	0.0056	0.102	0.754
Percent patches occupied	0.0050	0.091	0.767
Summer days ≥ 28 °C			
Number of pikas	0.1365	2.846	0.132
Percent patches occupied	0.0113	0.205	0.10

The model of White and Smith (2018) was run 1,000 times and was informed by census data from all 76 patches and the 3 mainland sites. Inclusion of the mainlands was based on our prior analysis in which model runs with and without the 3 mainland populations yielded no significant difference in model outcomes (White and Smith 2018). The putative lack of dispersal from mainland patches to isolated patches is initially counterintuitive, but our prior work with marked animals and comparative genotypes has also found little evidence of movement away from mainlands to nearby patches (Peacock and Smith 1997; Smith and Gilpin 1997). Apparently juveniles looking for new territories have more available vacancies on these large patches, so that they are unlikely to risk dispersal across inhospitable terrain.

Results

Temperature and climate.

BSHP is a warm environment for pikas; average monthly maximum temperatures during summer are in the top 16% of 760 occupied pika localities in the Great Basin—the warmest geographic region across the species range. Average monthly maximum temperatures at BSHP in July and August have increased significantly, approximately 1.5 °C from 1895 to 2022 (July R^2 = 0.064, P = 0.009; August R^2 = 0.039, P = 0.030; Fig. 4A). Particularly notable is the high variance in temperatures, with extreme high and low values among years. The number of extremely warm days (≥28 °C) increased marginally over time (R^2 = 0.028; P = 0.099; Fig. 4B), and again there was considerable variability among years. Notably, 3 years with the greatest number of extremely warm days occurred during the prior decade (Fig. 4B). The hottest temperatures recorded at BSHP (≥31 °C) were measured as early as 1895, and the hottest temperature, 32 °C, was recorded twice—in 1988 and 2002.

Summary of previous censuses.

In 1972, 81.8% of ore dumps in the northern constellation and 36.8% of ore dumps in the southern constellation were occupied (Fig. 5A). The corresponding total number of pikas occupying ore dumps in the north was 75, whereas 48 pikas were found in the south (Fig. 5B). Most occupied ore dumps contained fewer individuals than the apparent carrying capacity of the patch as indicated by patch perimeter (Smith 1974b). The pattern of occupancy of pikas on ore dumps apparently represented a dynamic equilibrium between extirpation of populations on a patch, which was indirectly related to patch size, and the ability of pikas to recolonize vacant patches, which was indirectly related to inter-patch distance (Smith 1974b). The distribution of unoccupied patches implied that distances greater than 300 m posed difficult barriers to dispersing juveniles (Smith 1974b).

Population metrics from the first follow-up census in 1977 were nearly identical to those from 1972: 78.1% of ore dumps in the north were occupied, whereas in the south 34.2% were occupied (Fig. 5A). The total number of occupied pika territories observed was 66 in the north and 44 in the south (Smith 1980; Fig. 5B). However, these figures masked the region-wide dynamics of the population: 53% of populations on ore dump islands across the entire study area differed between the 2 censuses. Eight previously unoccupied islands were recolonized and populations on 11 ore dumps were extirpated (Smith 1980).

The next 2 censuses in 1989 and 1991 differed significantly from the 1972 and 1977 censuses. Metrics from the northern constellation of pikas were similar to the earlier censuses (patch occupancy: 66.7% in 1989; 75% in 1991; number of pikas: 77 in 1989; 85 in 1991; Fig. 5A and B). In contrast, in the southern constellation, both patch occupancy (18.4% in 1989; 13.2% in 1991) and number of pikas (14 in 1989; 8 in 1991) were significantly reduced (Fig. 5A and B). These

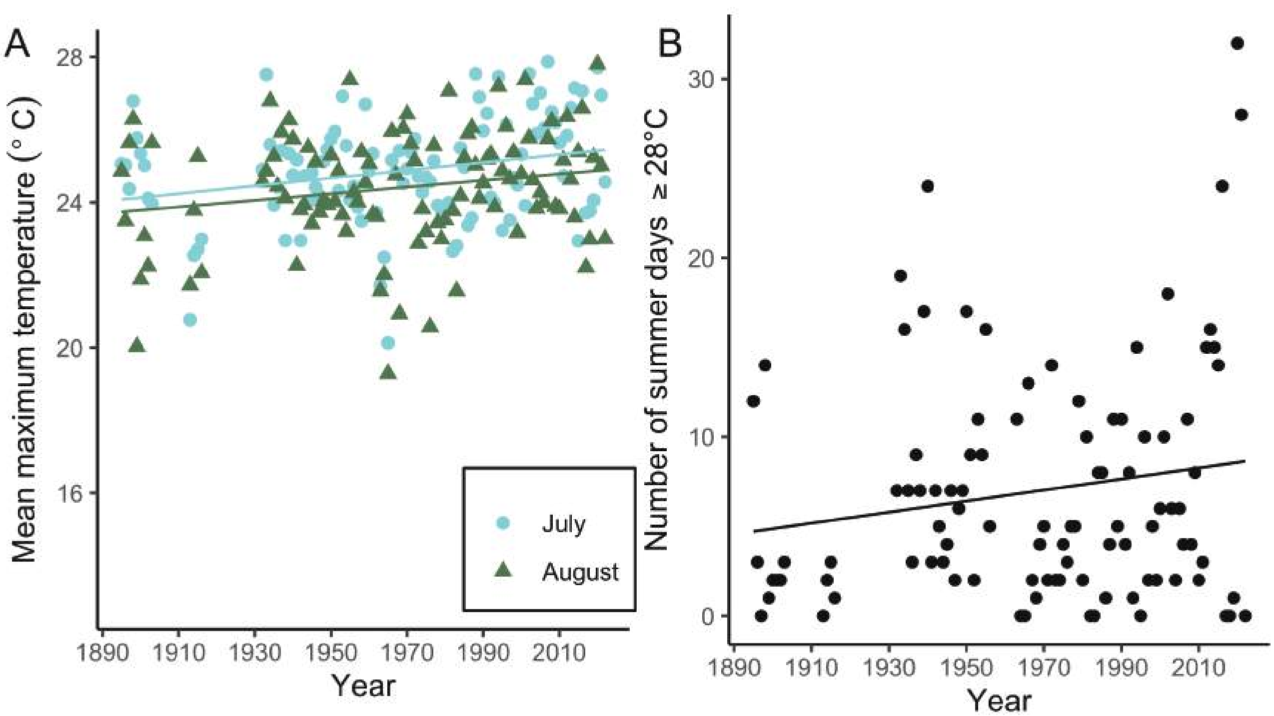

Fig. 4. Maximum temperature trends at BSHP, California, from 1895 to 2022. (A) Mean monthly maximum temperature for July (circles) and August (triangles); (B) number of maximum daily temperatures ≥ 28 °C during summer months (July and August).

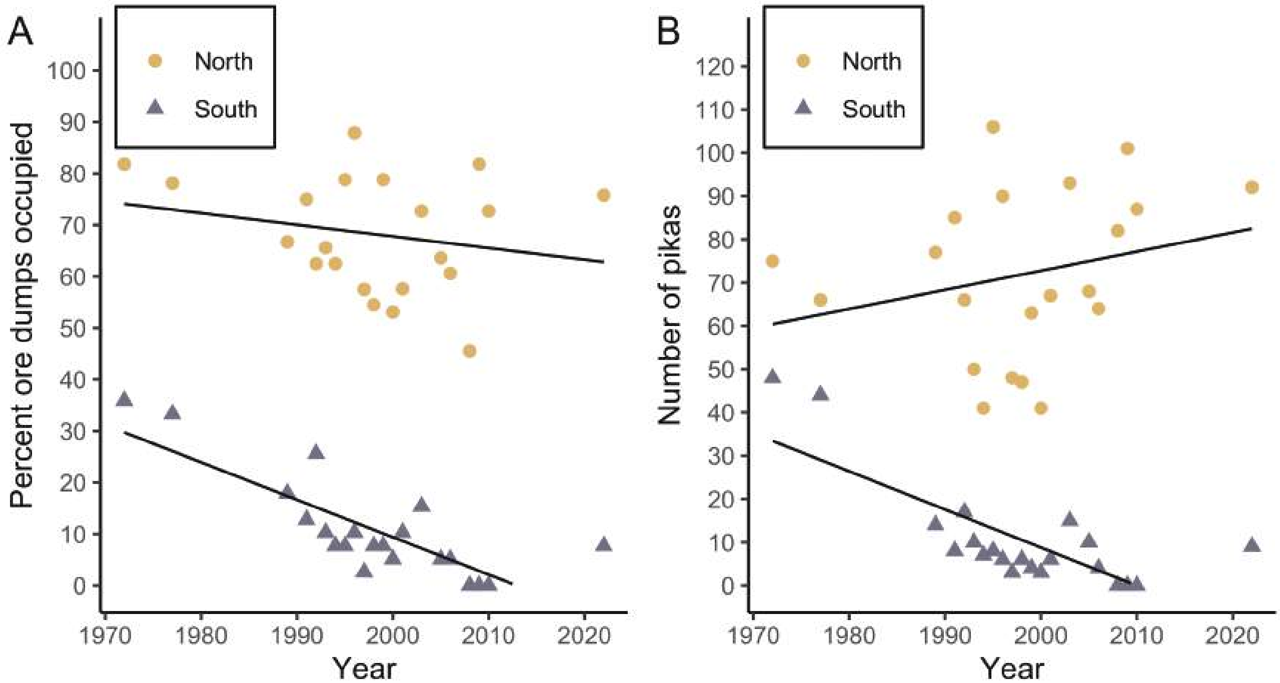

Fig. 5. Occupancy values on ore dump habitat by American pikas (*Ochotona princeps*) at BSHP, California, from annual censuses conducted over a span of 51 years, separated into northern and southern regions of the study area. (A) There was no change over time in percent occupancy in ore dumps in the northern constellation ($R^2 = 0.05$, $P = 0.335$), whereas occupancy in the southern constellation decreased significantly ($R^2 = 0.64$, $P < 0.001$); (B) there was no change over time in the total number of pikas on occupied ore dumps in the northern constellation ($R^2 = 0.06$, $P = 0.27$), whereas the number of pikas decreased significantly in the southern constellation ($R^2 = 0.59$, $P < 0.001$).

data led to our consideration to separate the 2 areas as representing different population trajectories. The combination of these 4 censuses also paved the way for the BSHP pika population to be considered a classic metapopulation (Smith and Gilpin 1977; Moilanen et al. 1998; n.b., Moilanen et al. separated the ore dumps into northern, middle, and southern patch networks).

Censuses conducted in the northern constellation of ore dumps between 1992 and 2010 yielded patch occupancy values between 45.5% and 87.9% and number of pikas from 41 to 106 (Smith and Nagy 2015; Fig. 5A and B). In the southern constellation from 1992 to 2006, the pika population reached very low numbers: occupancy ranged from 5.1% to 25.6% and number of pikas from 3 to 17 (Smith and Nagy 2015; Fig. 5A and B). Following 2006 no pikas were observed in the south for the next decade (Stewart et al. 2015; Nichols et al. 2016; Klingler 2017; Fig. 5A and B).

2022 census.

In 2022, occupation of ore dumps in the northern constellation was 75.8%, an occupancy rate comparable to that found in the previous censuses. Taken together with the prior 20 censuses, there was no change in percent occupancy over time ($R^2 = 0.05$, $P = 0.335$; Fig. 5A). The number of active pika territories observed in the north was 92, and there was no significant difference in the number of pikas located over time ($R^2 = 0.06$, $P = 0.27$; Fig. 5B).

In 2022, we found 9 active pika territories on 3 patches in the south (7.7% of patches): 1 on the Noonday mine (a large patch 1.3 km south of the closest large source ore dump in the north), 4 on the Red Cloud mine (a large patch 1.1 km south of the closest large source ore dump in the north), and 4 on a medium-sized patch 300 m south of the 2 closest northern source patches (Figs. 1, 5A and B). These findings contributed to a negative 21-year trajectory of percent patches occupied ($R^2 = 0.64$, $P < 0.001$; Fig. 5A) and number of pikas ($R^2 = 0.59$, $P < 0.001$; Fig. 5B) in the southern constellation over time. We had also found pikas in the southern constellation during our localized survey of the southern constellation in 2021: sightings, vocalizations, and abundant sign of pikas on the Noonday mine, although no pikas were found on either the Red Cloud mine or the medium-sized patch (Millar and Smith 2022).

In addition to examining the ore dumps for sign of active pika occupancy, in 2022, we also positioned 2 trail cameras for 3 months (July through September) at sites on southern ore dumps likely to be occupied by pikas. Images on 1 camera were exclusively of small rodents. At the camera on the Red Cloud mine, 2 pikas that could be clearly distinguished by their pelage were recorded by the camera consistently over the 3 months. When we conducted our survey, we spent considerable time examining the talus adjacent to the trail camera for active pika sign (fresh fecal pellets, stored green vegetation), without success.

In summary, our surveys over 50 years at BSHP indicate that the northern constellation of pikas remained robust, although fluctuating in numbers both spatially and temporally throughout this period, thus not showing any demonstrable effect due to climate change or other linear effect. In contrast, the southern constellation of populations contracted significantly, even becoming regionally extirpated for a period of approximately a decade, before becoming recolonized (Millar and Smith 2022). There were no instances where temperature appeared to directly affect pika population numbers or percent occupancy of ore dumps in either the southern or northern constellations based on regressions with temperature variables (monthly summer maximums or number of days ≥ 28 °C for each year; Table 1).

Metapopulation analysis.

Separate stochastic patch occupancy models based on the first 4 censuses (1972 to 2001) noted that the dynamics of the northern and southern constellations were decoupled and correctly determined that the observed decline in patch occupancy in the south would eventually lead to regional extirpation (Smith and Gilpin 1997; Moilanen et al. 1998). Similarly, model analyses of data through 2010 (White and Smith 2018) and the present study (Fig. 6) predicted the northern constellation to remain robust. In contrast, the model determined that landscape heterogeneity and the specific configuration of habitat at BSHP were together necessary and sufficient predictors of the eventual extirpation of the southern constellation of patches (White and Smith 2018; Fig. 6). An important take-home lesson from this analysis is that fragmentation alone can lead to regional extirpations within metapopulations, independent of climatic variables. As habitat conditions at BSHP (patch spacing and quality of ore dumps) have remained constant for decades, a key question becomes why did the south not become extirpated earlier?

The model of White and Smith (2018) further allows for setting different parameters for juvenile mortality during dispersal, a factor that may be affected by increasing temperatures, as pikas are physiologically sensitive to warm temperatures. Simulations incorporating higher dispersal mortality rates, as would be expected due to warming temperatures (MacArthur and Wang 1973; Smith 1974a), predicted declines in mean population size and patch occupancy, events that could have led to the eventual collapse of the southern constellation (Fig. 7).

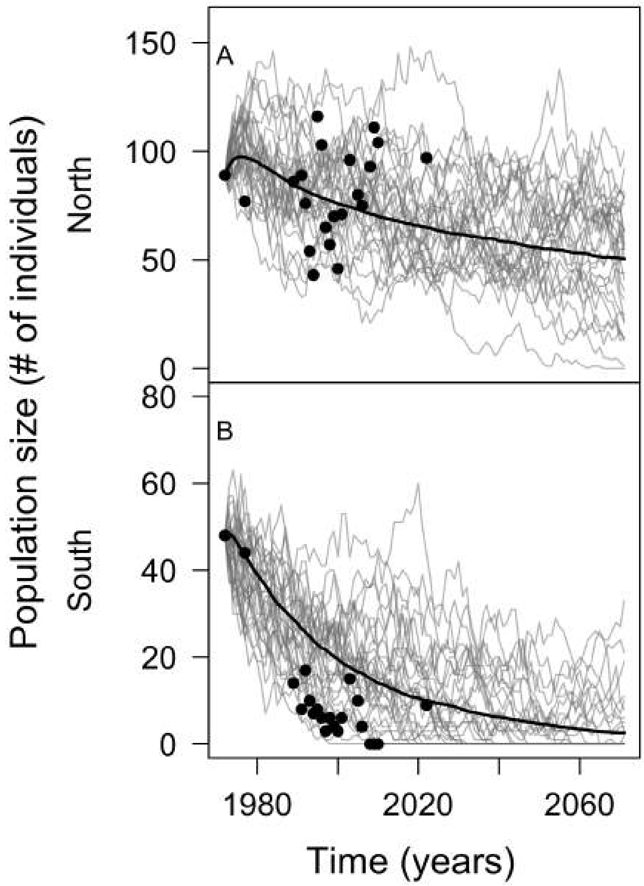

Fig. 6. Simulated time series of 30 typical runs for total population size of American pikas (*Ochotona princeps*) in the northern and southern constellations of ore dumps, respectively, at BSHP, California, based on the metapopulation model of White and Smith (2018). Black circles are data from field censuses conducted from 1972 to 2022. The solid line is the mean population size from 1,000 runs.

Discussion

The 10 warmest years in the historical record on earth have all occurred since 2010 (Lindsey and Dahlman 2023), and at BSHP the decade prior to our 2022 census was characterized by many years of extremely warm high average monthly summer temperatures (Fig. 4A). Most notably, 3 years during this period exhibited the greatest number of daily temperatures ≥ 28 °C compared with data extending back as far as 1895 (Fig. 4B). If these temperatures, reflecting the approximate onset of observable anthropogenic global warming, had negatively affected the BSHP pikas, we would expect a decline in occupancy rates and numbers of surviving animals, particularly during the past decade. Our initial observations in 1972 and 1977—effectively a baseline—were taken before awareness of the current rise in greenhouse-induced global temperatures associated with anthropogenic climate change began (Lindsey and Dahlman 2023). Even at that time, the climate at BSHP was warmer than habitats that typically characterize the core (montane/alpine) range of American pikas. As global warming accelerated, the metrics of the pika population in the northern constellation ore dump

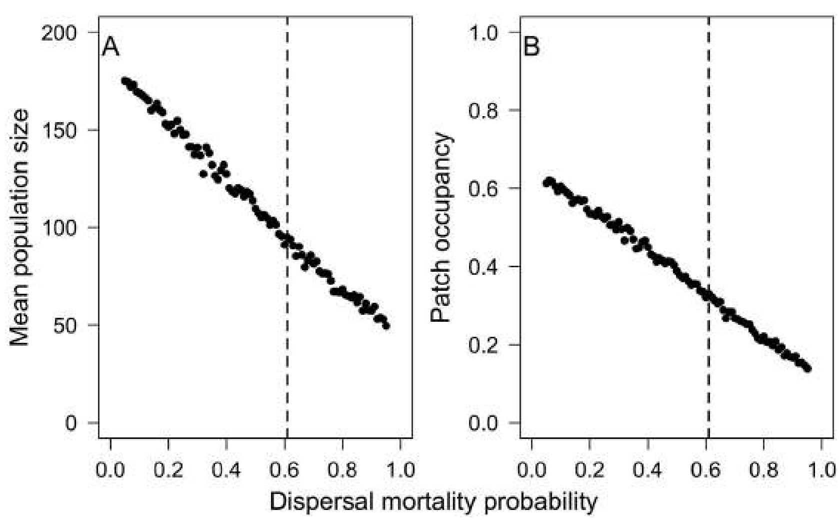

Fig. 7. Sensitivity of (A) total population size and (B) patch occupancy to reductions in dispersal mortality with increasing temperatures potentially encountered by American pikas (*Ochotona princeps*) at BSHP, California. Model parameterization from White and Smith (2018). The vertical dashed line is the default parameter value for the Bodie population based on observed pika life-history characteristics (White and Smith 2018).

patches have shown no decline over 5 decades, indicating that climate change during this time period has not directly affected this pika population, whereas the population in the southern constellation declined significantly during this period, leading to eventual regional extirpation (Fig. 5A and B). What do these separate trajectories, in what was originally considered a single population, tell us about climate change or other determinants of population persistence?

As the entire BSHP pika study area is small, the southern area is continuous with the northern area, and elevation, topography, and vegetation of the areas are similar (Fig. 1)—it is unlikely that temperatures in the 2 areas varied significantly. It is also difficult, looking at the extreme variability in our 2 measures of environmental temperature (Fig. 4A and B), to ascertain inflection points that would have led to the significant decline in pikas in the southern constellation prior to the 1989 and 1991 censuses and in the years immediately preceding the transient extirpation after 2006. Warm average monthly maximum temperatures and years with a large number of extremely hot days (≥28 °C) are scattered throughout the historical record of pikas at BSHP. Additionally, percent occupancy and number of pikas in both the northern and southern constellations were not influenced by average monthly maximum temperatures during summer or the number of days ≥ 28 °C for each year (Table 1). The variability in temperature metrics also allowed examination of whether climate could influence extirpations or recolonizations on ore dump patches (Smith and Nagy 2015). In 18 annual or biannual censuses (17 census intervals) between 1989 and 2010, there were 114 patch extirpations and 109 patch recolonizations. These events were not correlated with temperatures from either the current or previous census year. Patch extirpations were not more likely in warm years, and recolonizations of vacant patches were not more likely in cool years (Smith and Nagy 2015).

Our climate data are based on standard meteorological measurements. However, such data do not accurately reflect the thermal environment in which pikas live, particularly pikas that occupy warm environments like BSHP. When faced with the prospect of overheating, pikas retreat into the cool interstices of their talus habitat (Smith 1974a; Otto et al. 2015; Smith et al. 2016; Camp et al. 2020). In native habitat, it has been observed that warm localities occupied by pikas are normally characterized by rock-ice (periglacial) features (Millar and Westfall 2010; Millar et al. 2013b, 2014b, 2016; Wilkening et al. 2015; Smith et al. 2016). In these situations, temperatures deep in the talus may be significantly cooler than found in talus without ice-rock features. Thermal profiles on the ore dumps at BSHP are unavailable, but it is unlikely that they contain periglacial (ice) features. Apparently, the thermal profile deep in the ore dumps is sufficient for pikas to thermoregulate adequately.

If the prevailing climate is not responsible directly for the observed discrepancy between the population trajectories in the northern and southern constellations of pikas at BSHP, then what factors might come into play? Most contemporary pika studies amass a suite of climatic factors (Beever et al. 2010, 2011), but they rarely examine alternatives to the loss of local or regional populations independent of climate (but see Beever et al. 2003). The most likely alternative to climate involves metapopulation dynamics (Smith and Gilpin 1997; Moilanen et al. 1998; White and Smith 2018). The observed distribution of pikas at BSHP thus represents a control over the effect of climate, which is constant across the study population, versus metapopulation dynamics.

Metapopulation variables at BSHP include the configuration and spacing of available ore dump patches. A key difference between the southern and northern constellations is that available ore dumps in the south appear to be "strung out" more than the "clustered" patches in the north (Fig. 1). Also, at the time of the first census, the percent of ore dumps occupied and number of occupied pika territories in the southern constellation were fewer than those found in the northern constellation (Fig. 5A and B). Could the 15 small patches in the south that were never occupied since 1972 contribute to the downward trajectory of the southern pika population? The model of White and Smith (2018) allowed for a direct test of this hypothesis, and determined no difference in projected population dynamics with or without these patches. Our model simulations incorporating both the specific configuration of ore dump habitat and heterogeneity of the landscape were necessary and sufficient predictors of mean population size, patch occupancy, and total abundance through time for both the northern and southern constellations, as well as the timing of the collapse of the southern constellation, independent of any climatic factors (White and Smith 2018; Fig. 6).

Investigation of the pika metapopulation at BSHP has also documented the importance of patch size (patch carrying capacity) on the probability of pika occupancy. Small ore dumps were far less likely to be occupied than larger patches (Smith 1974b, 1980; Smith and Nagy 2015; present study). It is common for a high percentage of small patches to be responsible for documented extirpations in studies that have concluded climate to be the dominant factor responsible for the decline of American pikas (e.g., Beever et al. 2011; Stewart et al. 2015, 2017). However, what we do not know in these situations is whether or not a vacancy on a habitat patch is due to stochastic extirpation, without having been recolonized, independent of climatic variables (McCain et al. 2016).

The factor that ties together aspects of metapopulation dynamics and the prevailing influence of a warming climate is dispersal—one of the least understood life-history features in pikas (Tapper 1973; Smith 1974b; Smith and Ivins 1983a; Smith 1987; Peacock 1997; Peacock and Smith 1997). As Smith (2020:1484) concluded in his review of the status of American pikas: "The trait that puts pikas most at risk from climate change is their poor dispersal capability." Further, the metapopulation model of White and Smith (2018) highlights the impact that reduced dispersal, most likely resulting from warming temperatures affecting dispersal mortality, can have on regional population persistence (Fig. 7). However, while Stewart et al. (2015) listed the southern constellation at BSHP as extirpated, the area has been recently recolonized by pikas, perhaps repeatedly, beginning in 2015 (Nichols et al. 2016; Klingler 2017; Millar and Smith 2022; present study). This recolonization shows the importance of re-censusing extirpated sites (McCain et al. 2016) and the need to better understand the dynamics of pika dispersal.

Finally, in a study such as this with many natural history (observation) decisions made over the course of many censuses, it is important to discuss the issues of false positives and false negatives (Fournier et al. 2019). Due to the distinctive nature of pika sign (small spherical pellets, generally in a latrine; green haypile caches), and the wide spacing between haypiles and centers of activity due to territoriality, we believe that false positives in our data are negligible.

False negatives, however, are a distinct possibility. We had authorization to position only 2 camera traps in 2022, and one of these consistently recorded 2 distinctly different pikas over the period of measurement. When we collected the camera, however, we could find no clear sign of pika occupancy in the adjacent talus. It is possible for a pika to tuck its entire haypile deep in the talus, but pellets should be present, and they were not. Surface haypiles at BSHP vary greatly in size from huge to small vestiges of a cache that may mostly be out of sight, deep in the talus (Figs. 2 and 4C), and not all territories contain obvious latrines. Similarly, pika haypiles in other warm habitats, e.g., Lava Beds National Monument (Beever et al. 2008); the nearby Mono Craters (Smith et al. 2016; Millar and Smith 2022), may be cryptic or hidden. Thus, more pikas could inhabit BSHP than we tallied.

The possibility of false negatives, coupled with rapid surveys that are not repeated or are conducted without documentation of interobserver reliability measures, may have led to several instances where a pika population was considered extirpated when it was, in fact, extant (e.g., at Mono Craters; Millar and Smith 2022; see also Smith 2020). Additionally, the potential for recolonization of vacant habitat, such as observed throughout the BSHP pika metapopulation, and particularly in the southern constellation, shows that dispersal capability is an important consideration when assessing the potential status of pika populations (McCain et al. 2016; Smith 2020; Millar and Smith 2022).

It is unclear why most studies that have concluded American Pika populations may be on a downward trajectory have not evaluated unambiguous conflicting evidence from extant populations found at warm marginal sites such as BSHP; Mono Craters (Smith et al. 2016; Millar and Smith 2022); Craters of the Moon (Camp et al. 2020); Lava Beds National Monument (Ray et al. 2016); Newberry National Volcanic Monument (Shinderman 2015); northwest Nevada (Jeffress et al. 2017). A robust conservation and climate assessment of the American Pika is incomplete without considering the performance of the BSHP pika population over time and its resilience when confronted with high temperatures.

Acknowledgments

We thank the staff of Bodie State Historic Park for their support over the years. The 2022 census was conducted under California Department of Parks and Recreation permit 22-06. We appreciate the assistance of Badingqiuying, M. Gilpin, J. Nagy, L. Nichols, D. Quammen, C. Ray, R. Westfall, and M. Wilson who aided with various censuses. H. Smith and J. R. Smith provided valuable editorial suggestions. J. A. Smith drafted the 2 data figures, R. Westfall assisted with the climate data, and A. Musgrave kindly produced the study area map.

Author contributions

ATS and CIM conceived the study and designed the methodology. ATS and CIM conducted the field study and curated data, and ATS and ERW performed formal analyses. ATS and CIM led the writing of the manuscript, with key input from ERW. All authors contributed critically to the drafts and gave final approval for publication.

Funding

No external funding.

Conflict of interest

The authors declare no conflict of interest.

Data availability

Data available by request through the authors.

References

Beever EA, Brussard PF, Berger J. 2003. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. Journal of Mammalogy 84(1):37–54. https://doi.org/10.1644/1545-1542(2003)084<0037:poaeai>2.0.co;2

Beever EA, Perrine JD, Rickman T, Flores M, Clark JP, Waters C, Weber SS, Yardley B, Thoma D, Chesley-Preston T, *et al*. 2016. Pika (*Ochotona princeps*) losses from two isolated regions reflect temperature and water balance, but reflect habitat area in a mainland region. Journal of Mammalogy 97(6):1495–1511. https://doi.org/10.1093/jmammal/gyw128

Beever EA, Ray C, Mote PW, Wilkening JL. 2010. Testing alternative models of climate-mediated extirpations. Ecological Applications 20(1):164–178. https://doi.org/10.1890/08-1011.1

Beever EA, Ray C, Wilkening JL, Brussard PF, Mote PW. 2011. Contemporary climate change alters the pace and drivers of extinction. Global Change Biology 17(6):2054–2070. https://doi.org/10.1111/j.1365-2486.2010.02389.x

Beever EA, Wilkening JL, Billman PD, Thurman LI, Ernest KA, Wright DH, Gill AM, Craighead AC, Helmstetter NA, Svancara LK, *et al*. 2023. Geographic and taxonomic variation in adaptive capacity among mountain-dwelling small mammals: implications for conservation status and actions. Biological Conservation 282:109942. https://doi.org/10.1016/j.biocon.2023.109942

Beever EA, Wilkening JL, McIvor DE, Weber SS, Brussard PF. 2008. American pikas (*Ochotona princeps*) in northwestern Nevada: a newly discovered population at a low-elevation site. Western North American Naturalist 68(1):8–14. https://doi.org/10.3398/1527-0904(2008)68[8:apopin]2.0.co;2

Billman PD, Beever EA, McWethy DB, Thurman LL, Wilson KC. 2021. Factors influencing distributional shifts and abundance at the range core of a climate-sensitive mammal. Global Change Biology 27(19):4498–4515. https://doi.org/10.1111/gcb.15793

Camp MJ, Shipley LA, Varner J, Waterhouse BD. 2020. Activity patterns and foraging behavior of American pikas (*Ochotona princeps*) differ between Craters of the Moon and alpine talus in Idaho. Western North American Naturalist 80(1):49–69. https://scholarsarchive.byu.edu/wnan/vol80/iss1/6

Daly C, Neilson RP, Phillips DL. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33(2):140–158. https://doi.org/10.1175/1520-0450(1994)033<0140:astmfm>2.0.co;2

Fournier A, White ER, Heard SB. 2019. Site-selection bias and apparent population declines in long-term studies. Conservation Biology 33(6):1370–1379. https://doi.org/10.1111/cobi.13371

Grayson DK. 2005. A brief history of Great Basin pikas. Journal of Biogeography 32(12):2103–2111. https://doi.org/10.1111/j.1365-2699.2005.01341.x

Grinnell J. 1917. Field tests of theories concerning distributional control. The American Naturalist 51(602):115–128. https://doi.org/10.1086/279591

Hanski I. 1998. Metapopulation dynamics. Nature 396(6706):41–49. https://doi.org/10.1038/23876

Jeffress MR, Van Gunst KJ, Millar CI. 2017. A surprising discovery of American pika sites in the northwestern Great Basin. Western North American Naturalist 77(2):252–268. https://doi.org/10.3398/064.077.0213

Klingler KB. 2017. An integrated investigation of the population genetics, physiological stress, and movement patterns in the American pika (*Ochotona princeps*) [dissertation]. [Reno (NV, USA)]: University of Nevada, Reno.

Lindsey R, Dahlman L. 2023. Climate change: global temperature. [accessed 1 Feb 2023]. https://www.climate.gov/news-features/understanding-climate/climate-change-global-temperature

MacArthur RA, Wang LCH. 1973. Physiology of thermoregulation in the pika, *Ochotona princeps*. Canadian Journal of Zoology 51(1):11–16. https://doi.org/10.1139/z73-002

MacArthur RA, Wang LCH. 1974. Behavioral thermoregulation in the pika, *Ochotona princeps*: a field study using radiotelemetry. Canadian Journal of Zoology 52(3):353–358. https://doi.org/10.1139/z74-042

McCain C, Szewczyk T, Knight KB. 2016. Population variability complicates the accurate detection of climate change responses. Global Change Biology 22(6):2018–2093. https://doi.org/10.1111/gcb.13211

McKelvey KS, Perry RW, Mills LS. 2013. The effects of climate change on mammals. U.S. Department of Agriculture, Forest Service, Climate Change Resource Center. [accessed 1 Feb 2023]. https://www.fs.usda.gov/ccrc/topics/wildlife/mammals

Millar CI, Delaney DL, Hersey KA, Jeffress MR, Smith AT, Van Gunst KJ, Westfall RD. 2018. Distribution, climatic relationships, and status of American pikas (*Ochotona princeps*) in the Great Basin, USA. Arctic Antarctic and Alpine Research 50(1):e1436296. https://doi.org/10.1080/15230430.2018.1436296

Millar CI, Heckman K, Swanston C, Schmidt K, Westfall RD, Delany DL. 2014a. Radiocarbon dating of American pika fecal pellets provides insights into population extirpations and climate refugia. Ecological Applications 24(7):1748–1768. https://doi.org/10.1890/13-0520.1.

Millar CI, Hickman KT. 2021. Camera traps provide insights into American pika site occupancy, behavior, thermal relations, and associated wildlife diversity. Western North American Naturalist 81(2):141–170. https://doi.org/10.3398/064.081.0201

Millar CI, Smith AT. 2022. Return of the pika: American pikas re-occupy long-extirpated warm locations. Ecology and Evolution 12(9):e9295. https://doi.org/10.1002/ece3.9295

Millar CI, Westfall RD. 2010. Distribution and climatic relationships of the American pika (*Ochotona princeps*) in the Sierra Nevada and western Great Basin, U.S.A.; periglacial landforms as refugia in warming climates. Arctic Antarctic and Alpine Research 42(4):493–496. https://doi.org/10.1657/1938-4246-42.4.493

Millar CI, Westfall RD, Delany DL. 2013a. New records of marginal locations for American pika (*Ochotona princeps*) in the western Great Basin. Western North American Naturalist 73(4):457–476. https://doi.org/10.3398/064.073.0412

Millar CI, Westfall RD, Delany DL. 2013b. Thermal and hydrologic attributes of rock glaciers and periglacial talus landforms: Sierra Nevada, California, U.S.A. Quaternary International 310:169–180. https://doi.org/10.1016/j.quaint.2012.07.019

Millar CI, Westfall RD, Delany DL. 2014b. Thermal regimes and snowpack relations of periglacial talus slopes, Sierra Nevada, Calif. ornia, U.S.A. Arctic Antarctic and Alpine Research 46(2):483–504. https://doi.org/10.1657/1938-4246-46.2.483

Millar CI, Westfall RD, Delany DL. 2016. Thermal components of American pika habitat—how does a small lagomorph encounter climate? Arctic Antarctic and Alpine Research 48(2):327–343. https://doi.org/10.1657/aaar0015-046

Millar JS. 1973. Evolution of litter-size in the pika, *Ochotona princeps* (Richardson). Evolution 27(1):134–143. https://doi.org/10.1111/j.1558-5646.1973.tb05925.x

Millar JS. 1974. Success of reproduction in pikas, *Ochotona princeps* (Richardson). Journal of Mammalogy 55(3):527–542. https://doi.org/10.2307/1379544

Millar JS, Zwickel FC. 1972. Determination of age, age structure, and mortality of the pika, *Ochotona princeps* (Richardson). Canadian Journal of Zoology 50(2):229–232. https://doi.org/10.1139/z72-033

Moilanen A, Smith AT, Hanski I. 1998. Long-term dynamics in a metapopulation of the American pika. The American Naturalist 152(4):530–542. https://www.jstor.org/stable/10.1086/286188

Nichols LB. 2010. Fecal pellets of American pikas (*Ochotona princeps*) provide a crude chronometer for dating patch occupancy. Western North American Naturalist 70(4):500–507. https://doi.org/10.3398/064.070.0410

Nichols LB, Klingler KB, Peacock MM. 2016. American pikas (*Ochotona princeps*) extirpated from the historic Masonic Mining District of eastern California. Western North American Naturalist 76(2):163–171. https://doi.org/10.3398/064.076.0203

Otto HW, Wilson JA, Beever EA. 2015. Facing a changing world: thermal physiology of American pikas (*Ochotona princeps*). Western North American Naturalist 75(4):429–445. https://doi.org/10.3398/064.075.0402

Peacock MM. 1997. Determining natal dispersal patterns in a population of North American pikas (*Ochotona princeps*) using direct mark-resight and indirect genetic methods. Behavioral Ecology 8(3):340–350. https://doi.org/10.1093/beheco/8.3.340

Peacock MM, Smith AT. 1997. The effect of habitat fragmentation on dispersal patterns, mating behavior, and genetic variation in a pika (*Ochotona princeps*) metapopulation. Oecologia 112(4):524–533. https://www.jstor.org/stable/4221809

Ray C, Beever E, Loarie S. 2012. Retreat of the American pika: up the mountain or into the void? In: Brodie JF, Post E, Doak DF, editors. Wildlife conservation in a changing climate. Chicago (IL, USA): University of Chicago Press; p. 245–270.

Ray C, Beever EA, Rodhouse TJ. 2016. Distribution of a climate-sensitive species at an interior range margin. Ecosphere 7(6):e01379. https://doi.org/10.1002/ecs2.1379

Severaid JH. 1955. The natural history of the pikas (mammalian genus *Ochotona)* [dissertation]. [Berkeley (CA, USA)]: University of California, Berkeley.

Shinderman M. 2015. American pika in a low-elevation lava landscape: expanding the known distribution of a temperature-sensitive species. Ecology and Evolution 5(17):3666–3676. https://doi.org/10.1002/ece3.1626

Smith AB, Beever EA, Kessler AE, Johnston AN, Ray C, Epps CW, Lanier HC, Klinger RC, Rodhouse TJ, Varner J, *et al*. 2019. Alternatives to genetic affinity as a context for within-species response to climate. Nature Climate Change 9(10):787–794. https://doi.org/10.1038/s41558-019-0584-8

Smith AT. 1974a. The distribution and dispersal of pikas: influences of behavior and climate. Ecology 55(6):1368–1376. https://doi.org/10.2307/1935464

Smith AT. 1974b. The distribution and dispersal of pikas: consequences of insular population structure. Ecology 55(5):1112–1119. https://doi.org/10.2307/1940361

Smith AT. 1978. Comparative demography of pikas: effect of spatial and temporal age-specific mortality. Ecology 59(1):133–139. https://doi.org/10.2307/1936639

Smith AT. 1980. Temporal changes in insular populations of the pika (*Ochotona princeps*). Ecology 61(1):8–13. https://doi.org/10.2307/1937147

Smith AT. 1987. Population structure of pikas: dispersal versus philopatry. In: Chepko-Sade BD, Halpin ZT, editors. Mammalian dispersal patterns: the effects of social structure on population genetics. Chicago (IL, USA): University of Chicago Press; p. 128–142.

Smith AT. 2020. Conservation status of American pikas. Journal of Mammalogy 101(6):1466–1488. https://doi.org/10.1093/jmammal/gyaa110

Smith AT, Gilpin ME. 1997. Spatially correlated dynamics in a pika metapopulation. In: Hanski IA, Gilpin ME, editors. Metapopulation biology: ecology, genetics, and evolution. San Diego (CA, USA): Academic Press; p. 407–428.

Smith AT, Ivins BL. 1983a. Colonization in a pika population: dispersal versus philopatry. Behavioral Ecology and Sociobiology 13(1):37–47. https://doi.org/10.1007/bf00295074

Smith AT, Ivins BL. 1983b. Reproductive tactics of pikas: why have two litters? Canadian Journal of Zoology 61(7):1551–1559. https://doi.org/10.1139/z83-209

Smith AT, Ivins BL. 1984. Spatial relationships and social organization in adult pikas: a facultatively monogamous mammal. Zeitschrift für Tierpsychologie 66(4):289–308. https://doi.org/10.1111/j.1439-0310.1984.tb01370.x

Smith AT, Li W, Hik D. 2004. . Pikas as harbingers of global warming. Species 41:4–5.

Smith AT, Nagy JD. 2015. Population resilience in an American pika (*Ochotona princeps*) metapopulation. Journal of Mammalogy 96(2):394–404. https://doi.org/10.1093/jmammal/gyv040

Smith AT, Nagy JD, Millar CI. 2016. Behavioral ecology of American pikas (*Ochotona princeps*) at Mono Craters, California: living on the edge. Western North American Naturalist 76(4):459–484. http://www.jstor.org/stable/44651220

Smith AT, Weston ML. 1990. *Ochotona princeps*. Mammalian Species 352(352):1–8. https://doi.org/10.2307/3504319

Stewart JAE, Perrine JD, Nichols LB, Thorne JH, Millar CI, Goehring KE, Massing CP, Wright DH. 2015. Revisiting the past to foretell the future: summer temperature and habitat area predict pika extirpations in California. Journal of Biogeography 42(5):880–890. https://doi.org/10.1111/jbi.12466

Stewart JAE, Wright DH, Heckman KA. 2017. Apparent climate-mediated loss and fragmentation of core habitat of the American pika in the northern Sierra Nevada, California, USA. PLoS One 12(8):e0181834. https://doi.org/10.1371/journal.pone.0181834

Stuble KL, Bewick S, Fisher M, Forister ML, Harrison SP, Shapiro AM, Latimer AM, Fox LR. 2021. The promise and perils of resurveying to understand global change impacts. Ecological Monographs 91(2):e01435. https://doi.org/10.1002/ecm.1435

Tapper SC. 1973. The spatial organisation of pikas (*Ochotona*), and its effect on population recruitment [dissertation]. [Edmonton (AB, Canada)]: University of Alberta.

United States Department of Interior. 2015. 9 animals that are feeling the impacts of climate change. [accessed 1 Feb 2023]. https://www.doi.gov/blog/9-animals-are-feeling-impacts-climate-change

White ER. 2019. Minimum time required to detect population trends: the need for long-term monitoring programs. BioScience 69(1):40–46. https://doi.org/10.1093/biosci/biy144

White ER, Smith AT. 2018. The role of spatial structure in the collapse of regional metapopulations. Ecology 99(12):2815–2822. https://doi.org/10.1002/ecy.2546

Wilkening JL, Ray C, Varner J. 2015. Relating sub-surface ice features to physiological stress in a climate sensitive mammal, the American pika (*Ochotona princeps*). PLoS One 10(3):e0119327. https://doi.org/10.1371/journal.pone.0119327