

AMERICAN PIKAS (*OCHOTONA PRINCEPS*) EXTIRPATED FROM THE HISTORIC MASONIC MINING DISTRICT OF EASTERN CALIFORNIA

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ABSTRACT.—American pikas (*Ochotona princeps*) are small alpine lagomorphs and talus obligates with a narrow range of temperature tolerance, along with physiological and ecological characteristics that make them especially vulnerable to local extirpation in the face of climate change. Since their initial colonization of the Great Basin during the Pleistocene geological epoch, the distribution of pikas in this region has become more restricted, with population losses occurring especially in lower-elevation sites characterized by relatively low precipitation and high temperatures. Even where pikas have persisted, many populations are now restricted to higher elevations. We surveyed several sites in the Bodie Hills of eastern California known to have been recently occupied by pikas. Here we report the recent extirpations of 2 of these sites: one small cluster of anthropogenic patches in the historic Masonic Mining District and one natural patch on Masonic Mountain. These extirpations are consistent with those reported in California and across the Great Basin and may indicate the impending loss of pikas from this region due to impacts from global climate change.

RESUMEN.—La pica americana (*Ochotona princeps*), pequeños lagomorfos alpinos, viven en el talud alpino y toleran un estrecho margen de temperaturas. Sus características fisiológicas y ecológicas los hacen especialmente vulnerables a la extirpación local ante el cambio climático. Desde su colonización inicial de la Gran Cuenca (Great Basin) durante la época geológica del Pleistoceno, la distribución de las picas en esta región se ha vuelto más restringida, con pérdidas poblacionales que ocurren sobre todo en áreas con menor elevación, caracterizadas por un número relativamente bajo de precipitaciones y por sus altas temperaturas. Incluso en aquellos casos en los que las picas han resistido, muchas de estas poblaciones ahora están limitadas a las elevaciones más altas. Monitoreamos varias zonas en Bodie Hills al este de California conocidas por haber sido recientemente colonizadas por poblaciones de picas. En este estudio mostramos las extirpaciones más recientes de dos de estas áreas, un pequeño grupo de parches antropogénicos en el histórico distrito de Masonic Mining y un parche natural en Masonic Mountain. Estas extirpaciones concuerdan con aquellas registradas en California y en toda la Gran Cuenca, y pueden indicar la inminente pérdida de picas en esta región debido a los impactos del cambio climático global.

In recent decades, the distributional ranges of many montane species have retreated upslope (Parmesan and Yohe 2003, Parmesan 2006, Moritz et al. 2008, Chen et al. 2011). For many species, this range retraction is a response to anthropogenic global climate change mediated through an upslope shift in their lower elevational limits (Glick and Van-Putten 2002, Loarie et al. 2009, Leadley et al. 2010, Erb et al. 2011, Bellard et al. 2012). Climate change is predicted to drastically alter the availability of suitable habitat for many species across the western United States. The rapidity of such changes makes ecological adaptation to changing conditions challenging at best, and climate change will likely become the major threat to earth's biological diversity for the foreseeable future (Loarie et al. 2008, Ackerly et al. 2010). Protecting biodiversity in

the face of such rapid ecological changes represents a significant challenge for conservation science.

The American pika (*Ochotona princeps*) has become an iconic example of a species threatened by global climate change and as such, an important model organism to study the mechanisms by which environmental change impacts a species (Ray et al. 2012). A combination of life history characteristics (intolerance to high ambient temperatures, extreme habitat specificity, limited dispersal distance, and social intolerance) makes pikas very susceptible to local extirpation in the face of global warming (Beever et al. 2003, Erb et al. 2011). Pikas are currently experiencing range contractions linked to climate change, particularly in the Great Basin and Sierra Nevada where distributional shifts and extirpations have

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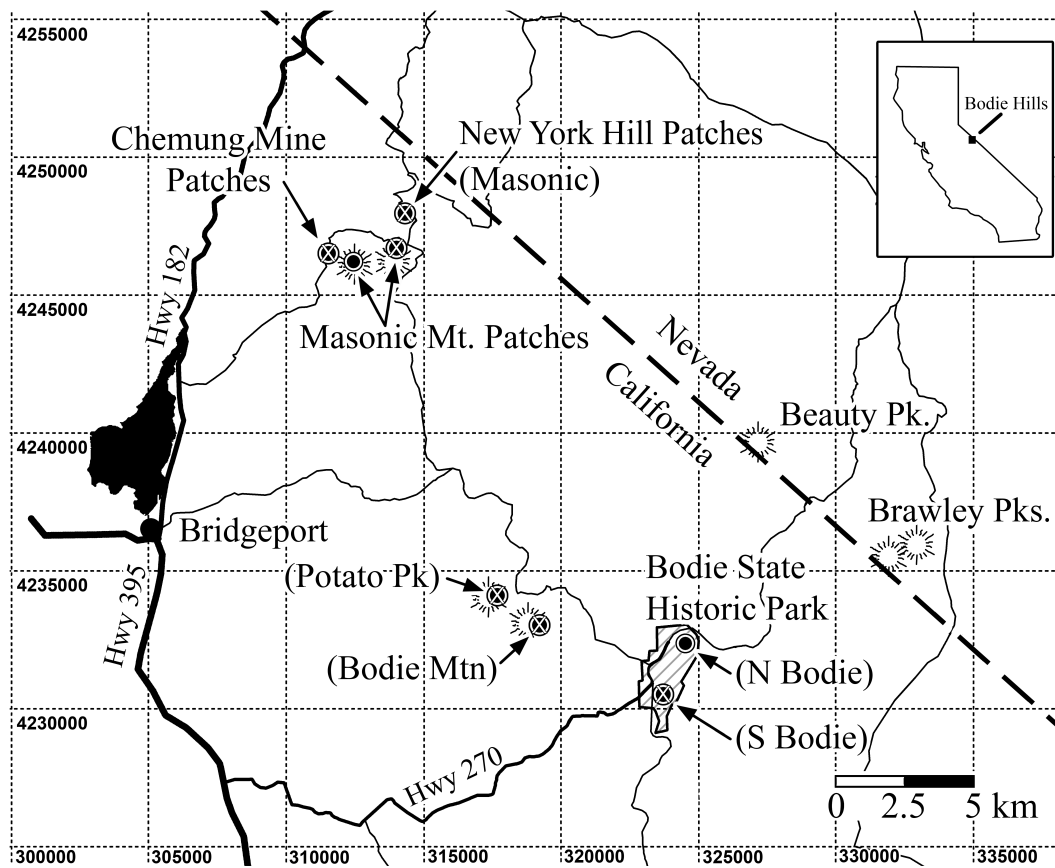


Fig. 1. Bodie Hills study area. ● indicates a site occupied by American pikas (*Ochotona princeps*) when surveyed. ⊗ indicates an extirpated site. Site names in parentheses correspond to those reported in Stewart et al. (2015). Coordinates are UTM grid 11S, WGS84.

been associated with both modern climate trends as well as glacial-interglacial dynamics during the Pleistocene (Beever et al. 2003, Grayson 2005, Beever et al. 2011, Erb et al. 2011, Wilkening et al. 2011, Stewart et al. 2015). Similar patterns are apparent in the southwest Yukon in the closely related collared pika, *Ochotona collaris*, that Canada has recently listed as a species of special concern (Morrison and Hik 2007, COSEWIC 2011). Although conservation groups have pressed for legal protection for American pikas in the United States, both state and federal agencies have so far refused to elevate the species to threatened or endangered status (USFWS 2010, Mastrup 2013). Here we report the very recent extirpations of 2 sites in the Bodie Hills of eastern California that were previously occupied by pikas.

STUDY AREA

New York Hill is located at 2500 m elevation in the northern Bodie Hills of Mono County, California, and is separated from the Sierra Nevada crest by approximately 37 km of Great Basin sage-scrub habitat dotted with limited natural rock outcroppings suitable for pika occupation (Fig. 1). This site is reported in Stewart et al. (2015) as “Masonic.” Pikas are currently extirpated from essentially all of the natural rock outcropping in the Bodie Hills despite evidence of occupation during the 20th century (Nichols 2010, Stewart et al. 2015). As part of the Masonic Mining District during the early 20th century, the area of New York Hill was actively mined for gold and silver by the Serita and Pittsburg–Liberty mines (Eakle et al. 1917). This hard

rock mining created anthropogenic ore dumps suitable for pika occupation adjacent to a few small natural talus patches. The habitat patches at New York Hill occur within an area approximately 600 m north to south and 800 m east to west and are centered at approximately 38.3612° N, 119.1264° W. Vegetation in the area of New York Hill is characterized as Great Basin sage scrub mixed with pinyon-juniper woodland. The plant community in the middle elevations across the Bodie Hills is dominated by several species of sagebrush (*Artemisia*), currant (*Ribes*), and buckwheat (*Eriogonum*), as well as antelope bitterbrush (*Purshia tridentata*) and rubber rabbitbrush (*Chrysothamnus nauseosus*; Severaid 1955). The New York Hill site occurs near the lower elevational limit of pika distribution at this latitude and as such, experiences relatively warm temperatures (approximately 8 °C higher) compared to higher-elevation populations in the nearby Sierra Nevada (Smith 1974b).

Millar et al. (2013) reported pika occupancy on 5 clustered sites with natural talus on Masonic Mountain. These sites ranged from 2673 to 2767 m in elevation (Millar et al. 2013) and were 1.3 to 2.5 km from the artificial patches at New York Hill. Four of these patches occur within an area approximately 850 m north to south and up to 300 m west to east (centered at approximately 38.3446° N, 119.1432° W). The remaining patch is approximately 1.3 km east-northeast of the other 4 patches (38.3484° N, 119.1278° W).

METHODS AND RESULTS

Potential pika habitat around New York Hill in the historic Masonic Mining District was initially surveyed by one of us (LBN) in 2009 and 2010 as part of an occupancy survey of pika habitat throughout the Bodie Hills (Fig. 1). A total of 17 patches suitable for pika occupation (3 natural talus and 14 anthropogenic ore dumps) were identified at New York Hill and surveyed for pika activity (either sightings or vocalizations) and for pika sign (fecal droppings, haypiles, and urine white-wash) for a mean time of 48 min per patch. Droppings were classified in the field as “fresh” or “old” based on criteria in Nichols (2010) and Prugh and Krebs (2004). Voucher samples of fecal pellets were collected from

latrines on every patch surveyed. Of the 17 surveyed patches, 7 were determined to be occupied based on the presence of fresh pellets, vocalizations, or sightings. Fresh haypiles constructed of vegetation characteristic of pika territories are not considered sufficient evidence on their own to indicate occupancy by pikas. Bushy-tailed woodrats (*Neotoma cinerea*) occur throughout the Bodie Hills on patches of occupied and unoccupied pika habitat and are known to make haypiles (Morton and Pereyra 2008) that could be misinterpreted as pika haypiles in the absence of corroborating evidence (i.e., fecal pellets, vocalizations, or sightings). The remaining 10 patches all contained evidence of prior occupation by pikas in the form of old pellets but were determined to be unoccupied at the time of the initial survey (2009, 2010).

In September 2013, one of us (KBK) revisited a subset of these patches to collect fresh pellets for genetic analysis. At that time no fresh pellets or other evidence of current pika occupation were observed. A complete resurvey of all 17 patches was conducted in summer and fall of 2014 and again in early summer of 2015 for a total of 3 independent visits to determine whether this site had been recolonized. Old fecal pellets were present and abundant but no pikas were sighted or heard, no fresh fecal pellets were found, and no recent haypiles were present. In contrast, abundant evidence of current woodrat occupation (probably *Neotoma cinerea*) was present in the form of fresh fecal pellets and midden construction.

In June 2015, 2 surveys were conducted to locate and assess pika occupation of sites on Masonic Mountain reported by Millar et al. (2013). Four of these sites are arrayed north to south on the west side of Masonic Mountain and were determined to be occupied based on pika vocalizations and presence of fresh pellets. One site isolated to the east-northeast of the others was determined to be recently extirpated. This site is approximately 1.3 km from the cluster of patches at New York Hill and 1.3 km from the nearest occupied site on Masonic Mountain. After spending a total of 5.8 observer hours over 2 days on site, no pikas were sighted or heard, no fresh haypiles were observed, and only 2 latrines were located with moderately fresh fecal pellets (*sensu* Nichols 2010).

DISCUSSION

Anthropogenic climate change is likely to have a disproportionate effect on montane environments and on alpine specialists in particular due to their limited capacity to respond to unpredictable environmental change (Parmesan 2006, Varner and Dearing 2014). Indirect effects of anthropogenic change, such as altered composition or availability of forage, may also contribute to population decline (Cahill et al. 2012). As alpine specialists, pikas may experience not only contracting ranges but also altered food availability, direct thermal stress from increasing temperatures (Varner and Dearing 2014), and exposure to extreme cold temperatures during winter months with limited snowpack (Beever et al. 2010). Other indirect effects of anthropogenic climate change may negatively impact pika populations but have not yet been tested. These include increased competition with species that have less restrictive habitat requirements (e.g., bushy-tailed woodrats, *Neotoma cinerea*), changing ecological relationships with sympatric species (pikas shifting to nocturnal foraging and becoming more exposed to nocturnal predators), and changing species composition in communities due to upward range expansions of previously allopatric competitors, predators, or plants.

The local extirpation of pikas at New York Hill, Masonic Mountain, and nearby ore dumps of the inactive Chemung Mine (reported by Millar et al. 2013) is consistent with range contractions observed across the Great Basin (Beever et al. 2003, Beever et al. 2011). Limited information exists about the length of time pikas have occupied New York Hill, but the species was first reported in the Masonic Mining District (which includes New York Hill) during the early 1970s (Smith 1974b), and pikas presumably occupied natural talus patches in this area for much of the Holocene. Stewart et al. (2015) identified 5 historically occupied pika populations in the Bodie Hills: 2 at Bodie State Historic Park (North Bodie and South Bodie), 1 at Potato Peak, 1 at Bodie Mountain, and 1 at Masonic Mountain (Fig. 1). The New York Hill site reported here is the same as the Masonic site reported in Stewart et al. (2015). Although all 5 sites were known to have been occupied in the 20th century, only 2 (North Bodie and

Masonic) remained occupied when resurveyed. Therefore, in the small amount of time between completion of resurvey fieldwork and publication of Stewart et al. (2015), at least one more historical pika site in California (New York Hill/Masonic) became unoccupied. This changes the total of historical pika sites in California that are currently unoccupied from the 10 of 67 (15%) reported in Stewart et al. (2015) to 11 of 67 (16%).

The extirpation of the New York Hill/Masonic population leaves only 2 documented surviving pika populations in the Bodie Hills: the recently reported population occupying a few small patches on Masonic Mountain (Millar et al. 2013) and the north end of the Bodie Mining District (now part of Bodie State Historic Park and surrounding Bureau of Land Management lands). The Masonic Mountain population is 2.5 km southwest of the extirpated New York Hill population. Bodie is southeast of New York Hill and is separated from this site by approximately 20 km of Great Basin sage-scrub habitat with widely spaced patches of natural talus that have evidence of prior pika occupation but are currently extirpated (L.B. Nichols, personal observation).

The Bodie Hills have long been considered an unusual and marginal habitat for pikas due to small highly fragmented habitat patches and arid climate compared to nearby alpine sites in the Sierra Nevada and Sweetwater Mountains (Severaid 1955, Smith 1974b). The demographics and genetics of small populations tend to push populations on individual patches toward extirpation in the absence of interpatch dispersal events. Populations on even the larger patches would be subject to extirpation without an influx of dispersing individuals. It is therefore expected that in the face of a widespread environmental stress like global climate change, pika populations in these marginal habitats would be impacted before those in core parts of their distributional range.

The observed decline in pika distribution in the Bodie Hills reported here may represent either a permanent, long-term decline or the low point in a cyclical pattern of extirpations and recolonizations. Old fecal pellets are abundant throughout natural talus patches. Urine whitewash left by pikas is thick and obvious on rocks in natural talus in the Bodie Hills, but this evidence is barely noticeable on

rocks in artificial talus patches that have existed for over 100 years at Bodie State Historic Park and at New York Hill/Masonic site (L.B. Nichols, personal observation). Survey work across the Bodie Hills found that suitable pika habitat was occupied in the recent past (latter half of the 20th century) but was extirpated by 2010, except for populations persisting at the north end of Bodie State Historic Park and the 2 neighboring populations of Masonic Mountain (Millar et al. 2013) and New York Hill (Stewart et al. 2015). At present, the only known occupied natural pika habitat in the Bodie Hills is the 4 clustered sites on Masonic Mountain. Collectively these observations suggest that the extirpation of pika populations in the Bodie Hills represents long-term decline in the regional distribution of these animals rather than a low point in a natural cyclical pattern of local extirpations to be soon followed by a wave of patch recolonizations.

Stewart et al. (2015) found mean summer temperatures and amount of talus habitat within a 1-km radius to be the best predictors of pika occupancy at historically occupied pika sites in California. The New York Hill population was comprised of 17 relatively small habitat patches with a possible recent demographic connection to the Masonic Mountain population (Millar et al. 2013), whereas the Bodie population has over 100 habitat patches, including several large “mainland” patches (Smith 1974a, Peacock and Smith 1997). Both populations are at relatively low elevations for pikas in the region (2560 m at New York Hill and 2630 m at Bodie). That the pika population at Bodie has persisted longer than at New York Hill is consistent with the model in Stewart et al. (2015), since the Bodie population occupies a much larger array of habitat islands.

This study did not attempt to determine what factors are related to the local extirpations we report here. However, given the available evidence, some potentially useful inferences may be made. The extant pika population in the Bodie Hills has always been highly fragmented due to the inherently patchy distribution of natural talus habitat and the continued loss of lower-elevation populations during late Holocene warming (Grayson 2005). Pikas colonized the prehistoric Great Basin during the Pleistocene; and with the

lack of successful recolonization after initial extinction events, this region has been experiencing a consistent upslope range contraction ever since (Grayson 2005). The recent rise in global temperatures caused by anthropogenic climate change has likely only exacerbated this trend. Although these patches were probably demographically connected by regular (although possibly infrequent) interpatch dispersal events, it is difficult to determine the frequency of patch extirpation/recolonization events given the absence of regular historic survey data. Unfortunately, the ecological and environmental factors that contribute to the colonization process in pikas are not well understood (Lanier et al. 2015). Recent field observations of abundant old fecal pellets and thick urine whitewash suggest that many natural talus patches in the Bodie Hills were occupied by pikas continuously for long periods rather than intermittently.

Pikas are believed to have limited dispersal ability; however, a wide range of maximum dispersal distances has been reported in the literature. Generally, studies that have relied solely on observations of known individuals report shorter maximum dispersal distances than those studies that have used genetic data to estimate dispersal distances (e.g., Smith 1974a vs. Peacock 1997). Reported maximum dispersal distances for pikas range up to 20 km (Hafner 1994); however, this estimate is based on millennial timescales, and most estimates (whether genetic or observed) range between 2 and 5 km (Tapper 1973, Peacock 1997, Peacock and Ray 2001, Henry et al. 2012).

The Bodie Hills do not provide optimal conditions for successful pika dispersal. Pikas must have access to cool talus piles to behaviorally thermoregulate at ambient temperatures above 27 °C (MacArthur and Wang 1974). With a warming climate, populations on patches that would have otherwise been maintained or recolonized by dispersers may become permanently extirpated. The Bodie Hills have high diurnal temperatures combined with widely spaced natural talus patches that create an unfavorable landscape for dispersal. Peacock and Smith (1997) observed a marked Bodie pika move 396 m from its natal territory. However, during an annual survey in August 2015, a pika was observed on a previously extirpated patch at Bodie State Historic Park that was over 1.2 km

from the nearest occupied patch (L.B. Nichols and K.B. Klingler, personal observation). Pikas are diurnally or crepuscularly active, and they are not shy about vocalizing to defend their territory from investigators. In addition, despite large variation among individuals, especially at Bodie, pikas maintain visible haypiles and latrines easily detected by trained researchers. This individual was initially detected by LBN through observation of fresh fecal material, a small haypile, and a camera trap and then later confirmed by live trapping (KBK).

Given this empirical observation of a dispersal event among fragmented habitat patches separated by Great Basin sage-scrub, it is clearly possible for an individual pika to disperse at least 1.2 km and find suitable habitat despite high habitat fragmentation, warming temperatures, vulnerability to predation, and lack of visual or aural cues (e.g., no other pikas were present on this extremely isolated patch). Previous work has demonstrated that there are other significant factors besides temperature that interact to influence pika persistence, such as amount of habitat, anthropogenic disturbance, precipitation, and snow cover (Smith 1978, Beever et al. 2003, Morrison and Hik 2007, Beever et al. 2008). Therefore, when conditions are favorable, this example shows that it is possible for individual pikas at Bodie to successfully disperse across distances approaching 2 km.

If the observed maximum dispersal distance in the Bodie Mining District is 1.2 km, it is reasonable to suggest that a similar maximum dispersal distance may be possible in the greater Bodie Hills even though natural talus patches in the Bodie Hills tend to be widely spaced. In contrast, anthropogenic sites like Bodie provide many small and closely spaced "stepping stone" patches that may make long-distance dispersal easier. The rarity of a dispersal event similar to this should not be understated. This dispersal event recorded during summer 2015 is the greatest dispersal distance observed and quantified over the past 27 years from data collected for both a mark-resight study conducted from 1988 to 1991 (Peacock and Smith 1997) and annual surveys conducted by LBN beginning in the late 1990s at this site. Hence, based on this empirical evidence and the reported dispersal distances in the literature, it is likely that populations separated by greater than 2 km

are demographically isolated and fairly prone to extinction in the Great Basin. However, as suggested previously by Beever et al. (2008), it may be important to consider occupancy patterns as site-specific in the Great Basin and avoid generalizing the ability of pikas to disperse without considering the unique conditions present within each population.

In the recent past, there may have been a demographic connection between the small cluster of medium-sized natural patches on Masonic Mountain and the cluster of small anthropogenic patches at New York Hill (approximately 2.5 km apart) either directly or through the isolated Masonic Mountain patch that sits between the two (approximately 1.3 km south-southwest of New York Hill and 1.3 km east-northeast of Masonic Mountain patches; Fig. 1). Recent environmental changes (especially anthropogenic climate change) may have reduced the number of successful dispersers among these patches enough to demographically isolate them. However, this theory is difficult to empirically test. In most cases, American pika dispersal can be defined as the act of a juvenile leaving its mother's territory and securing a new territory as close to its natal territory as possible (Smith and Ivins 1983, Peacock 1997). Once an animal has claimed a new territory and started haying, it is extremely rare that secondary dispersal will occur within its lifetime (Peacock 1997, Zgurski and Hik 2012). The dispersal of an animal away from its natal talus slope or habitat patch, even to pursue mating opportunities, is probably rarely successful for pikas, which makes researcher observations of long-distance dispersal extremely infrequent.

Dispersal habits are known to differ between the 2 pika species in North America (both obligate talus dwellers), perhaps as a function of population density (Zgurski and Hik 2012). Despite a similarity in even-sexed dispersal, the American pika differs significantly in reported mean dispersal distances (50–91 m; Smith and Ivins 1983, Peacock and Smith 1997) from the collared pika (500 m; Zgurski and Hik 2012). Differences in population densities may influence movement patterns, with juveniles from American pika populations (6–10 pikas \cdot ha⁻¹; Smith et al. 1990) failing to disperse long distances perhaps due to aggression from neighboring conspecifics (Zgurski and Hik 2012). In collared

pikas, Zgurski and Hik (2012) reported an average dispersal distance of just 536 m, with the distribution of distances biased toward much shorter distances (<300 m). A maximum of 1.8 km was reported based on genetic evidence (Zgurski and Hik 2014), making collared pikas relatively poor dispersers.

American pika populations exhibit much shorter mean dispersal distances of approximately 50–91 m (Smith and Ivins 1983, Peacock and Smith 1997), with mean distance between haypiles of nearest neighbors at about 32 m (Peacock 1997). These shorter dispersal distances typical in the American pika (especially in the Great Basin), and even in the collared pika, mean that dispersal events greater than 1 km are probably extremely uncommon (Peacock 1997, Zgurski and Hik 2014, Lanier et al. 2015). Therefore, the possibility that the New York Hill/Masonic pika population will become rescued due to metapopulation dynamics seems unlikely under a global warming scenario. In addition, there is the problem of distance: the minimum dispersal distance required at present is at least 2.5 km from the small patches on Masonic Mountain and the next closest (and much denser) population in the Bodie Mining District is 20 km away.

Losses of these small isolated populations at the lower elevations and southern fringes of the pika distributional range, as well as in atypical habitat, represent a significant genetic diversity cost, whether this loss is due to metapopulation dynamics or anthropogenic climate change or an interaction between these 2 factors. It is reasonable to expect that such populations harbor locally adapted and unique genetic variation, which is important for an evolutionary response to environmental disturbance and for the management of this species' persistence across its range (Lanier and Olsen 2013). In fact, the continuing extirpation of locally adapted populations and the decreasing geographic proximity among them is likely to significantly alter the distribution and maintenance of regional genetic diversity. It is also likely that fine-scale population structure within and among local populations is largely being erased by extirpation events such as the one reported here (Galbreath et al. 2009, 2010). The role of historic factors in shaping extant population connectivity and levels of shared ancestry means that we can-

not assume populations will respond similarly to the effects of global climate change (Lanier et al. 2015).

For highly isolated populations, such as New York Hill in the Masonic Mining District, decreased gene flow with other populations may have elevated the extirpation risk through losses of genetic variation due to inbreeding depression and/or genetic drift (Frankham 2005). Although the relative contribution of genetic effects on a populations' extinction risk is unknown, it is certain that the continuing disappearance of small populations in the Great Basin and California represents serious reductions in the genetic diversity within the Sierra Nevada pika lineage of the American pika. In addition, these extirpations limit the species' evolutionary potential in the face of global climate change.

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