Conservation status of American pikas (*Ochotona princeps*)

ANDREW T. SMITH*

School of Life Sciences, Arizona State University, P.O. Box 874501, Tempe, AZ 85287, USA

*Correspondent: a.smith@asu.edu

The American pika (*Ochotona princeps*) is commonly perceived as a species that is at high risk of extinction due to climate change. The purpose of this review is two-fold: to evaluate the claim that climate change is threatening pikas with extinction, and to summarize the conservation status of the American pika. Most American pikas inhabit major cordilleras, such as the Rocky Mountain, Sierra Nevada, and Cascade ranges. Occupancy of potential pika habitat in these ranges is uniformly high and no discernible climate signal has been found that discriminates between the many occupied and relatively few unoccupied sites that have been recently surveyed. Pikas therefore are thriving across most of their range. The story differs in more marginal parts of the species range, primarily across the Great Basin, where a higher percentage of available habitat is unoccupied. A comprehensive review of Great Basin pikas revealed that occupied sites, sites of recent extirpation, and old sites, were regularly found within the same geographic and climatic space as extant sites, and suggested that pikas in the Great Basin tolerated a broader set of habitat and climatic conditions than previously understood. Studies of a small subset of extirpated sites in the Great Basin and in California found that climate variables (most notably measures of hot temperature) were associated more often with extirpated sites than occupied sites. Importantly, upward contraction of the lower elevation boundary also was found at some sites. However, models that incorporated variables other than climate (such as availability of upslope talus habitat) often were better predictors of site persistence. Many extirpations occurred on small habitat patches, which were subject to stochastic extinction, as informed by a long-term pika metapopulation study in Bodie, California. In addition, several sites may have been compromised by cattle grazing or other anthropogenic factors. In contrast, several low, hot sites (Bodie, Mono Craters, Craters of the Moon National Monument and Preserve, Lava Beds National Monument, Columbia River Gorge) retain active pika populations, demonstrating the adaptive capacity and resilience of pikas in response to adverse environmental conditions. Pikas cope with warm temperatures by retreating into cool interstices of their talus habitat and augment their restricted daytime foraging with nocturnal activity. Pikas exhibit significant flexibility in their foraging tactics and are highly selective in their choice of available vegetation. The trait that places pikas at greatest risk from climate change is their poor dispersal capability. Dispersal is more restricted in hotter environments, and isolated low-elevation sites that become extirpated are unlikely to be recolonized in a warming climate. The narrative that American pikas are going extinct appears to be an overreach. Pikas are doing well across most of their range, but there are limited, low-elevation losses that are likely to be permanent in what is currently marginal pika habitat. The resilience of pikas in the face of climate change, and their ability or inability to persist in marginal, hot environments, will continue to contribute to our understanding of the impact of climate change on individual species.

Key words: adaptive capacity, American pika, climate change, metapopulation, *Ochotona princeps*, resiliency

The American pika (*Ochotona princeps*) has received disproportionate attention in the public media compared with most small mammals, and most accounts share the following sentiment: “The evidence seems unequivocal: The American pika is rapidly vanishing from the mountains of the western U.S., and scientists say it is climate change that has imperiled these tiny mammals” (Mosbergen 2016). Millar et al. (2018:Appendix I) listed over 40 media releases claiming that the American pika is at risk of extinction due to climate change. The question before us is: to what degree are pikas at risk of extinction, and if they are at risk, is contemporary climate change responsible? The answers to these questions are complicated—a result that should come as no surprise to most biologists. So why then is the public perception of the fate of pikas so uniformly
negative? It could be due in part to the tendency of contemporary media to focus on sensational topics. But it may also be true that some researchers are presenting an exaggerated or biased narrative—that climate change is compromising pikas and may lead to their extinction. For example, the US National Park Service (2020) initiated a study of pikas entitled “Pikas in Peril,” a title that suggests the researchers knew the outcome before their study began.

Climate change is the most pressing environmental issue of our time, and it is overwhelmingly supported by scientific data (Collins et al. 2013). Whether or not pikas currently are being adversely affected by climate change does not negate the existential threat that climate change imposes on the world, and studies concerning how pikas respond to a changing climate certainly are warranted. Overreaching or unsupported claims about pikas and climate change, however, may do significant damage if they lead the public to question the credibility of science. It is incumbent upon scientists to present their results objectively, particularly in interactions with the press and general public.

Much of the narrative regarding pikas and climate change has been based on studies from a restricted and marginal part of their geographic range. But because responses of pikas to their environment can vary greatly across their broad geographic range (Millar et al. 2018; Smith et al. 2019), care should be taken when generalizing from one region to another.

In this review I 1) review the paleontological history of the American pika in North America; 2) outline why pikas are an exceptional species to study with regard to environmental change; 3) summarize relevant information on the status of pikas across the species’ range; 4) highlight aspects of the resilience of pikas living in extreme environments; 5) review how relevant traits of pikas may be impacted by environmental change; and 6) present the current conservation status of the pika. My goal is to integrate our knowledge about this important species and set a benchmark for ongoing investigations.

**Early North American Pikas**

The paleontological record of pikas is one of adjustment to warm temperatures. Pikas (*Ochotona*) have occupied North America since the late Miocene/early Pliocene following colonization from their center of origin in Asia. The earliest known North American fossil pika is the late Miocene/early Pliocene *O. spanglei* from Oregon (Shotwell 1956). By the late Pleistocene two morphological forms of *Ochotona* lived in northeastern North America: a large form, *O. whartoni*, found in deposits in Alaska, Yukon, and Ontario, and a small *O. princeps*-like form from deposits in Appalachia (Mead 1987; Mead and Grady 1996). These eastern forms persisted into the early Holocene before postglacial climate warming and increasing fragmentation of their habitat lead to their extinction (Mead and Grady 1996).

American pikas were common and widespread across western North America during the Wisconsin Glaciation (Mead 1987). In spite of the absence of pre-Wisconsin Glaciation fossils of pikas, allozymic patterns among populations indicate a pre-Wisconsin Glaciation divergence (>120,000 years BP) of four major genetic units (northern Rocky Mountains, southern Rocky Mountains, Cascade Range, and Sierra Nevada—Hafner and Sullivan 1995; later expanded to a fifth, central Utah unit—Galbreath et al. 2009; Hafner and Smith 2010). Hafner and Sullivan (1995) posited that pikas initially spread south along cordilleran dispersal corridors and subsequently became fragmented into isolated montane refugia during post-Wisconsin Glaciation warming. A more detailed examination of this dynamic in the southern Rocky Mountains found that altithermal warming accounted for 66.7% of post-Wisconsin Glaciation extinctions of insular pika populations in the region. Populations remaining in larger altithermal refugia (>100 km²) exhibited high survivorship (93.8%) compared with smaller refugia (6.1–15.2%—Hafner 1994). The resulting pattern of occupancy of pika populations has persisted over time, as recolonization of extirped sites within even 20 km has been rare (<7.8% of sites—Hafner 1994).

The prehistoric record of pikas also is well-documented in the Great Basin. Pikas were widespread in the Great Basin during the Pleistocene, reaching as far south as the Mojave Desert (Mead and Spaulding 1995; Grayson 2005, 2006). Pikas at that time apparently were not as predictably associated with talus as they are today, as evidenced by Pleistocene pika remains originating from valley bottoms (Mead and Spaulding 1995). Extirpation of Mojave Desert populations began as early as 14,000 years BP, consistent with the increase in temperatures before the close of the Wisconsin Glaciation, and nearly all southern and east-central Great Basin populations were gone by the end of the Pleistocene (Mead and Spaulding 1995; Grayson 2005, 2006). Pika extirpations and concomitant upslope movement of populations continued through the distinctly warm and dry Middle Holocene. This pattern of loss continued through the Holocene and to the present resulting in the establishment of the relatively impoverished modern distribution of pikas in the Great Basin (Mead and Spaulding 1995; Grayson 2005, 2006). The paleontological record also clearly documents that the current restriction to talus habitat by American pikas is fairly recent (Grayson 2006), although nearly all species in the subgenus *Pika*, which includes the American pika, are obligate rock-dwelling species (Smith 2018).

**Regional Status Summaries**

**Detection of Pika Populations**

 Detecting a climate change signal in a species’ response is directly related to the quality of the sampling effort (McCain et al. 2016). Presented below are several distinctive elements of pika natural history (Smith and Weston 1990) that inform accurate censuses of pika populations.

American pikas occupy a specific habitat of talus, or piles of broken rock, fringed by vegetation. They also may occupy lava flows, inselbergs, and anthropogenic habitats such as mining ore dumps, and roadside riprap. Pikas occur at relatively low density, and each sex defends a widely spaced territory (Smith...
Pikas are generalized herbivores that forage in two ways: feeding close to the talus–meadow interface, and haying—storing vegetation in a haypile during summer to serve as a source of food over winter (Millar and Zwickel 1972a; Conner 1983; Dearing 1997). Haypiles are the figurative center of a pika’s territory, and are most commonly positioned under an overhanging rock close to the talus–vegetation interface. A green (fresh vegetation) haypile indicates an occupied pika territory, while a dried brown haypile suggests that the site was previously but currently is not occupied. Pikas are diurnal and are surface-active about one-third of the time (although they are not always visible due to the disruptive nature of their talus habitat—Smith and Ivins 1984; Smith et al. 2016). Pikas also utter characteristic vocalizations (Ivins and Smith 1983; Conner 1985). Another way to assess the presence of pikas is finding their latrines of small round fecal pellets (distinctly different from the oblong scats deposited by rodents). Green, soft pellets reveal active pika presence, while dry yellowish-brown pellets signify that the site was occupied previously (Nichols 2010; Millar et al. 2014a). Contemporary occupancy surveys for presence/absence of pikas rely on sightings, vocalizations, green haypiles, and fresh fecal pellets.

The seemingly high detectability of pikas is one reason why pikas have attracted significant attention in the recent ecological literature. However, false negatives have been reported in several studies, requiring extensive repeat surveys (Beever et al. 2011; Millar et al. 2013a; Stewart et al. 2015). Extirpations are most difficult to detect when populations are small, and the possibility of false negatives increases in marginal (low, hot) habitats where reliable detection of pikas is more difficult (Smith et al. 2016). Examples include a “functionally extinct” site in Beever et al. (2003) that was later determined to host a “robust” pika population (Beever et al. 2010), and five occupied sites documented by Stewart et al. (2015) that had initially been classified as vacant.

Rocky Mountain Region

The Rocky Mountain region provides some of the best habitat for pikas, with many large, continuous talus slopes and high connectivity above 3,000 m. A number of studies in this region over the last decade have examined the distribution and abundance of pikas. Erb et al. (2011) censused 69 sites with historical records of pika occupancy from southern Wyoming to northern New Mexico. Of these sites, 65 (94%) were occupied, although two of the four sites labeled as extirpated were occupied the following summer. The four original extirpated sites possessed the lowest annual precipitation among all survey sites, but no temperature signal was apparent among the sites (Erb et al. 2011). Erb et al. (2014) estimated pika density at 18 of these sites. Two measures of vegetation quality—diversity and relative cover of forbs—predicted pika density better than climatic factors.

A comprehensive survey of pika occupancy in Colorado was carried out in 2015 (A. Seglund, Colorado Parks and Wildlife, pers. comm.). Potential pika localities (n = 858) throughout the state were identified and stratified into three geographic bands (north to south) and three elevational zones (< 3,353 m; between 3,353 and 3,658 m; > 3,658 m). From this matrix 112 sites were selected randomly and censused. Three sites did not contain appropriate pika habitat; of the remaining 109 sites, 107 (98.2%) were occupied. The two unoccupied sites, while containing sign of previous occupants, were small and in sub-optimal pika habitat.

Yandow et al. (2015) examined relative pika abundance as determined by fresh pellet density across two north-central Rocky Mountain ranges: the Wind River and Bighorns, Wyoming. In each range the identification of sites involved stratification by elevation, aspect, and timing of snowmelt. Pikas were found at all 40 sites in the Wind River and at 37/40 (92.5%) of sites in the Bighorns. Summer temperatures had no apparent influence on pika abundance at this latitude (Yandow et al. 2015). Farther north, in Glacier National Park, Montana, Moyer-Horner et al. (2016) detected evidence of pika occupancy (old, current, or both) in 274 sites, and 235 (85.8%) of these were occupied.

Utah

Four of five subspecies of pikas occur in Utah (Hafner and Smith 2010); these have recently been censused at 3-year intervals in 165 monitoring sites established across the state (K. A. Hershey, Utah Division of Wildlife, pers. comm.). Monitoring criteria included seeing or hearing pikas and presence of green haypiles. Conservatively, sites where only fresh green pellets were found during surveys were not counted as occupied. All sites were surveyed twice to confirm occupancy, and there were no significant changes in occupancy levels among years (2008: 74%; 2011: 73%; 2014: 73%; 2017: 78%).

These surveys starkly contrast with the declines in historic pika populations in the relatively isolated protected areas of Zion National Park and Cedar Breaks National Monument, Utah, at the southern edge of the species’ distribution (Beever et al. 2016a). In Zion, talus areas cover less than 5% of the park and are found in five distinct areas. Within these areas, evidence of prior pika occupancy was found in 30 discrete talus habitat patches, one of which was occupied as recently as 2011; in 2015 no evidence of current occupation was found (Beever et al. 2016a). At Cedar Breaks no pikas were found at three historic sites occupied as recently as 2012. Pikas occupied two of four newly discovered talus habitats within the monument, and 12 of 19 talus areas in adjoining Dixie National Forest; thus, regional occupancy was 53.8% (Beever et al. 2016a).

California Mountains

In the early 20th century, Joseph Grinnell and colleagues at the Museum of Vertebrate Zoology, University of California, Berkeley, conducted extensive surveys in the mountains of California, and these sites serve as historic localities for comparisons with modern surveys to determine potential climate change impacts. Moritz et al. (2008) reported the current status of pikas in Yosemite National Park, California, compared with Grinnell’s baseline observations. A single small (0.6 ha) historical site at low elevation (2,380 m) at Glen Aulin initially was classified as vacant, but subsequently found to be...
occupied (J. L. Patton, Museum of Vertebrate Zoology, U.C. Berkeley, pers. comm.). Although their sampling approach for pikas precluded from testing whether elevation was a significant predictor of occupancy, this paper (Moritz et al. 2008) has been cited widely and inappropriately as a demonstration of the negative effect of climate on pikas. Evidence for a range shift by pikas in California mountains was later addressed by Rowe et al. (2015), who expanded the comparison of modern versus historical Grinnell-era data on mammals to include Lassen, Yosemite, Kings Canyon, and Sequoia National Parks, California. They concluded that pikas exhibited no significant range limit shifts due to climate change; elevational ranges of the pika were stable across each of these regions.

Additional surveys have explored the occurrence and potential response of pikas to climate change in the mountains of California. Millar and Westfall (2010) identified and surveyed 329 habitats conducive to pika occupancy in the central Sierra Nevada; 98% were occupied, and the remaining 2% contained old pika sign. Occupied sites were predominantly characterized by RIF (rock-ice-feature) till landforms, contained diverse vegetation associations, and had a wide range of climatic conditions (Millar and Westfall 2010).

Stewart and Wright (2012) and Stewart et al. (2015) recensused 67 historical sites across the mountains of California, including sites within the Sierra Nevada, Lassen, and Mt. Shasta regions. All 19 sites in the central Sierra region (some of which presumably duplicated the survey of Moritz et al. 2008) were occupied (Stewart et al. 2015). Of 18 unique sites in the northern Sierra, 16 (89%) were occupied (only 17 sites were reported in Stewart et al. 2015). The two sites from which pikas had been extirpated each were very small (Stewart and Wright 2012). Stewart and Wright (2012) detected no strong climate signal in this region. Thirteen sites were recensused in the Lassen region; an unknown number of these duplicated the surveys included in Rowe et al. (2015). Pikas had been extirpated from two sites; regional occupancy thus was 84.6% (Stewart et al. 2015). Nine historic sites have been censused for pika occupancy in the vicinity of Mt. Shasta, northern California, eight of which (88.8%) were occupied (Stewart et al. 2015; Beever et al. 2016a).

Northern Cascade Mountains and Coastal Ranges

While there are no comparisons with historic location data in this region, Castillo et al. (2014) describe widespread occupancy of pikas in Crater Lake National Park, Oregon. Manning and Hagar (2011) documented that pikas have a greater distribution along the western slope of the Cascades of central Oregon than previously recognized. They documented 42 new occupied pika sites, most of which were found at relatively low elevations and in anthropogenic (roadside riprap and quarry) habitats.

In Washington’s North Cascades National Park, Bruggeman (2010) found active pika presence in 85/99 (85.8%) sites with current or old pika sign, and pika presence at a subset of these sites remained high through 2016 (Johnston et al. 2019). Two studies document current pika occupancy in British Columbia. Waterhouse et al. (2017) and Blair (2019) monitored 174 pikas on relatively dry natural (n = 7) and anthropogenic (mine ore dump; n = 8) habitats in the southern interior of British Columbia, where temperatures ranged from average maximum highs in July of 34°C to average minimum lows in winter of −9.1°C. At the northern distributional limit of the species in the coastal mountains of British Columbia, Henry and Russello (2013) sampled pikas from 10 populations from sea level to 1,500 m—and a corresponding gradient of 6°C in mean summer temperatures.

Volcanic Sites

Pikas also inhabit several distinctly different localities from the more typical montane talus habitat occupied throughout the species range. These sites are hotter, drier, found at lower elevation, and consist of atypical rock and talus habitat. Ranging from 2,092 to 2,565 m, various sites in the Mono and Inyo Crater region of eastern California were surveyed from 2009 to 2015 (Smith et al. 2016). Here the habitat resembles a moonscape, consisting of gray rhyolite pumice, obsidian, and solidified lava. Mean ambient shade temperature at the southern end of the Mono Craters in July was 25.4°C (Millar et al. 2014b), shade temperatures on the talus surface were consistently >30°C and commonly approached or exceeded 40°C (Millar et al. 2016; Smith et al. 2016). Several localities had active pika populations in each year surveyed, some showed signs of occupancy in some but not all years, and one site—Wilson Butte, midway between Mono and Inyo Craters—was devoid of pikas or any old pika sign in spite of its suitable habitat (Smith et al. 2016).

At Craters of the Moon National Monument and Preserve, Idaho, the habitat is comprised of two types of basalt lava flows (a’a, characterized by blocks of rough lava, and pahoehoe, characterized by smooth, undulating lava) that span an elevation gradient from 1,301 to 1,985 m. Maximum summer temperature averages 29°C (Camp et al. 2020). Beever (2002) found pikas at nine of 16 (56%) sites surveyed and five of nine (62%) historic sites in the preserve. Subsequent surveys detected pikas in 45 of 145 sites (31%), predominantly in areas with pahoehoe lava and above 1,605 m (Rodhouse et al. 2010). At Lava Beds National Monument in northeastern California, elevation 1,454 m, pikas inhabit both lava caves and noncave habitat. Here maximum temperatures in July average 29.3°C (Ray et al. 2016). Beever (2002) detected pikas at eight of 12 (67%) sites surveyed; four of five (80%) historic sites were occupied. Ray et al. (2016) found a pika occupancy rate of 45% from surveys of 143 randomly selected sites. Pika occupancy was similarly low in the four main lava formations at Newberry National Volcanic Monument, Oregon, base elevation 1,417 m. Temperature during the growing season averages 38.1°C. Here pikas were detected at 37 of 146 sites (26%). Rate of detections increased with elevation and tended to occur in the most complicated lava formations (Shinderman 2015).

Great Basin

In contrast to the large cordilleras that support continuous pika habitat, the Great Basin provides a unique network of 635 small
and isolated mountain ranges separated by basins that pikas cannot traverse under current conditions. Compared to the high level of pika occupancy throughout most of the species range, like a hole in a doughnut, pika occupancy in the hydrographic Great Basin appears to be more compromised. Understanding the distribution and biology of pikas in this region may help us understand the response of pikas in other regions when confronted with climate change.

Range-wide survey.—A recent overarching analysis compiled all available records and provided additional new locations to inform the pattern of pika distribution in the Great Basin region (Millar et al. 2018). This analysis included observations from 40 mountain ranges, spanned 2,378 m in elevation (1,631–4,009 m), and encompassed three of the five recognized pika subspecies (Hafner and Smith 2010). We compiled 3,250 site records based on published literature and unpublished inventories dated from 2005 or later. Of these, 2,387 sites (73.4%) were occupied, 89 sites (2.7%) were documented as extirpated since 2005, and 774 sites (23.8%) contained only old pika sign (Millar et al. 2018). Full documentation for each site is presented in three appendices, including the data source for each site (California, Nevada, and Utah, state wildlife databases, unique observations by authors, and published literature—Millar et al. 2018). Key sources among the supporting literature included Galbreath et al. (2009), Millar and Westfall (2010), Beever et al. (2011, 2016a), Wilkening et al. (2011), Collins and Bauman (2012), Millar et al. (2013a), Stewart et al. (2015), Castillo et al. (2016), Nichols et al. (2016), and Jeffress et al. (2017). Due to the large number of sources in this compilation and the fact that some extirpated or old sites were censused only once, the percent loss in the region may be an overestimate (Millar et al. 2018). Recently Stewart et al. (2017) added an additional 21 occupied and 16 recently extirpated sites from the western Great Basin; 10 of the extirpated sites were small, with talus areas ranging from 0.7 to 3.5 ha.

The large number of pika extant, extirpated, and old-sign, sites across the Great Basin documented by Millar et al. (2018) allowed a robust evaluation of how climatic features (temperature and precipitation determined from the PRISM climate model) may have affected pika occupancy. While there were differences in climate values across six subregions of the Great Basin, for all extant sites the model expanded the range of both temperature and precipitation values compared with most other regions across the range of the species (Millar et al. 2018). Further, sites from which pikas have been extirpated and sites with old pika sign only mostly were found within the geographic and climatic space of extant sites, albeit often in warmer and drier portions (Millar et al. 2018: Fig. 1). Some sites with extant populations, however, were warmer, drier, or occurred at lower elevation than sites that no longer contained pikas. These data indicate that nonclimatic factors also have contributed to observed population losses, and that pikas are “able to tolerate a broader set of habitat conditions than previously understood” (Millar et al. 2018:1). Our analysis did not include inspection of what those other conditions could be, nor did we evaluate talus patch size or aspects of connectivity. Interestingly, many sites in the Great Basin where pikas are no longer found were concentrated in a few regions where pikas may be particularly vulnerable, for example,
northeastern California/northwestern Oregon (Beever et al. 2011, 2016a; Collins and Bauman 2012; Jeffress et al. 2017; Millar et al. 2018), and the Bodie Plateau (Nichols et al. 2016; Millar et al. 2018).

Historical site resurveys.—Additional understanding of conditions promoting occupancy or extirpation of pika populations in the Great Basin follows from a series of studies on a small number of sites with historically documented presence of pikas (Beever et al. 2003, 2010, 2011, 2013, 2016a; Wilkening et al. 2011, 2019; Ray et al. 2012). These studies merit special consideration as they have contributed significantly to the narrative that pikas are imperiled due to impending climate change. Beever et al. (2003) surveyed 25 sites, and subsequently included a 26th site (Hays Canyon—Beever et al. 2008). These investigations were designed to resurvey known pika localities reported from early 20th century records. Unfortunately, this means that the sites are not representative of the full distribution of pikas in the Great Basin; they represent a narrower geographic distribution and a bias toward lower elevations than the comprehensive data set in Millar et al. (2018). It also is possible that elevations reported on voucher specimens of pikas reflected campsite locations, which might have been lower than the actual collection locality (Beever et al. 2011). In addition, identification of one of these sites (Peterson Creek: 39.19°N; −118.30°W) in Beever et al. (2003:Appendix I; repeated in Beever et al. 2011:Appendix V and in Wilkening et al. 2011:Appendix I) places the locality in the middle of a desert playa far from any talus, and ~50 km west of and approximately 1,280 m lower in elevation than the true site (39.1594°N; −117.4802°W—Millar et al. 2018). If these coordinates were used to inform any climate models such as PRISM, the conditions found at the significantly lower site could have biased subsequent statistical analyses, given the small number of sites. Also, as cautioned by Fournier et al. (2019:1371): “…when researchers revisit historically known populations but do not search for new populations, local extinctions can be documented but newly founded populations cannot.”

In the initial 1990’s surveys, six (24%) historic sites were reported as extirpated (Beever et al. 2003 noted seven extirpations, although subsequently one of these sites was found to have a robust population—Beever et al. 2010). Surveys undertaken in the early 2000s documented an additional three extirpations (Beever et al. 2010, 2011), elevating to 34.6% (9/26) the prevalence of extirpations at the historic sites. Beever et al. (2011) listed a 10th site, Pinchot Creek, as being “functionally extirpated,” although that site is not considered extirpated in Wilkening et al. (2011). I treat this site as extant in Appendix I. Because the small number of sites means that each documented extirpation in these studies carries significant weight in subsequent analyses, it is important to understand the environmental attributes of each site. Extensive direct human disturbance was noted at three of the nine sites of extirpated pika populations (at one site, half of the talus area had been excavated and used as a “borrow pit” for road maintenance; a second site had been used extensively as a dump; and a third site was scattered with gun shell casings—Beever et al. 2003), making it difficult to conclusively determine the mechanisms responsible for population extirpation.

Influence of livestock grazing.—Significant grazing activity was observed at seven of the nine sites of pika extirpation (Beever et al. 2003, 2011). Grazing could negatively impact pika populations by severely reducing available forage near the lower talus edge of a pika’s talus habitat where they prefer to forage for food and gather vegetation for their haypiles (Hafner and Sullivan 1995; Millar 2011). Ray et al. (2012) found that pika density was lower at grazed sites with smaller talus patches. Millar (2011) found that where vegetation in the forefield adjacent to talus was grazed, pika haypiles were located much higher in the talus (x = 30.1 m upslope compared with a mean of 1.8 m upslope in ungrazed areas). As highlighted by Hafner and Sullivan (1995):

…pikas in summer-drought regions are more vulnerable to adverse human impact, particularly over-grazing by livestock. … Pikas are more dependent upon the often-narrow band of vegetation, that itself depends on runoff from the talus slope. Competition with domestic livestock for that critical vegetation, particularly during drought years, could result in immediate and widespread extinction of local populations and, yet, leave little evidence if followed by a wetter year.

Beever et al. (2011) concluded that anthropogenic influences were not important factors leading to documented extirpations of pika populations in their investigations, failing to mention that a third of all pika-extirpated sites were heavily impacted by humans (evidenced by shotgun shells, etc.), and that most extirpated sites also were grazed by livestock.

Influence of habitat size.—Compared with occupied sites, sites from which pikas had been extirpated were smaller, more isolated, and located at lower, hotter elevations (Beever et al. 2003). While talus patch size is not presented in Beever et al. (2003) or in subsequent papers, the talus area within a 0.8-km radius of historic sites was described as small, medium, or large. Only five sites were classified as “small,” and four of these were sites from which pikas had been extirpated (Beever et al. 2003). Five sites were considered isolated (not found in a mountain range), and four of these were sites of extirpation. Amount of talus at the mountain-range scale was the strongest univariate predictor of persistence within the suite of historical sites (Beever et al. 2003).

Influence of temperature.—Surveys in the 2000s incorporated data from sensors (mini-thermochrons) placed to measure talus surface and subsurface temperatures (Beever et al. 2010, 2011; Wilkening et al. 2011; Ray et al. 2012). Analysis of climate metrics differentiated a pattern of persistence between occupied and unoccupied sites. Daily temperatures exceeding 28°C were more common (9 days more on average) at sites of pika extirpation than sites with extant pika populations, and average summer temperature (5.7°C higher at extirpated than extant pika population sites) was a strong predictor of pika population persistence (Beever et al.
Sites with extant pika populations were more likely to experience continuous snow cover in winter than sites with extirpated populations, thus providing resident pikas with an insulating blanket for much of the winter (Beever et al. 2011; Ray et al. 2012), although Wilkening et al. (2011) found less support for this hypothesis from the same data set.

The above climate metrics, however, were not consistent (see Fig. 1). For example, the talus matrix temperatures at the extirpated Duffer Peak site were several degrees cooler than at extant sites (Beever et al. 2010; Wilkening et al. 2011; Jeffress et al. 2017), whereas the high mean summer temperature at the occupied Hays Canyon site led Beever et al. (2008:11) to claim “…temperature is not a perfect predictor of persistence.” Jeffress et al. (2017:265–266), working in the northwest Great Basin concluded that “…no single variable distinguished currently occupied sites from relict sites” and that “Our results provide further evidence of the seemingly weak predictive power of thermal indices alone in many of these low-elevation and warm mountain ranges…” The local availability nearby of high-elevation talus habitat continued to be an important predictor of pika persistence in the Great Basin in many of the models evaluating this system (Beever et al. 2011; Ray et al. 2012). Similarly, the absence of probable dispersal corridors and the low elevation of mountains that could potentially serve as refugia were the leading predictors of extirpation in western Great Basin sites (Stewart et al. 2017).

Range expansion and contraction.—Comprehensive sampling upslope of historic Great Basin sites documented that the upper elevation boundaries of pika occupancy (range expansion) largely were unchanged (Beever et al. 2011). Thus, pikas were not found to be colonizing upslope habitat, as frequently claimed in media releases. The most convincing data that higher temperatures at lower elevations due to climate change could affect modern pika populations were range contractions at some sites (Beever et al. 2011)—although the magnitude of these population movements appears to be exaggerated in the data presentation. Beever et al. (2011) analyzed the changes in the lower elevational distribution of pika populations over time by comparing data from the historic record to surveys in the 1990s and 2000s. These results were calculated as the difference between the lowest occupied elevation for each paired record, then averaged by time period (data from Beever et al. 2011:Appendix V; data reproduced here in Appendix I, with modifications to include pika observations excluded by Beever et al. 2011). Beever et al. (2011:2060) concluded: “Within 10 sites at which we have detected pikas since 1999, minimum elevation of the species’ range has risen at least 145 m (mean = 364 m) since historical surveys.” This summary does not conform with the data from that study as presented in Appendix I, and it is unclear why only 10 sites are included in the above summary. In the historical to 1990s comparison: n = 15 sites (four sites occurred at a lower elevation than reported in the historic record), upslope \( \bar{x} = 51.93 \) m. In the historical to 2000s comparison: n = 14 (five sites occurred at a lower elevation than reported in the historic record), upslope \( \bar{x} = 102.14 \) (Appendix I). Beever et al. (2011) assumed that if a pika was detected at a lower elevation in a later survey, it had also occupied that elevation in earlier surveys, and adjusted the elevational data accordingly. The only possible outcomes, therefore, were no change in elevation or an upward range contraction, artificially lowering measures of central tendency. But setting downslope observation differences to zero still yields an average upslope contraction far less than claimed (Appendix I). While these computations of range contraction are interesting, the comparison of historical data with modern comprehensive surveys at best is an estimate, because it is unknown if the historical data document elevations pikas occupied at that time.

Beever et al. (2011) stated that upslope range contraction in the decade spanning the comprehensive surveys undertaken from 1999 to 2008 averaged 145.1 m compared with an upslope average of 13.3 m/decade during the 20th century. These findings have been widely cited in the media. But, comparing historic-era contractions with the modern surveys is problematic. First, baseline lower elevation data for the historical records are approximate. Second, data presented in Beever et al. (2011; see Appendix I) indicated that only 10 of 16 populations demonstrated upslope contractions, and the mean increase in elevation among all occupied sites was 55.0 m ± 69.88 SD (or 69.9 m if all 2008 downslope observation differences are set to 0). The overall mean elevation increase in 2008 compared with the 1990s was 17 m (Appendix I). Although some pika populations in this environment moved upward from the previous lowest level observed, the magnitude of this shift is variable among populations and the mean value is considerably lower than claimed in Beever et al. (2011).

**Characteristics of Pikas in Stressful Environments**

Our understanding of the current distribution and local abundance of American pika populations is contingent on a thorough understanding of the natural history of the species, notably missing from most of the contemporary work on pikas involving regional surveys. The dynamics of pika populations, particularly in stressful environments, influence the degree to which pikas are resilient in the face of environmental change.

**Metapopulation dynamics.**—Pikas occur in disjunct habitats at several different spatial scales, from mountain chains, to widely dispersed talus habitats (in mountains or in nonmontane areas), to small talus patches clustered within a local area. Although studies conducted at each of these scales have identified pikas as a species with metapopulation structure (cf. Hafner 1994; Hafner and Sullivan 1995; Beever et al. 2003), only the local patch scale contains characteristics of a classic metapopulation. Classic metapopulations include the following components: 1) a species that lives in spatially distinct habitat patches scattered across an open landscape; 2) all local populations are small and have a significant risk of extirpation (patch extinction); 3) dispersal among patches appears to be distance-dependent; and 4) the dynamics of local populations appear to be asynchronous (Hanski 1999). The interplay of
these elements determine the frequency of patch turnover and the resulting pattern of patch occupancy across the landscape. Pikas living on ore dumps at the abandoned mining town of Bodie, California (~2,550 m and only 30 km east of the Sierra Nevada escarpment), meet the conditions of a classic metapopulation. I investigated this metapopulation from 1969 to 2010 (Smith 1974a, 1974b, 1980; Peacock and Smith 1997a; Smith and Gilpin 1997; Moilanen et al. 1998; Smith and Nagy 2015; White and Smith 2018). The relatively small ore dump patches varied in size and spacing across a sea of Great Basin sage vegetation, and offered a natural laboratory in which to investigate metapopulation dynamics (Smith and Gilpin 1997; Smith and Nagy 2015; White and Smith 2018).

The climate at Bodie ranges from extreme cold (~30°C) and deep snow in winter (Smith and Millar 2018) to hot summers. Smith and Nagy (2015) present summer climate records from 1895 to 2010 (84 years with complete temperature records for June, July, and August; Figs. 2 and 3). Over this interval the average monthly maximum temperature in summer months increased approximately 1°C, and within each month there was considerable variability among years throughout the record (Fig. 2). Similarly, the number of extreme hot days (≥ 25°C or ≥ 28°C) within a summer varied greatly among years (Fig. 3).

Pikas apparently colonized the anthropogenic ore dumps from nearby lava rock outcrops sometime before 1900. They were first studied in the late 1940s by Severaid (1955), who noted, based on sign, that pikas had at one time occupied all available ore dump patches. He further clarified (Severaid 1955:150) that “the average stable population was never equal to the carrying capacity of the habitat.” Severaid (1955) also removed all pikas from select ore dumps and determined that they were very slow to recolonize these areas.

In 1972 I conducted my first comprehensive survey of pika occupancy on 76 ore dumps across the Bodie landscape. The ore dumps were relatively uniform in structure; thus, my measure of size was the perimeter in meters of each patch: small (n = 45, perimeter ≤ 75 m, potential habitat for 1–3 pikas); medium (n = 17, 76–150 m, 4–6 pikas); and large (n = 14, ≥ 151 m, seven or more pikas). Like Severaid, I found that, based on sign, pikas had at one time occupied all 76 patches, but that they currently occupied only 60% of available patches; most patches contained fewer individuals than the patch carrying capacity (Smith 1974a). Small patches and those at distances greater than 300 m from occupied ore dumps were most likely to be unoccupied. I repeated the Bodie pika census in 1977 with a similar result: 58% of the ore dumps were occupied, and small and isolated habitat patches were again those most likely to be unoccupied. Interestingly, significant turnover had occurred in this 5-year interval between censuses. Populations on 11 patches went extinct, and eight previously unoccupied patches were recolonized (Smith 1978). The Bodie metapopulation appeared to represent a dynamic equilibrium between patch extinction (inversely related to patch size) and recolonization (inversely related to patch isolation—Smith 1974a, 1978).

We initiated a series of annual or biannual censuses of the Bodie metapopulation in 1989, and a profound difference was found. The spatial configuration of the study area is roughly a figure-eight, with a constriction in the middle, and the southern constellation of ore dumps appeared to be on the verge of collapse. The number of occupied ore dumps (and of active pika territories) in the southern constellation was greatly reduced compared with the two earlier surveys (Smith and Gilpin 1997; Moilanen et al. 1998). The pika population in the southern constellation of ore dumps continued to decline for several years, with only a small number of patches occupied each year, until 2006 when we recorded the last pika in that region (Smith and Nagy 2015). Meanwhile, the pattern of occupancy in the northern constellation of patches, while variable from year to year, was unchanged; in fact, the documented number of pikas in the north in our 2009 and 2010 surveys exceeded the number of pikas counted in the north in 1972 or 1977 (Smith and Nagy 2015). Finally, the number of pika extinctions and recolonization events on patches was highly variable from year to year, but overall nearly equivalent during the time span from 1989 to 2010; in this interval we tallied 114 patch extinctions and 109 recolonizations (Smith and Nagy 2015: Fig. 4).

Two questions arose from the results of the Bodie pika metapopulation study: why did the southern constellation of pikas become extirpated while populations in the north remained healthy, and could climate change explain this outcome? First, extinctions happen at the local scale, and many of the extinctions we tallied were on ore dumps larger than some of the site extinctions highlighted in the preceding section (cf. Beever et al. 2011; Stewart et al. 2015, 2017) that have been attributed to climate change. Second, many lines of evidence argue against climate being a force leading to extirpation of the southern constellation of ore dumps at Bodie (although Stewart et al. 2015 treat Bodie south as a climate extinction). The straight-line distance from the two most distal ore dumps censused at Bodie is 3 km; thus, most patches are even closer together. Climate could not differ so significantly over this spatial scale to explain such a disparate pattern of occupancy. The collapse of the southern patches also did not happen all at once—it was a drawn out affair from 1989 to 2006; an extremely hot summer or an exceptionally hot day could not be responsible for the observed result (this also rules out an epidemic—Smith and Gilpin 1997). Further, we tested the hypotheses that years with higher extinction rates (see Fig. 4) would be correlated with warmer weather (average daily high temperature or number of extremely hot days), and that recolonizations would be correlated with cooler weather, and found no significant results (Smith and Nagy 2015). Finally, the loss of the southern constellation of ore dumps is a recent event, yet the long-term climate data (Figs. 2 and 3) show that several periods earlier in the 20th century were just as hot as during the modern period. But occupancy data from Severaid’s investigations in the 1940s through to my 1970s investigations show no pattern of decline in the south.

Three very different models have explored the issue of the extirpation of the southern constellation of pikas at Bodie (Smith and Gilpin 1997; Moilanen et al. 1998; White and Smith 2018). All three approaches concluded that this pattern resulted...
Fig. 2.—Average monthly high temperatures at Bodie, California, from 1985 to 2010. A) June, B) July, and C) August (from Smith and Nagy 2015).
Fig. 3.—Number of threshold maximum daily temperatures at Bodie, California, from 1985 to 2010. A) number of days ≥ 25°C, and B) number of days ≥ 28°C (from Smith and Nagy 2015).
from a regional extension of the spatial autocorrelation among patches exhibited in earlier censuses. The most precise model, that of White and Smith (2018), suggests that the specific configuration of habitat and landscape heterogeneity both are necessary and sufficient predictors of the eventual extirpation of the southern constellation. This model predicts that the probability of the entire Bodie population going extinct over the next 100 years is relatively low, but that in isolation, the southern population would go extinct in two decades—strikingly similar to what we observed (White and Smith 2018).

The biological feature implicit in these models is that pikas are poor dispersers. The original surveys concluded that pikas were unlikely to disperse long distances, particularly in a hot and hostile environment such as that found at Bodie (Smith 1974a, 1974b, 1980). Subsequent studies with marked animals demonstrated that adults were highly reluctant to disperse (see below). Thus, even if the southern constellation at Bodie did not become extirpated due to direct climate change effects, today’s warmer temperatures could impede potential dispersal from north to south and thereby contribute to the overall loss of pikas in the Bodie metapopulation (Smith and Nagy 2015).

Behavioral ecology.—Observing how populations behaviorally adapt to stressful environments is the most direct approach to understanding their ability to cope with changing environmental conditions (Beever et al. 2016b, 2017). The following case studies highlight significant differences in the ecology and behavior of pikas living in stressful or atypical environments, compared with pika populations living at cool, high-elevation sites. These studies also document that features traditionally used to census pikas (activity, vocalizations, haypiles, latrines) may be compromised or lacking in some of these areas, thus making detectability of the presence of pikas more difficult. The three low, hot sites are: 1) Bodie (Smith and Nagy 2015); 2) Mono Craters (Smith et al. 2016); and 3) Craters of the Moon National Monument and Preserve (Camp et al. 2020). At the Mono Craters site, despite surface temperatures that commonly approached or exceeded 40°C, matrix temperatures (taken approximately 1 m deep in the talus) averaged 8°C lower during the hottest part of the day (Smith et al. 2016). At Craters of the Moon, mean surface temperature was significantly warmer than mean subsurface (crevice) temperature during midday and evening (Camp et al. 2020).

Pikas generally avoid high environmental temperatures such as those encountered in summer at the Bodie, Mono Craters, and Craters of the Moon sites. I measured pika activity by counting the number of pikas seen on standardized semihourly transects at Bodie, and compared these findings with a similar protocol at a high-elevation site in late summer (Fig. 5). Bodie
Fig. 5.—Activity of American pikas (*Ochotona princeps*) throughout the day at different elevations and seasons in relation to ambient temperature. Low-elevation data are from Bodie, California (2,550 m), high-elevation data from Kuna Lake, California (3,350 m). Solid lines = shade temperature; dashed lines = black-bulb temperature (from Smith 1974b).
pikas were essentially inactive during the hot midday hours in August, but were active throughout the day along the same transect the following May when it was cooler. In summer, pikas at a cooler high-elevation site in the Sierra Nevada were active throughout the day (Smith 1974b; Fig. 5). I also compared the relationship between ambient temperature and the percentage of time individual pikas were active. Due to the hot midday temperatures at Bodie, there were highly significant negative relationships between temperature and pika activity during both August ($r = -0.78; P < 0.001$) and September ($r = -0.63; P < 0.001$). At the high-altitude site, pikas showed some inhibition of activity in August when temperatures were warm during midday ($r = -0.29; P < 0.05$), but this difference was not significant in September when it was cooler (Smith 1974b). Pika activity at Mono Craters was similarly depressed during the hot midday hours, and pikas were most active in the early morning and late afternoon (Smith et al. 2016).

As Craters of the Moon, pika activity decreased as surface temperature increased, and again, activity was highest during the morning and evening (Camp et al. 2020). Camp et al. (2020) compared their results at Craters of the Moon with a nearby high-elevation typical pika population at Grays Peak. Surface temperature at Grays Peak had no influence on aboveground pika activity, and pikas there were most active in the morning, but equally active in midday and late afternoon (Camp et al. 2020).

The overall level of diurnal activity of pikas therefore is reduced at low hot sites compared with cooler sites at high elevation. There were fewer detections of pikas per hour at Bodie than at Lost Lake in the nearby Sierra Nevada for all observed behaviors (e.g., vocalizations, locomotion, surveillance—Smith et al. 2016). At Mono Craters, pikas were observed in only 10.3% of all minutes of focal animal observation, whereas in the nearby High Sierra they were observed 36% of the time (Smith et al. 2016). During June, July, and August, there were significantly fewer detections of pikas/hour for all time periods at Craters of the Moon compared with the high-elevation Grays Peak site (Camp et al. 2020). Pikas at Craters of the Moon were observed during only 7% of observation minutes, compared with 33% of observation minutes at Grays Peak. Similarly, the frequency of vocalizations was nearly three times greater at Grays Peak (7.85 calls/h) than at Craters of the Moon (2.89 calls/h—Camp et al. 2020).

While it has been assumed that pikas are primarily active during the day, they also can be active at night. I have observed Bodie pikas feeding, calling, and running about in the middle of the night under a full moon (Smith 1974b). Pikas at the Mono Craters site exhibited activity rates at night comparable to those for morning and late afternoon (Smith et al. 2016), and pikas at Craters of the Moon were more nocturnal than at the higher elevation Grays Peak site (Camp et al. 2020). Hall and Chalfoun (2019) also have documented nocturnal pika activity in the Rocky Mountains in Wyoming. Recent camera trap data in the Sierra Nevada, Bodie Mountains, and Mono Craters further confirm that nocturnal activity is a characteristic of American pikas, even those that live at high elevations (C. I. Millar, US Forest Service, and K. T. Hickman, pers. comm.). Millar and Hickman found that significant pika activity in the Sierra Nevada could occur at night; one high-elevation pika was nocturnally active 36% of the time from June to October.

Foraging is the most distinctive behavior of American pikas, and the significant differences between pika foraging behaviors at hot, low-elevation sites and cooler, higher elevation sites facilitate our understanding of the response of pikas to environmental change (Table 1). Pikas at Bodie, the Mono Craters, and Craters of the Moon, all have been observed to feed at lower rates than at nearby high-elevation sites (Table 1). Pikas at the Mono Craters and Craters of the Moon engaged in very low rates of haying compared with pikas at nearby high-elevation sites (Table 1). Half of all haying trips at Mono were performed by one of the nine pikas in the study population; many other individuals never left the talus to gather hay. The vegetation at Mono was sparse or even absent in the forefield of several territories. Pikas at Mono primarily foraged on widely dispersed shrubs on the steep talus (Smith et al. 2016).

The product of haying behavior is a large cache of vegetation (the haypile), a dominant feature of a pika’s territory (Millar and Zwickel 1972a; Conner 1983; Dearing 1997). Bodie pikas construct huge haypiles, similar to those found at high-elevation sites. In contrast, haypiles at Craters of the Moon were cryptic, and although most individuals constructed

<table>
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<tr>
<th>Behavior</th>
<th>Elevation</th>
<th>Rate per hour</th>
<th>Region</th>
<th>Source</th>
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<tbody>
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<td>Feeding</td>
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<td>1.31</td>
<td>Bodie, California</td>
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<td></td>
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<td>0.73</td>
<td>Mono Craters, California</td>
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<td>0.27</td>
<td>Craters of the Moon, Idaho</td>
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<td>Sierra Nevada, California</td>
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<td>Grays Peak, Idaho</td>
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<td>2.62</td>
<td>Grays Peak, Idaho</td>
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one to three haypiles, one pika scatter-hoarded vegetation to 12 different locations (Camp et al. 2020). Similarly, haypiles rarely were detected during multiple surveys at Lava Beds National Monument (Beever et al. 2008). All Mono Craters pikas scatter-hoarded and none constructed a central-place haypile, the norm for most pikas. I have observed the Mono study site annually since 2009, and only one typical haypile was constructed during that time, although haypiles are present in other sites in the Mono Craters.

The xerophytic vegetation consumed and collected by pikas at the Bodie, Mono Craters, and Craters of the Moon sites is distinctively different from that found in typical alpine or subalpine pika habitats. Bodie haypiles almost totally consisted of dominant Great Basin vegetation (big sagebrush *Artemisia tridentata*, bitterbrush *Purshia tridentata*, and gray rabbitbrush *Ericameria nauseosa*—Smith 1974b). The diet of pikas at the Mono Craters consisted primarily of gray rabbitbrush, oceanspray (*Holodiscus discolor*), currants (*Ribes* spp.), and Sierra angelica (*Angelica lineariloba*), most of which were widely distributed across the talus (Smith et al. 2016). Camp et al. (2020) documented that fernbush (*Chamaebatiaria miliifolium*), cushion buckwheat (*Eriogonum olivilium*), sticky cinquefoil (*Potentilla glandulosa*), and scabland beardtongue (*Pensetemnon deustus*) were the dominant plants used by pikas at Craters of the Moon.

There also are interesting comparisons of pika territoriality among these low-elevation sites, and between these sites and high-elevation pika populations. Pika territoriality at Bodie was similar in most respects to characteristics of pikas living at high elevation. Bodie pikas constructed single large haypiles close to the ore dump/vegetation interface, frequented favored sites within their territory where they deposited cones of their round fecal pellets (latrines), and vocalized frequently (Smith 1974b; Smith et al. 2016).

Territories were uncharacteristically large at the Mono Craters site (Smith et al. 2016). Mono pikas did not construct characteristic haypiles, so it was difficult to identify centers of individual activity. In addition, Mono pikas did not favor sitting on specific rocks and thus did not accumulate distinctive hard pellet latrines; behaviors indicative of territory defense (aggression, cheek rubbing) were rare (Smith et al. 2016).

Pikas at Craters of the Moon displayed poorly defined terri-


toricality and consequently used larger areas than pikas in typ-
ical alpine habitats, although the disruptive nature of the lava habitat made it difficult to quantify territory size (Camp et al. 2020). Behaviors indicative of territorial defense were rare: aggression never was observed, cheek rubbing was seen only once, and vocalizations were uncommon. Each of these behaviors occurred more frequently at the nearby high-elevation Grays Peak site (Camp et al. 2020).

Another atypical pika population occurs near sea level in the Columbia River Gorge, Oregon (Horsefall 1925). Here pika ecology is distinctly different from that of more montane pikas in that they spend more time consuming vegetation and less time building large haypiles (Varner et al. 2016). Moss, which is available year-round, comprises more than 60% of their diet—more than any other wild mammalian herbivore (Varner and Dearing 2014a). The high availability of moss also allows the Columbia River Gorge pikas to defend the smallest territo-


dies of any American pika population. In spite of the resulting increase in density, territorial behaviors (aggression and cheek rubbing) were rare, accounting for < 0.1% of all observations (Varner et al. 2016). Pikas at this site also frequently used the surrounding shaded moist forest as a thermal refugia (38.6% of midday detections—Varner et al. 2016).

### A Trait-Based Approach to Assessing Pika Vulnerability to Climate Change

Three approaches address the ability to measure vulnerability of a species to climate change: correlative, mechanistic, and trait-based (Foden and Young 2016). Correlative approaches estimate current climatic conditions for a species and then use future climatic models to predict potential regions that could be occupied by that species. Correlative approaches, also known as niche-based or species distribution models, are problematic for a variety of reasons (Franklin 2013; Foden and Young 2016). First, the methodology ignores possible impacts other than climate change. Second, this approach does not consider biological traits or microclimates, both known to play an important role in shaping the capacity of a species to behaviorally adapt to climate change (Millar et al. 2016). Third, MaxEnt modeling, used in most species distribution models, may mischaracterize the range of a species (Franklin 2013; Foden and Young 2016). Each of these issues influences projections of future environments that could be occupied by pikas (e.g., Galbreath et al. 2009; Calkins et al. 2012) thus resulting in misleading (exaggerated) predictions of future pika decline.

Mechanistic approaches aim explicitly to incorporate known biological processes and thresholds, and require extensive field and laboratory experimentation (Foden and Young 2016). Based on pika temperature thresholds (see below), Mathewson et al. (2017) provided mechanistic predictive models of the species’ past, current, and future climates. Their models closely matched the paleontological distribution of pikas; however, they only approximated their current distribution, failing to pre-
dict the occurrence of pikas at Craters of the Moon, Lava Beds National Monument, Newberry National Volcanic Monument, or along the Columbia River Gorge (Mathewson et al. 2017).

Trait-based approaches use the biological characteristics of a species to estimate its sensitivity and adaptive capacity to climate change, typically combining these with estimates of the extent of the species’ exposure to climate change (Foden and Young 2016). Because of our current understanding of the ecology of pikas, a trait-based approach appears best suited to interpreting pikas’ relationship with climate change, as presented below.

**Vulnerability to hot temperature.**—Climate change may directly impact pikas by physiologically stressing them when ambient temperatures exceed the species’ tolerance (e.g., Foden and Young 2016). Pikas maintain a relatively high body
temperature (> 40°C) over a wide range of ambient temperatures (MacArthur and Wang 1973; Smith 1974b). Due to their thick fur, pikas also have a relatively high basal metabolic rate coupled with a low thermal conductance (MacArthur and Wang 1973; Smith 1974b; Otto et al. 2015). These factors prevent dissipation of metabolic heat and cause thermal stress at modestly warm environmental temperatures. Two field experiments have tested the response of pikas to warming temperatures. In Alberta, two pikas died in metabolic chambers after exposure for 2 h at temperatures of 28-30°C (MacArthur and Wang 1973). In 1970 I conducted a series of experiments in which pikas were trapped at dawn and confined in large outside wire-mesh cages provisioned with fresh green vegetation and a rock to sit on. At a high-elevation site in the Sierra Nevada two pikas survived a full day confined in the sun with ambient shade temperatures reaching 17.2°C. At the low-elevation Bodie site, the initial ambient temperature of 17°C rose gradually throughout the morning; each animal died at 1230 h when ambient temperature reached 29.4°C and 25.5°C, respectively (Smith 1974b).

These cage experiments demonstrate that when pikas are deprived of their behavioral mechanisms for avoiding high temperatures and are exposed to direct solar radiation, they are unable to regulate their temperature physiologically (Smith 1974b). Pikas typically accommodate to high temperatures by behaviorally retreating into the interstices of the talus where they cool down. This behavior results in a bimodal activity profile, with pikas primarily being active in the morning or late afternoon, a response that becomes even more exaggerated as ambient temperatures increase (Fig. 5; MacArthur and Wang 1974; Smith 1974b; Otto 2015). The results of the cage experiments are consistently misinterpreted in press releases concerning pikas and climate change. Press releases state that pikas die at temperatures as low as 77°F (25°C), but fail to mention that the animals in the study were confined and unable to behaviorally thermoregulate by retreating into the talus.

The degree to which hot temperatures (either mean summer maximum temperatures or the number of days the temperature exceeds a hot threshold such as 28°C) have led to extirpation of pika populations is unclear. All status surveys conducted in core pika habitat throughout the intermontane west indicated that no climate signal could differentiate successfully between occupied and unoccupied sites. The meta-analysis by Millar et al. (2018) similarly found that climate failed to differentiate between occupied and previously occupied sites in the Great Basin. Furthermore, models presented by Beever et al. (2010, 2011), Wilkening et al. (2011), and Ray et al. (2012) evaluating pika presence and absence on historic sites in the Great Basin found that elevated temperatures were not consistently the top performing variables. The strongest case for how climate may adversely have affected pika persistence is the demonstration of upslope contraction in some of the historic Great Basin populations (Beever et al. 2011; see also Grayson 2005), although as indicated above, the magnitude of this effect appears to be exaggerated.

Vulnerability to cold temperature.—Although counterintuitive, very cold temperatures could be physiologically intolerable to pikas. I suggested that pika populations might experience high density-independent mortality in years lacking sufficient snow cover to provide thermal insulation of subnivean habitats during cold winters, because of the additional energy pikas would have to expend to maintain homeostasis (Smith 1978).

As precipitation and potential snow cover have declined in the intermontane west of North America (Mote et al. 2005), this hypothesis has gained significant traction. Several studies have looked at the responses of pikas to cold by recording temperatures 1 m deep in the talus throughout the winter (Beever et al. 2011; Wilkening et al. 2011; Millar et al. 2014b; Yandow et al. 2015). When temperatures remain relatively constant at ~0°C, researchers assume the site is buffered by a blanket of snow; conversely, absence of a snowpack is assumed when temperatures plunge to negative values.

Yandow et al. (2015) found that pika abundance in the north-central Rocky Mountains could be reduced when low temperatures and weak thermal insulation occurred on a relatively high number of days. Pika density in relation to snow cover was examined by Johnston et al. (2019) in North Cascades National Park, capitalizing on the record-low snowpack during winter 2014–2015. The following summer all sites were occupied by pikas; cold exposure during the winter did not cause high mortality. Cold stress, due to a lack of insulation provided by snow, only was apparent within a narrow mid-elevation band as indicated by reduced abundance from prior years (Johnston et al. 2019).

Beever et al. (2011) compared winter snowpack between sites in the Great Basin determined to be extirpated and sites with extant pika populations. Most extirpated sites were not covered with snow for more than 2 weeks during winter, and temperatures as low as −22°C were recorded at some of these sites (Beever et al. 2011). In contrast, most extant populations “had continuous snow cover for 0.5 - 8.2 months per year” (Beever et al. 2011:9). The arbitrary threshold of 0.5 months (2 weeks) between pika extirpated and extant sites, however, means that an unknown number of the extant sites could have been uncovered by snow for much of the winter. Furthermore, Wilkening et al. (2011) analyzed the same Great Basin data set and came to a different conclusion; they found no support for the hypothesis that site extirpation results from acute cold stress during the winter.

The most direct test of the prediction that pika mortality increases during winters with little-or-no snow was given by Smith and Millar (2018). During the winter of 2014–2015, the central Sierra Nevada had the lowest snowfall in recorded history; in many areas there was no snow. We recorded the presence of fresh green haypiles to examine pika survivorship from summer 2014 (before the drought winter) to the following summers of 2015 and 2016. Pikas occupied 36 of 37 sites (97%) in 2015. To examine whether there was a cumulative effect, in 2016 we recensused 33 of the sites and found 29 (88%) occupied. The nearly total absence of snow over the winter of 2014–2015 did not precipitate unusual overwinter mortality in these Sierra Nevada pikas (Smith and Millar 2018).
**Habitat specialization.**—Species tightly coupled to particular environmental conditions are thought to be less resilient to climate change, and thus at high risk of extinction, because of the narrower range of habitat and microhabitat options available to them (Foden and Young 2016). Although pikas occupy a very specific habitat, talus is widely distributed across the range of pikas and is unlikely to degrade over time. Talus therefore is suitably abundant to support large pika populations. In addition, because pikas also occupy anthropogenic habitats such as mine ore dumps, roadside riprap, wood piles, etc. (Smith 1974a; Manning and Hagar 2011; Beever et al. 2017), total available pika habitat in North America is likely to be larger today than in the recent past.

A crucial characteristic of the talus environment is the degree to which it buffers temperature. Talus matrices in summer are cooler and have lower daily variances than hot surface temperatures during the day, and remain warmer than surface temperatures at night (Varner and Dearing 2014b; Hall et al. 2016; Millar et al. 2016; Rodhouse et al. 2017). These variations in temperature above and below the talus reveal how pikas behaviorally manage their sensitivity to high temperatures (Millar et al. 2016; Smith et al. 2016).

Not all talus is created equal. Thermal attributes of rock glaciers and periglacial talus landforms may further moderate temperatures in the talus matrix (Millar et al. 2013b; Wilkening et al. 2015). For example, a lens of permafrost lies beneath the talus at the Mono Craters site, and cool air vents reach the talus surface. This “air-conditioner” underneath the talus may help pikas cool down after exposure to hot surface temperatures and may explain how pikas persist at this hot site (Smith et al. 2015). Wilkening et al. (2015) compared pika stress levels with an assay of glucocorticoid metabolite (GCM) concentration at sites with and without subsurface ice. Pikas living at sites without subsurface ice had higher GCM levels, and thus showed higher levels of physiological stress than pikas inhabiting sites with subsurface ice (Wilkening et al. 2015).

The Dollar Lake forest fire on the north face of Mt. Hood, Oregon, in fall 2011, provided an extreme example of how talus buffers hot temperatures. Varner et al. (2015) had tagged animals and measured prefire temperatures within the talus matrix at several of their study sites, one of which was severely burned by the fire. Subsurface temperature at this site rose to 18–19°C during the fire compared to 7–14°C immediately before and after the fire, but the fire temperature fell within the thermal capacity of pikas. The four tagged animals were not seen after the fire, but the severely burned site maintained an occupancy of 83% the following spring compared with 89% before the fire (Varner et al. 2015).

**Low density species.**—Small patch sizes (containing few animals) increase extinction risk through demographic stochasticity (Diamond 1984; Lande 1988; Harrison 1991). Because pikas are individually territorial and widely spaced on their obligate talus habitat, they live at a low density compared with most other small mammals (Smith and Weston 1990). Adjacent territories of similar size tend to be occupied by individuals of the opposite sex, and this pattern persists over time (Smith and Ivins 1983a, 1984). The increased risk of stochastic extinction on small habitat patches has been well-documented in the Bodie pika metapopulation (Smith and Gilpin 1997; Smith and Nagy 2015; White and Smith 2018). The most common characteristic of reported extirpations across the range of pikas is that they occurred on small patches. For example, seven of 10 extirpated sites documented by Stewart et al. (2015) were very small (one measuring only 20 × 20 m—Stewart and Wright 2012), and what best distinguished occupied from unoccupied sites was a model that incorporated both talus area and mean summer temperature. Beever et al. (2017) reported that two of their extirpated sites had insufficient talus to support three pikas, and that fewer than 10 pikas were detected at nearly 40% of their historic sites occupied throughout the 1990s and 2000s (thus they presumably lived on small patches). Given the documented importance of the relationship of patch size to the probability of patch extinction in the long-term Bodie metapopulation study (Smith 1974a; Smith 1980; Smith and Gilpin 1997), it is notable that patch size on the 26 historic sites was not a variable considered by Beever et al. (2003, 2011).

**Poor dispersal capability.**—“Species with low dispersal rates or low potential for long distance dispersal...have lowest adaptive capacity since they are unlikely to be able to keep up with a shifting climate envelope” (Foden and Young 2016:40). Pikas are poor dispersers, particularly between habitat patches where they are at increased risk of predation and of overheating because they cannot retreat to the cool interstices of the talus to behaviorally thermoregulate (Smith 1987). The vulnerability of pikas during dispersal thus intensifies with increasing temperatures, such as found at low-elevation sites or with climate change (Smith 1974a; Millar et al. 2016). Juveniles are the predominant dispersers in pikas, and most dispersal occurs in late summer following their weaning and subsequent independence; adult dispersal within or between patches is rare (Smith 1987). Most juveniles are philopatric and settle on their natal territory (following the death of a putative parent) or on the next closest vacant territory or patch. In the Bodie metapopulation, pika dispersal was particularly restricted and natal site fidelity was strong (Peacock and Smith 1997a; Smith and Gilpin 1997), due to hot summer temperatures that put pikas at risk of overheating.

High percentages of same-patch philopatry in high-elevation pika populations have been documented across their range (Smith and Ivins 1983a; Peacock 1997; Kreuzer and Huntly 2003), and result from aggressive territorial behavior between patch occupants and vagrant pikas (juveniles during their birth summer or immigrants from other patches—Smith and Ivins 1983a, 1984). However, limited adult dispersal may occur when a pika moves within a patch to a vacant territory to improve its breeding status following death of the resident, or when pikas immigrate to a new patch overwinter when territorial defense is relaxed (Smith and Ivins 1983a; Peacock 1997). Maximum dispersal distances by pikas are farther at cooler, high-elevation sites, where pikas are not at as high a risk of overheating, compared with hotter, low-elevation sites (Tapper 1973; Smith 1974a; Peacock 1997).
Restricted dispersal among regional pika populations also may be inferred from genetic analyses. At the northern limit of their range in British Columbia, Henry et al. (2012) genotyped pikas at 10 sites separated by 1–70 km along three elevational gradients ranging from sea level to 1,500 m. They detected marked genetic structure both within and among sites, and also found low levels of gene flow, thus restricted dispersal, within individual transects (Henry et al. 2012). In southern British Columbia, Waterhouse et al. (2017) found two distinct genetic units within a cluster of 15 sites, and pikas in two patches separated by only 500 m had different genetic profiles. Waterhouse et al. (2018) documented limited gene flow along two elevational transects in North Cascades National Park. Along the Columbia River Gorge, microsatellite genotypic data separated a cluster of five low-elevation pika populations from a cluster of six populations only 2.5–6 km upslope, suggesting that little gene flow was occurring (Robson et al. 2016). These researchers further suggested limited gene flow among populations within each cluster, highlighting the restricted dispersal of pikas in this region.

A fundamental assumption concerning genetic risk in conservation biology is that inbreeding may decrease fitness within populations (Pusey and Wolf 1996; but see Smith 1993), and the studies discussed above address this likelihood for American pikas. Due to reduced dispersal, Henry et al. (2012) detected significant levels of inbreeding both within and among the sites they studied. Similarly, Robson et al. (2016) found high inbreeding coefficients in populations at all sites. In the Sierra Nevada, Peacock and Smith (1997b) found that pikas avoided close inbreeding, but commonly mated with individuals of intermediate genetic similarity. At Bodie, perhaps because of the frequent turnover in the metapopulation, mating appeared to be random (Peacock and Smith 1997a). The potential indirect effect of warming temperatures on pika population persistence due to inbreeding may be underappreciated and warrants further investigation.

Demographic constraints.—The annual reproductive rate of pikas is low for a small mammal, reducing their potential resiliency following population losses. Average litter size is three, and most mothers successfully wean two young per summer (Millar 1973, 1974; Smith 1978). Females initiate two litters each summer breeding season, but normally wean only the first successfully. If the first litter is lost, the second one acts as a safety valve (Smith and Ivins 1983b). Interestingly, the largest documented pika litter size was at Bodie (\(\bar{x}\) litter size = 3.7), suggesting that mother pikas are in a positive energy balance with the stressful thermal environment there, in spite of the demands on mothers during reproduction.

Pikas are relatively long-lived for a small (125–175 g) mammal, a feature that reduces the probability of local random patch extirpations. Populations are commonly comprised of 3- to 5-year-old animals, and they may live to age seven or older (Millar and Zwickel 1972b; Smith 1978).

Foraging considerations.—Understanding the responses of pikas to current vegetation will help us understand how their foraging practices could facilitate coping with climate change or conversely lead to extirpations. Pikas are generalist herbivores, but foraging by individual pikas is restricted to the cafeteria of plants available in the talus forefield or isolated plants growing on their territory’s talus slope. Vegetation available to pikas varies across the local habitat, within a region, across their geographic range, and potentially over time as vegetative communities adapt due to climate change.

Foraging by pikas can be highly selective; they prefer harvesting plants with a higher caloric, protein, lipid, or water content than nonselected plants (Millar and Zwickel 1972a; Smith and Erb 2013; Hall and Chalfoun 2018). Selectivity and which plant components pikas preferentially harvest varies with environmental conditions, and the degree of selectivity increases with decreasing plant quality (Smith and Erb 2013). For example, pikas selected plants higher in nitrogen (indicative of protein content) at warmer sites (Smith and Erb 2013; Hall and Chalfoun 2018), and preferentially harvested high-moisture plants at lower elevations in Colorado (Smith and Erb 2013).

Three arguments address how climate change could negatively impact pika fitness with regard to their ability to forage. First, it is claimed that higher temperatures will restrict the amount of time pikas can spend foraging (Mathewson et al. 2017; Hall and Chalfoun 2018). This argument follows from the increasingly crepuscular nature of pikas at low, hot, sites (Fig. 5), but ignores the fact that pikas can forage at night. Large haypiles are found at some of the hottest sites in the Great Basin (Hays Canyon—Beever et al. 2008; Bodie—Smith 1974b), suggesting that available foraging time is sufficient. The pika population at the Mono Craters site does not even make haypiles, yet persists in an environment with extremely hot summer temperatures and sparse vegetative resources (Smith et al. 2016). We can thus conclude that pikas are capable of harvesting sufficient vegetation at hot localities despite the restriction of daytime activity.

Second, it has been claimed that “Rapidly increasing temperatures could change the composition or relative abundance of plants in and around talus areas to a mix with which pikas have not evolved” (Beever et al. 2003: 48). Thus, Wilkening et al. (2019) predicted that pika persistence and occupancy would be negatively associated with the presence of big sagebrush, rabbitbrush, and invasive cheatgrass (Bromus tectorum), plants found at low, hot sites, compared with plant species characteristically found in the Rocky Mountains or Sierra Nevada. Available data, however, refute this hypothesis. Cheatgrass was abundant in all but one of the large haypiles at Hays Canyon (Beever et al. 2008). Haypiles at Bodie (Smith 1974b) and Craters of the Moon (Camp et al. 2020) were comprised almost exclusively of xerophytic vegetation (see above). Ray et al. (2016) similarly found that presence of fernbush and big sagebrush was the best predictor of site use by pikas at Lava Beds National Monument.

Third, some suggest that pika persistence is positively related to relative forb cover in the environment and anticipate that a projected reduction in forbs resulting from increasing temperatures will increase the risk of pika decline (Wilkening et al. 2011, 2019; Bhattacharyya and Ray 2015). Wilkening et al.
found that relative forb cover was significantly higher at extant sites (29%) compared with extirpated sites (9%), but that there was no discernible difference in relative graminoid cover. However, pikas currently thrive in areas dominated by shrubs. Graminoids, the third major class of vegetation consumed by pikas, is a common pika staple. Pikas preferentially feed on graminoids during the summer (Huntly et al. 1986), and they constitute a high percentage of pika haypiles (36% in Alberta—Millar and Zwicker 1972a; 35% in Montana—Bhattacharyya and Ray 2015). It is common for haypiles in the Sierra Nevada to contain 100% graminoids, sometimes in territories adjoining a pika whose haypile consists of 100% forbs (personal observations).

In addition, given the potential impact of livestock grazing on vegetation, and that nearly all extirpated sites among the 26 Great Basin historic sites were grazed and most occupied sites were not, it is notable that the variable grazing was not included in any of the models relating vegetation to site persistence (Wilkening et al. 2011, 2019). This omission restricts our understanding of the role forage could have played in determining pika persistence at these sites. Furthermore, cattle grazing is one of the few variables amenable to management in the Great Basin (Ray et al. 2012).

Finally, it is important to recognize that plants and climate co-vary, and that pikas are quite flexible in adapting to different vegetative regimes. Predictions about how pikas will respond to vegetative changes associated with a changing climate are so far unsupported by available data.

Discussion

“Many species face extinction as warming outpaces their ability to adapt or to move – particularly for species that butt up against a geographic limit, such as …on mountains. Pikas… that live…in high-elevation boulder fields — have no place left to go; they are essentially already extinct…” (Terry Root, quoted in Powell 2008). “By some arguments, the pika may be nearly doomed” (Ray et al. 2012:261). At an earlier time, I have made similar claims myself (Smith et al. 2004). The problem with these statements is that they are not consistent with the evidence that I have presented. Let us review that evidence.

Most of the extensive occupied range of pikas in the intermontane west of North America is in major cordilleras, such as the Rocky Mountains, Sierra Nevada, and Cascade Range. Occupancy of potential pika habitat within this core distribution of pikas is uniformly high and has been constant over time. No studies have found a discernible climate signal that discriminated between occupied and unoccupied sites in these regions. The small number of suitable, but unoccupied, talus sites mostly fell within the range of potential stochasticity (population variability) of pikas. It is highly unlikely that any species will occupy all available habitat at all times (McCain et al. 2016).

In contrast, pikas were absent from several marginal sites where they once had been present. Most of these marginal sites are not on the periphery of the species range, but occur across the Great Basin, and their total area is small in comparison to the extent of core pika habitat. Marginal sites are the most difficult to census and have the potential to produce false negatives, as discussed above. The surveys by Jeffress et al. (2017) and Millar et al. (2018) revealed many previously unknown pika populations across the Great Basin, primarily at low, hot elevations, and it is likely that there are many more. There also are confounding effects of anthropogenic variables, including cattle grazing, at many of the sites from which pikas have been extirpated, which makes it difficult to ascertain which variable or combination of variables may have been responsible for the extirpations.

Our previous work on the Bodie pika metapopulation led to predictions of frequent patch extirpations at low, hot marginal sites. The Bodie metapopulation (with observations going back to the late 1940s) is a natural laboratory demonstrating the dynamics of extinction of populations on patches (inversely related to patch size) and subsequent patch recolonizations (inversely related to interpatch distances), and presents a model for understanding the interplay of these dynamics near the range limit for pikas (Fig. 4; Smith 1974a). It is unfortunate that these variables were not explicitly included in the studies of pika persistence that I have reviewed, as such analyses might have clarified which factors best predicted site extinctions, including stochastic extinction on small, isolated patches.

The pika has been in retrenchment due to a warming climate since the Pleistocene, and most reported extirpations have occurred in the warmest areas of the pika’s range. Thus, it is unsurprising that models based on climate variables showed that extirpated sites had hotter temperatures than occupied sites in several studies (Beever et al. 2010; Wilkening et al. 2011; Stewart et al. 2015, 2017). These studies had small sample sizes, however, and models that incorporated variables other than climate (such as availability of upslope talus habitat) were often stronger predictors of persistence. The sites from which pikas had been extirpated that were surveyed by Beever, Wilkening, and Stewart are surrounded by the occupied sites at Bodie, Mono Craters, Craters of the Moon, and Lava Beds National Monument, but the climate metrics from these sites are not included in any of their models. More importantly, the comprehensive review by Millar et al. (2018) showed that all known extant, extirpated, and old sites across the Great Basin occupied the same climate space (Fig. 1). The mechanistic climatic models of Mathewson et al. (2017) correctly predicted the prehistoric retrenchment of pikas in the Great Basin, as well as the current distribution of pikas, but failed to account for the presence of pikas at Craters of the Moon, Lava Beds National Monument, Newberry National Volcanic Monument, or along the Columbia River Gorge (and presumably also at Bodie and the Mono Craters; collectively “outlier sites”). Would these models have made different predictions if they had included data from each of the outlier sites?

An increasing number of peer-reviewed studies, including those I have cited here, have demonstrated the adaptive capacity of pikas and how resilient they actually are. The persistence of pikas living at outlier sites is a glaring exception to the argument that contemporary climate change is the primary
determinant of documented site extirpations. Pikas facultatively adjust to warm temperatures by retreating into the cool interstices of their talus habitat (Fig. 5), and augment their restricted daytime foraging time with nocturnal activity. We may assume that these behaviors have been present for a long time, as we have detailed long-term temperature data from Bodie showing that throughout the 20th century there have been periods with temperatures equally hot to those at present (Figs. 3 and 4). The forecasting models of Mathewson et al. (2017) that incorporate the ability of pikas to adjust their activity level to daytime temperatures predict 8–19% more habitat in the future than models based on temperature alone. If their models included the current conditions at outlier sites, these percentages likely would be even higher. Finally, pikas appear to demonstrate significant flexibility in their foraging tactics. They are highly selective when necessary, but also are capable of subsisting on a diet of all graminoids, all shrubs, all forbs, or any combination of plant type (including mosses at the Columbia River Gorge), depending on what is available.

The trait that puts pikas most at risk from climate change is their poor dispersal capability. Dispersal is best understood as the ability of pikas to overcome a behavioral–physiological barrier; in hotter environments dispersal is more restricted than in cooler core pika habitat. In terms of current pika biogeography, small sites at low elevation that are extirpated for whatever reason are less likely to be recolonized. The vagility of pikas may be more directly related to climate change than any other factor (Millar et al. 2016). It is no surprise, therefore, that the model variable that often explained pika site persistence better than temperature among historic sites was the amount of talus upslope—a measure of connectivity (Beever et al. 2011; Ray et al. 2012; Stewart et al. 2017). Interestingly, most of the outlier sites do not have significant upslope habitat; thus, these marginal populations may be at increased risk as temperatures warm. The current inability of pikas at Bodie to colonize the extirpated southern constellation in the metapopulation is indicative of this problem. A reduction in the overall range of pikas due to this gradual loss of small peripheral sites is highly likely. Fortunately, talus habitat is more extensive, and possesses greater connectivity at higher elevations in mountain ranges across the intermontane west, and this factor should mitigate further impacts of climate change on pikas in the future.

As I began, determining to what degree climate change will influence pikas across their range in the future remains complicated. A worst-case scenario is that temperatures will increase by 4°C by the end of the 21st century (Collins et al. 2013). However, pikas living today at hot, low-elevation sites that I have discussed experience significantly higher average summer daytime high temperatures than pika populations in nearby mountains, and yet they persist. We have no certainty as to the direction or impact of future climate change. As highlighted by Beever et al. (2011:2068): understanding the current dimensions of climate change “may provide few clues about how future losses may occur.”

In summary, the narrative that pikas are going extinct, supported by a restricted and somewhat compromised data set at the margins of the species’ range, appears to be an overreach. All available evidence shows that pikas are doing well across most of their range, but that there are limited, low-elevation losses in some marginal pika habitats. As pikas today continue to survive in some marginal environments, their adaptive capacity appears to be keeping up with the challenge of the current environment. We should expect variability in occupancy at the range edge for pikas (Smith 1974a), just as is the case for most North American small mammals (McCain et al. 2016). Pikas are showing us that their behavioral adaptations are, thus far, facilitating their ability to cope with a warming climate. The pika’s resilience in the face of climate change demonstrates how crucial it is to understand the natural history of a species in order to assess how it will be impacted by climate change.

Finally, I want to address the messaging that the public has received from scientists regarding the status of the American pika. When people I meet learn that I work on pikas, the first thing they say is “Oh I am so sorry; you must be sad that they are going extinct.” This information comes from press releases written by journalists after interviewing pika researchers who I believe have overstated their findings. The press releases warn that pikas are being forced off mountain tops; they are not. The discrepancies between available data and their interpretation could be used as evidence that the climate story is manufactured. The credibility of science should be of great concern to all of us.

ACKNOWLEDGMENTS

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LITERATURE CITED


APPENDIX I

Characteristics of sites in the hydrological Great Basin, western United States, used in relevant analyses, 1994–2008, as presented by Beever et al. (2011: Appendix V), with calculations of range retraction. Modifications from Beever et al. (2011) annotated and described in text.

<table>
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<tr>
<th>Site location</th>
<th>Status historic to 1999</th>
<th>Status 2000s</th>
<th>Historical minimum elevation (m)</th>
<th>Minimum elevation 1999 (m)</th>
<th>Minimum elevation 2008 (m)</th>
<th>Change historical to 1999</th>
<th>Change historical to 2008</th>
<th>Change 1999 to 2008</th>
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<td>2,599</td>
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<td>465</td>
<td>−24</td>
</tr>
<tr>
<td>Big Indian Mountain</td>
<td>Extant</td>
<td>Extant</td>
<td>2,391</td>
<td>2,713</td>
<td>2,527</td>
<td>122</td>
<td>−64</td>
<td>−186</td>
</tr>
<tr>
<td>Thomas Creek</td>
<td>Extant</td>
<td>Extant</td>
<td>2,377</td>
<td>2,683</td>
<td>2,686</td>
<td>306</td>
<td>309</td>
<td>3</td>
</tr>
<tr>
<td>Kiger Gorge</td>
<td>Extant</td>
<td>Extant</td>
<td>1,920</td>
<td>1,938</td>
<td>1,938</td>
<td>18</td>
<td>18</td>
<td>0</td>
</tr>
<tr>
<td>Stockade Creek</td>
<td>Extant</td>
<td>Extant</td>
<td>1,676</td>
<td>1,798</td>
<td>1,872</td>
<td>122</td>
<td>196</td>
<td>74</td>
</tr>
<tr>
<td>Cougar Peak</td>
<td>Extant</td>
<td>Extant</td>
<td>2,416</td>
<td>2,073</td>
<td>2,222</td>
<td>−343</td>
<td>−194</td>
<td>149</td>
</tr>
<tr>
<td>Crane Mountain</td>
<td>Extant</td>
<td>Extant</td>
<td>2,316</td>
<td>2,360</td>
<td></td>
<td></td>
<td>44</td>
<td></td>
</tr>
<tr>
<td>Hays Canyon Range</td>
<td>Extant</td>
<td>Extant</td>
<td>1,949</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>

\( n = 22 \), \( X^2 = 2,255 \), \( SE = 83.18 \)

\( ^a \) Beever et al. (2011) included 2008 elevation of 2,886 m; inappropriate to count as extirpated and also with a measured upslope retraction. Millar et al. (2018) show evidence of pikas at this site at 2,750 m.

\( ^b \) Beever et al. (2011) classified this site as “functionally extirpated” in 2008 while also giving a minimum elevation. Wilkening et al. (2011) do not classify this population as extirpated, and it is included as an extant site in Millar et al. (2018).

\( ^c \) Beever et al. (2011) included 2008 elevation as 2,776 m; herein this elevation is given as 2,234 because pikas were detected at that elevation although discounted by Beever et al. (2011).

\( ^d \) Classified as functionally extinct in 1999 in Beever et al. (2003); corrected as extant in Beever et al. (2010).

\( ^e \) Site not included in Beever et al. (2003); first identified as an historic site in Beever et al. (2008).

\( ^f \) Values in brackets reflect modification of all negative trends between years to zero, per Beever et al. (2011). See text.