Journal of Mammalogy, 97(6):1495–1511, 2016
DOI:10.1093/jmammal/gyw128
Published online August 25, 2016

Pika (*Ochotona princeps*) losses from two isolated regions reflect temperature and water balance, but reflect habitat area in a mainland region

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Although biotic responses to contemporary climate change are spatially pervasive and often reflect synergies between climate and other ecological disturbances, the relative importance of climatic factors versus habitat extent for species persistence remains poorly understood. To address this shortcoming, we performed surveys for American pikas (*Ochotona princeps*) at > 910 locations in 3 geographic regions of western North America during 2014 and 2015, complementing earlier modern (1994–2013) and historical (1898–1990) surveys. We sought to compare extirpation rates and the relative importance of climatic factors versus habitat area for pikas in a mainland-versus-islands framework. In each region, we found widespread evidence of distributional loss—local extirpations, upslope retractions, and encounter of only old sign. Locally comprehensive surveys suggest extirpation of *O. princeps* from 5 of 9 new sites from the hydrographic Great Basin and from 11 of 29 sites in northeastern California. Although American pikas were recorded as recently as 2011 in Zion National Park and in 2012 from Cedar Breaks National Monument in Utah, *O. princeps* now appears extirpated from all reported localities in both park units. Multiple logistic regressions for each region suggested that both temperature-related and water-balance-related variables estimated from DAYMET strongly explained pika persistence at sites in the Great Basin and in Utah but not in the Sierra-Cascade "mainland" portion of northeastern California. Conversely, talus-habitat area did not predict American pika persistence in the Great Basin or Utah but strongly predicted persistence in the Sierra-Cascade mainland. These results not only add new areas to our understanding of

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long-term trend of the American pika's distribution, but also can inform decisions regarding allocation of conservation effort and management actions. Burgeoning research on species such as *O. princeps* has collectively demonstrated the heterogeneity and nuance with which climate can act on the distribution of mountain-dwelling mammals.

Aunque las respuestas bióticas al cambio climático contemporáneo son espacialmente generalizadas y frecuentemente reflejan sinergias entre el clima y otros disturbios ecológicos, la importancia relativa de factores climáticos frente al área de hábitat para el mantenimiento de especies sigue siendo poco conocida. Para subsanar esta deficiencia, realizamos muestreos de la pika Americana (*Ochotona princeps*) en más de 910 sitios en 3 regiones geográficas del oeste de Norteamérica durante 2014 y 2015, complementando muestreos realizados en tiempos recientes (1994–2013) e históricos (1898–1990). Comparamos las tasas de extirpación para dilucidar la importancia relativa de los factores climáticos con respeto al área del hábitat disponible de las pikas bajo un marco conceptual de áreas continentales frente a zonas aisladas. En cada región, encontramos amplia evidencia en la pérdida de área de distribución - extinciones locales, desapariciones de las zonas bajas, y encuentro sólo de evidencia de ocupación pasada. Estudios localmente exhaustivos sugieren la extirpación de *O. princeps* en 5 de las 9 localidades nuevas muestreadas de la Gran Cuenca Hidrográfica (Great Basin), y en 11 de las 29 localidades en el noreste de California. Aunque las pikas todavía se encontraban en fechas recientes como en 2011 en el Parque Nacional Zion y en el Monumento Nacional Cedar Breaks en Utah en 2012, *O. princeps* ahora parece extirpada de todas las localidades donde fue encontrada anteriormente en ambos parques. Regresiones logísticas múltiples para cada región basados en factores ambientales como la temperatura y los factores relacionados con el balance del agua (ambos estimados por el DAYMET) explicaron claramente el patrón de persistencia de la pika en localidades de la Gran Cuenca y en Utah, pero no en el noreste de California, en el área "continental" de la montañas de Sierra Nevada y Cascades. Por el contrario, el hábitat de talud no predijo la persistencia de la pika en los sitios aislados en la Gran Cuenca y en Utah, pero lo predijo significativamente en el área continental (i.e., en las montañas de Sierra Nevada y Cascades). Estos resultados incrementan el conocimiento sobre la distribución histórica y la tendencia a largo plazo de la pika Americana. Este conocimiento también puede ayudar en la toma de decisiones sobre las prioridades en las acciones en conservación y manejo. El avance en conjunto en investigaciones de especies como *O. princeps* ha demostrado la heterogeneidad y la forma con que el clima actúa de diferente manera sobre la distribución de los mamíferos de montaña.

Key words: climatic water balance, DAYMET, habitat area, hydrographic Great Basin, local range contraction, logistic regression, northeastern California, *Ochotona*, pika, Utah national parks

Island Biogeography Theory (MacArthur and Wilson 1963) has provided a useful framework that has helped develop numerous conservation-oriented hypotheses related to species–area relationships, species occurrence and persistence, nestedness of island faunas, and other phenomena. Early application of this theory to floras and faunas of insular mountaintops of western North America (e.g., Brown 1971; Patterson and Atmar 1986; Lomolino et al. 1989; Charlet 1996) led to 3 fundamental predictions: 1) species richness on isolated mountaintop islands will be a subset of the richness found on (Sierra Nevada-Cascade and Rocky Mountain) mainlands; 2) species richness on insular mountaintops will reflect the balance of the rates of extinction and recolonization (but see the nonequilibrium model of Brown (1971) and subsequent authors), processes which are governed by mountaintop area and isolation from the mainlands, respectively; and 3) rates of local extinction are assumed to be higher on insular mountaintops than on the mainland, due to the latter's greater high-elevation area, and consequently, presumed greater total population size of any focal species, typically wider elevation gradients, diverse habitats and microclimates, and greater connectedness among populations (and thus, more frequent rescue effects—Brown and Kodric-Brown 1977).

Recent investigations (e.g., Fleishman et al. 2001; Beever et al. 2003; Ditto and Frey 2007) have documented contemporary climate change as another force shaping montane faunas and extinction rates. It may exert influence biogeographically (e.g., by influencing extent and isolation of suitable habitat area) or more directly (e.g., via physiological stress or effects on forage plants). Generally, high-elevation specialist and poorly dispersing species have been predicted (Thomas et al. 2004) and shown (e.g., Wilson et al. 2005; Sekercioglu et al. 2008; Rowe et al. 2015) to experience large range contractions under contemporary climate change. A relatively understudied question germane to conservation of all montane species, however, is whether the relative influence of climate and finer-scale factors (such as local amount of habitat) will vary in their importance in mediating extirpations between mainlands and insular areas. Climate may bring about extirpations through numerous direct and indirect mechanisms, such as physiological, disease-based, competitor-based, and forage-based pathways. In contrast, habitat area can affect persistence through aspects of Caughley's (1994) small-population paradigm by inducing local extinctions through demographic, environmental, or genetic stochasticity. Habitat area can also govern processes such as metapopulation and source–sink dynamics;

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positively influence the diversity of habitats and microclimates; and affect a patch's area:edge ratio, which in turn may affect access to forage and exposure to predation.

To test the assumption of higher extinction rates on insular mountaintops than in the mainland and the influence of climate and habitat area on these rates, we performed resurveys for a montane mammal, the American pika, *Ochotona princeps* Richardson, at sites of historical pika records in 3 regions—1 that included a portion of the Sierra Nevada-southern Cascade mainland, and 2 from more insular areas (i.e., the hydrographic Great Basin, and national parks of southern Utah). Whereas a single round of surveys provides some understanding of the distribution of a particular species (i.e., its distributional status), resurveys also provide investigators and conservation practitioners with the additional information of distributional changes through time. Similarly, with ≥ 3 sampling events, trends can begin to be estimated. Recent and historical records at our sample locations reflected detections of American pikas (hereafter referred to as pikas) from 1898 to as recently as 2012. In particular, our objectives included: 1) assessing whether the frequency of pika extirpations from areas at and near each historical record was greater in a portion of the Sierra Nevada-Cascade chain or in our more isolated regions, and 2) comparing across regions the relative importance of climatic factors and areal extent of local habitat.

Materials and Methods

Resurveys: historical data sources, geographical descriptions, and definitions of sites for each region.—We resurveyed areas with historical records of American pika occurrence in the Great Basin (Table 1), southern Utah, and northeastern California (Table 2) to assess patterns of persistence and to evaluate some variables that we hypothesized could explain those patterns (Fig. 1). Great Basin records came from a previously untapped resource (Howell 1924), and land-managing agencies in Utah and northeastern California expressed interest in 2014 in resurveys in those regions. Howell (1924) provided 9 sites in the Great Basin with historical pika records (Table 1) that have not been part of previous Great Basin persistence analyses (e.g., Beever et al. 2008, 2011). Within northeastern California, we used all records from the area's counties in the California Natural Diversity Database (CNDD; Table 2). The 5 counties that comprise northeastern California provided an interesting test because their geography allows the decoupling of elevation from aridity and water balance as potential mediators of extinction dynamics. This is because their geography spans an aridity gradient from the eastern part of the Sierra Nevada-southern Cascades massif to drier, more eastern mountain ranges of the Great Basin, allowing a subtest of dynamics in mainland versus isolated areas within the California study area. Within these mountains that overlap greatly in the elevations that they span, elevation constitutes a local proxy of temperature, given environmental lapse rates. California elevations were originally estimated in the CNDD from specimen records, field collectors' notes, and map interpretation by the Museum of Vertebrate Zoology at the University of California, Berkeley. We verified all site locations and elevations by the combination of inspecting the original field notes ourselves, exhaustive review of aerial imagery at CalTopo.com in 2015 to identify talus areas, and extensive discussions with local professionals, historical societies, and historical archives. In Utah, we spoke directly with the individuals who made the pika observations in 2009–2012. In the Great Basin and in northeastern California, we excluded several sites from Howell (1924) and earlier Great Basin analyses (such as from records in Verts and Carraway 1998) that were too vague to ascribe the record to a location clearly within our 3- or 1-km sampling radius and were not associated with field notes (or had field notes that provided insufficient precision to allow confidence of resurvey with our sampling design).

Because *O. princeps* exhibits metapopulation dynamics (Hanski 1998) and because we have observed changes in occupancy status of individual patches within and across years, we have defined a "site" as all talus patches within 3 km (in the Great Basin) or 1 km (within northeastern California, for consistency with our earlier surveys in that region), to distinguish this patch-level "noise" from landscape-level signal. In contrast, in Utah, our primary objective was to survey all patches at which pikas had been previously reported in both park units (Zion National Park [ZION] and Cedar Breaks National Monument [CEBR]). However, we surveyed extensively around CEBR (i.e., in Dixie National Forest) to assess the possibility of dispersal events (and recolonization, if any patches had been extirpated); comparable surveys could not be performed outside ZION due to private land ownership. Consequently, because we surveyed some patches that had no previous records (nor recorded surveys), our analyses for Utah examine patterns in occupancy rather than in persistence. Because *O. princeps* is generally quite philopatric (e.g., Peacock 1997) and is a relatively poor disperser (particularly in hot, dry contexts—Castillo et al. 2014), our definition of sites and extensive sampling likely avoided not detecting the species simply because it had temporarily moved. Strong support for this inference comes from the Great Basin, in which numerous surveys after a site's extirpation of pikas have subsequently never detected the species at any patch within the 3-km radius around the historical record (Beever et al. 2011). The pika's extensive geographic distribution, which is disjunct at multiple spatial resolutions, allows for a more nuanced understanding of trend than a species simply being a climate-change "winner" or "loser" (O'Brien and Leichenko 2003).

Study organism.—*Ochotona princeps*, a dietary-generalist lagomorph weighing 125–200 g, constitutes an excellent mammal species for study of wildlife responses to climate for many reasons. Pikas can be locally abundant and highly detectable (p usually > 0.90—e.g., Rodhouse et al. 2010; Beever et al. 2011); collectively, these attributes allow for greater statistical power to understand patterns and trends and to identify causal mechanisms of change. Compared to other lagomorphs and small mammals, relatively stable pika population sizes (Southwick et al. 1986) further increase the signal:noise ratio. In *O. princeps*, acute heat stress can cause death in < 6 h when

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Table 1.—Characteristics of sites added in 2014 and 2015 to investigation of *Ochotona princeps* across the hydrographic Great Basin, western United States. Records appear in Howell (1924), and we used historical field notes from the museums at which voucher specimens were deposited to pinpoint historical collecting locations. Home ranges were determined following methods described in text. E = east; S = south; W = west. NW = northwest; SE = southeast; SW = southwest. MEO = minimum elevation of occupancy; USFS = United States Forest Service. dec. deg. = decimal degrees; Hwy = highway; mi = miles; Mtn. = mountain; Rd. = road.

Location	Year(s) of historic record(s)	County, State	Elevation (m)	Latitude (dec. deg.)	Longitude (dec. deg.)	Approximate number of home ranges	Elevations surveyed for pikas	# of Historic specimens documented	Status of *O. princeps* at site in 2014	Owner or management jurisdiction	Sampling date(s) in 2014, 2015
Vicinity of Sugar Hill, 7.5 mi S of Fandango Pass Rd. (County Rd. 9) at Hwy 395, between Goose and Upper Lakes	1894, 1910	Modoc, California	2,203	41.81	−120.34	52	1,671–2,213	4 (1894); 2 (1910)	Extirpated	USFS-Modoc National Forest	8 Aug., 13 and 14 Sept.
Ruby Mtns., SW of Ruby Valley Post Office, 10,500′ (Green Mtn.)	1898	Elko, Nevada	3,200	40.40	−115.51	777	2,740–3,255	3	Very high density; extensively distributed (1.63 individuals per 50-m transect); MEO: 2,774 m[a]	USFS-Toiyabe National Forest	26 July, 8 Aug. 2014
Near Fandango Peak, ~4.4 mi W of Fort Bidwell, between Goose and Upper Lakes	1917	Modoc, California	2,338	41.86	−120.24	312	2,115–2,374	4	Widely distributed, but low density (0.247 individuals per 50-m transect); MEO: 2,150 m	USFS-Modoc National Forest	15 Sept. 2014
4 mi SW of McDonald Peak	1924	Lassen, California	1,632	40.91	−120.46	599	1,651–1,996	1	Extirpated	Mixed	29 and 30 July 2014
2 mi E of SE end of Eagle Lake (above W end of Bly Tunnel; S side of Black Mtn.)	1925	Lassen, California	2,009	40.60	−120.73	733	1,559–1,919	1 (+1 seen and heard)	Extirpated	Mixed	31 July, 1 Aug., 17 Sept. 2014
5 mi NW of Eagle Peak	1926	Modoc, California	2,227	41.34	−120.27	91	1,964–2,646	33	Low occupancy (pikas detected at 2 of 5 patches) and low density (0.094 individuals per 50-m transect); MEO: 2,558 m	USFS-Modoc National Forest	12 and 14 June 2015
Wisconsin Creek, at base of South Fork	1932	Nye, Nevada	2,160	38.95	−117.26	256	1,940–2,893	0 (1 seen and heard)	Extirpated	USFS-Toiyabe National Forest	20 July 2014; 27 and 28 July 2013; 30 July–1 Aug. 2012
Highgrade Springs area	1932	Modoc, California	2,326	41.95	−120.23	245	2,240–2,365	1	Low occupancy (pikas detected at 2 of 14 patches) and very low density (0.043 individuals per 50-m transect); MEO: 2,375 m	USFS-Modoc National Forest	14 Sep. and 5 Nov. 2014; 12 June and 6 July 2015
Warner Mtns.	1935	Modoc, California	1,811	41.59	−120.24	79	1,829–2,456	9	Extirpated	USFS-Modoc National Forest	11 and 12 Sep. 2014; 13 June and 6 July 2015

[a] Due to extensiveness of talus at this site, surveyors could not search all habitat within the site during the standardized search effort. MEO may be as low as 2,472 m, the lowest-elevation talus habitat within the site.

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Table 2.—Sites in northeastern California (Lassen, Modoc, Shasta, Siskiyou, and Tehama Counties), with historic records of *Ochotona princeps* that we resurveyed in 2014, 2015, or both years. At American pika-extirpated sites, we surveyed all talus patches within 1 km of the historic collecting location. Unless noted, all historic specimens were collected and preserved as museum voucher specimens. E = east; N = north; S = south; W = west. NE = northeast; NW = northwest; SE = southeast; SW = southwest. NNE = north-northeast; NNW = north-northwest; WSW = west-southwest. NPS = (United States) National Park Service; USFS = United States Forest Service. dec. deg. = decimal degrees; Hwy = highway; mi = miles; Mtn. = mountain; Rd. = road.

Location	Date of most recent specimen	County	Latitude (dec. deg.)	Longitude (dec. deg.)	Elevation (m)	# of Historic specimens documented	Pika-occupancy status, within the site	Management jurisdiction	Sampling date(s)
Vicinity of Sugar Hill, 7.5 mi S of Fandango Pass Rd. (County Rd. 9) at Hwy 395, between Goose and Upper Lakes, Modoc National Forest	1 June 1910	Modoc[a]	41.81	−120.34	2,203	4 (1894); 2 (1910)	Extirpated	USFS-Modoc National Forest	8 Aug. and 13–14 Sep. 2014
In the vicinity of Mt. Shasta (N slope of Shastina cone)	24 July 1898	Siskiyou	41.42	−122.24	2,912	1 (1898)	Occupied	USFS-Shasta-Trinity National Forest	28 July 2008
In the vicinity of Grey and Red Buttes, ~3.5 mi S of Mt. Shasta Summit, Shasta National Forest	6 July 1988	Siskiyou	41.36	−122.20	2,217	13 (1898); 1 (1939); 9 (1988)	Occupied	USFS-Shasta-Trinity National Forest	9 July 2014; 17 Sep. 2011; 16 Aug. 2010; 29 July 2006
In the vicinity of Lassen Peak and headwaters of West Fork of Hat Creek, Lassen Volcanic National Park	16 Sep. 1923	Shasta	40.48	−121.50	2,309	3 (1898); heard in 1923	Occupied	NPS-Lassen Volcanic National Park	16 Sep. 2014
In the vicinity of Goosenest Peak, ~5.5 mi NNW of Grass Lake	16 July 1899	Siskiyou	41.72	−122.23	2,483	3 (1899)	Occupied	USFS-Klamath National Forest	14 June 2015
Along Mill Creek, 1.7 mi NE of Christine Hill, ~6 mi S of Lassen Peak	29 July 1899	Tehama	40.40	−121.51	1,524	1 (1899)	Extirpated	Mixed	10, 11, and 16 June 2015
In the vicinity of Warren Peak, ~7 mi NW of Eagleville, Warner Mtns.	21 July 2005	Modoc	41.37	−120.22	2,807	7 (1910); 6 (1988); 2 (2005)	Occupied	USFS-Modoc National Forest	17 Sep. 2014
In the vicinity of Upper Ice Cave, 2.9 mi SW of Hill Rd. at Medicine Lake, Lava Beds National Monument	16 Oct. 1912	Siskiyou	41.70	−121.57	1,558	1 (1912)	Occupied	NPS-Lava Beds National Monument	27 Aug. 2014
Near Fandango Peak, ~4.4 mi W of Fort Bidwell, between Goose and Upper Lakes, Modoc National Forest	10 Sep. 1917	Modoc[a]	41.86	−120.24	2,338	4 (1917)	Occupied	USFS-Modoc National Forest	27 Aug. and 15 Sep. 2014
Near head of Little Shasta River	15 May 1918	Siskiyou	41.81	−122.24	1,844	1 (1918)	Extirpated	USFS-Klamath National Forest	12 and 13 June 2015

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Table 2.—*Continued*

Location	Date of most recent specimen	County	Latitude (dec. deg.)	Longitude (dec. deg.)	Elevation (m)	# of Historic specimens documented	Pika-occupancy status, within the site	Management jurisdiction	Sampling date(s)
Upper Kings Creek Meadow and Kings Creek Falls, 2.7 mi SE of Lassen Peak, and ~2 mi E of Bumpass Hell, Lassen Volcanic National Park	10 Aug. 1958	Shasta	40.46	−121.45	2,274	4 at King Meadow, 6 at King Falls (1923)	Occupied	NPS-Lassen Volcanic National Park	16 Sep. 2014
4 mi SW of McDonald Peak	10 Oct. 1924	Lassen[a]	40.91	−120.46	1,632	1 (1924)	Extirpated	Mixed	29 and 30 July 2014
12–13 mi SW of Eagleville	8 Oct. 1924	Modoc	41.18	−120.28	1,738	7 (1924); 1 (1926)	Occupied	USFS-Modoc National Forest	8 and 16 Sep. 2014
Emerald Lake	7 Sep. 2006	Shasta	40.47	−121.52	2,504	1 + 2 (1924); 1 (2006)	Occupied	NPS-Lassen Volcanic National Park	21 Aug. 2014; 10 Oct. 2010
N slope of Flatiron Ridge, Kings Creek, 1 mi NW of Kelly's Camp	29 July 1924	Plumas/Shasta	40.44	−121.37	1,649	1 (1924)	Occupied	NPS-Lassen Volcanic National Park	17 Sep. 2014; 18 Oct. 2010; 28 Aug. 2009
Mount Lassen Rd., 2 mi W of Black Butte (Mt. Conard), at Bluff Falls	8 July 1924	Tehama	40.41	−121.53	2,073	3 (1924)	Extirpated	NPS-Lassen Volcanic National Park	13 Oct. 2010; 6 Aug. 2009
2 mi E of the SE end of Eagle Lake (above Bly Tunnel intake)	28 May 1925	Lassen[a]	40.61	−120.73	1,585	0 (1 individual heard in 1925, by same collector as record below)	Extirpated	Mixed	31 July 2014; 21 Oct. 2010; 9 Aug. 2009
2 mi E of the SE end of Eagle Lake (S face of Black Mtn.)	30 May 1925	Lassen[a]	40.59	−120.73	2,009	1 (1925)	Extirpated	Mixed	1 Aug. and 17 Sep. 2014; 19 Oct. 2010; 9 Aug. 2009
Butte Lake	4 Aug. 2007	Lassen	40.57	−121.29	1,847	21 + 1 (1926); 1 (2007)	Occupied	NPS-Lassen Volcanic National Park	30 Aug. 2009
5 mi NW of Eagle Peak	5 July 1926	Modoc[a]	41.34	−120.27	2,227	31 + 2 (1926)	Occupied	USFS-Modoc National Forest	18 Aug. 2014; 12 and 14 June 2015
W end of Battle Creek Meadows (i.e., 2 mi W of Mineral)	12 June 1928	Tehama	40.34	−121.62	1,468	1 (1928); 1 (1927)	Extirpated	USFS-Lassen National Forest	17 Aug. 2010
6 mi N of Mineral	8 June 1928	Shasta/ Tehama	40.43	−121.60	2,108	1 (1928)	Extirpated	USFS-Lassen National Forest	15 Sep. and 14 Oct. 2014; 10 Oct. 2010; 5 Sep. 2009
Highgrade Springs area, Modoc County	1 Sep. 1932	Modoc[a]	41.95	−120.23	2,326	1 (1932)	Extirpated	USFS-Modoc National Forest	14 Sep. and 5 Oct. 2014; 12 June 2015
3.5 mi E of Weed	22 Dec. 1934	Siskiyou	41.42	−122.32	1,445	2 (1934)	Occupied	USFS-Shasta-Trinity National Forest	9 Oct. 2014; 8 Jan. and 21 Apr. 2012
Warner Mtns.	21 June 1935	Modoc[a]	41.59	−120.24	1,811	9 (1935)	Extirpated	USFS-Modoc National Forest	11 and 12 Sep. 2014; 13 June 2015
3 mi N of summit of Goose Nest Mtn.	22 May 1935	Siskiyou	41.76	−122.22	1,463	2 (1935)	Unknown	USFS-Klamath National Forest	Not sampled

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Table 2.—*Continued*

Location	Date of most recent specimen	County	Latitude (dec. deg.)	Longitude (dec. deg.)	Elevation (m)	# of Historic specimens documented	Pika-occupancy status, within the site	Management jurisdiction	Sampling date(s)
2 mi N of Medicine Lake	10 May 1935	Siskiyou	41.61	−121.60	2,179	4 (1935)	Occupied	USFS-Modoc National Forest	15 June 2015
Whitney Butte, Lava Beds National Monument	8 May 1936	Siskiyou	41.74	−121.59	1,493	1 (1936)	Occupied	NPS-Lava Beds National Monument	14 Oct. 2014
Near Mayfield Ice Cave, 1.6 mi NW of Indian Springs Mtn., 13.4 mi NNE of Hwy 89 at McArthur Rd.	4 Apr. 1991	Siskiyou	41.32	−121.54	1,177	1 (1991)	Occupied	USFS-Modoc National Forest	1, 2, and 7 Nov. 2014
1.4 mi WSW of Warren Peak, and ~7.4 mi NW of Eagleville, Warner Mtns.	22 June 2005	Modoc	41.37	−120.24	2,429	1 (2005)	Occupied	USFS-Modoc National Forest	15 Aug., 17 Sep., and 7 Nov. 2014

[a] Sites that occurred in the insular portion of northeastern California: i.e., not biogeographically connected via a high-elevation landbridge to the Sierra Nevada-Cascade mountain chain.

individuals are prevented from behavioral thermoregulation, and its distribution appears to be shaped by climatic factors at numerous scales (e.g., Smith 1974; Beever et al. 2011; Erb et al. 2011). *O. princeps* inhabits easily identifiable habitats—taluses, boulder fields, lava-flow margins, and analogous sites—which usually do not change in extent or spatial distribution over the decadal timescales that correspond to our investigation. Consequently, results are not confounded by alterations to habitat structure (Beever et al. 2010). The species has been used widely as a model organism for demonstrating and testing ecological theory, including metapopulation dynamics (Hanski 1998), source–sink and stepping-stone dynamics (Kreuzer and Huntly 2003), and Island Biogeography Theory (MacArthur and Wilson 1963; e.g., Brown 1971). Thus, *O. princeps* has high potential to inform conservation research and efforts across many contexts.

Surveys occurred on 30 June–3 July, 25–28 August, 26 September 2014, and 30 August–6 September 2015 in Utah and June–November 2014 and June–July 2015 in the Great Basin and northeastern California (Tables 1 and 2). Limited Great Basin surveys also occurred in July 2012 and July–August 2013 (Tables 1). Our sampling closely followed principles and methods described by Beever et al. (2003, 2010, 2011, 2013). These included focusing searches around the cooler times of the day, especially from 0.5 h before sunrise until 3–4 h after sunrise, and in the last 3–4 h of daylight and 0.5 h after sundown. Additionally, at sites suspected to have suffered pika extirpations, we performed repeat surveys on 2 different days, and using increased transect density to search under nearly every pika-occupiable rock. Finally, we tallied the number of 50-m transects walked along elevational contours while using distance sampling and independent-observer double counts to quantify detectability and density of individuals (Table 1). Because contours were walked in continuous fashion up through the elevational extent of talus within sites, we were able to quite accurately establish the low-elevation limit of pika occupancy within each site (also see Beever et al. 2011, for more information). We used WAAS- and GLONASS-enabled handheld GPS units to record the minimum and maximum elevations of talus habitat we searched.

Individuals were indicated by a sighting, vocalization, or fresh haypile. We used several criteria to avoid double-counting multiple evidences of the same animal and to estimate density, following Beever et al. (2013; see Table 1). Low pika densities at many of our sites led us to more thoroughly develop a novel, ordered classification of the relative age of evidence of past occupancy (Table 3). Our field research protocols on *O. princeps* followed Sikes et al. (2011); we did not handle any pikas, nor did we noticeably disrupt any habitats (other than temporarily moving rocks at locations of sign detection).

Analytical approaches.—Predictor variables: We quantified amount of talus habitat by tallying, in situ, the number of 20-m-diameter circles of pika-occupiable talus (rock diameter 0.2–1.0 m) within each site, aided with laser range finders. Each circle approximates 1 home range (Smith and Weston 1990) and estimation with larger diameters has proven less

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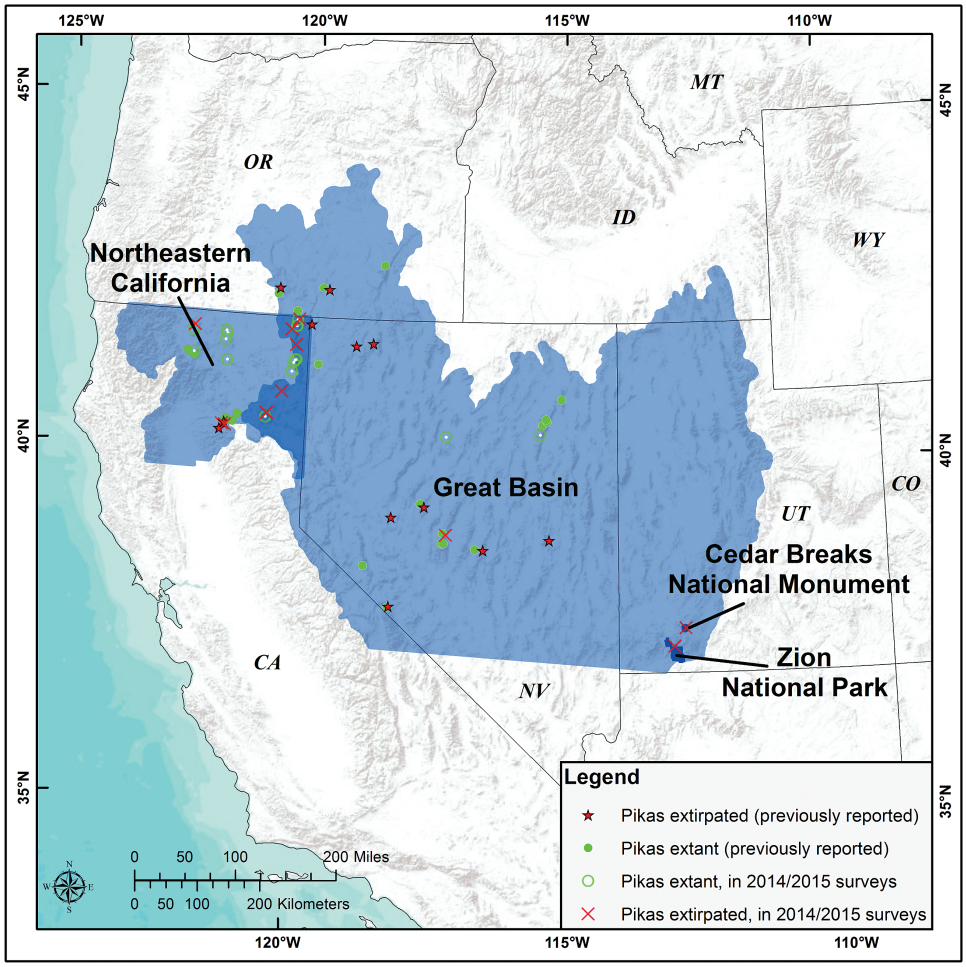

Fig. 1.—Map displaying sites of American pika (*Ochotona princeps*) resurveys (and their outcomes) from each of 3 regions (shown in blue). For context with past work in the Great Basin and northeastern California (Stewart et al. 2015), we included results from previous reports in those regions. Because there are no historical American pika records in the hydrographic Great Basin south of the indicated line, we truncated that portion of the region. CA = California; CO = Colorado; ID = Idaho; MT = Montana; OR = Oregon; UT = Utah; WY = Wyoming.

Table 3.—Classes of evidence of former occupancy of a site by *Ochotona princeps* found during extensive searches within talus (or analogous) habitat, ordered by how recently pikas are suspected to have occupied a site.

Evidence	Identification	Interpretation of evidence
No pika-relevant evidence		Either pikas never inhabited the target patch or occupied it so long ago that all evidences have decayed or disappeared.
Pika-created urine stains	Stains are generally circular, < 5 cm in diameter, or if along a rock ridge, < 3.5 cm in length: markedly different from woodrat and bird stains.	Most likely, most recent occupancy by *O. princeps* occurred many years to over a century ago.
Urine stains and old, hidden pika pellets (spherical, 2–3 mm in diameter)	In this category, pellets can be only discovered by excavating numerous rocks to uncover highly sheltered icrosites.	Age of pellets reflects a predictable sequence of colors, though rate of aging and decrease in pellet diameter will vary by ecoregion (e.g., more slowly, in drier regions—Nichols 2010). Most likely, most recent occupancy by *O. princeps* occurred many years to decades ago.
Urine stains and old pellets resting atop talus rocks	As in above category, but pellets are not all hidden.	Recent occupancy by pikas, from 1 year to multiple decades ago—depending on site factors.
Urine stains and old pellets resting atop talus rocks, plus old haypile(s)	Vegetation in haypile is not green (i.e., does not contain chlorophyll).	Most recent occupancy by pikas, from 1 year to multiple decades ago—depending on site factors.
Any combination of sighting(s), vocalization(s), or active haypile(s) present	Vegetation in haypile is green (i.e., contains chlorophyll), and there are ≥ 10 pieces of vegetation.	Current occupancy by *O. princeps* or use by *O. princeps* in the current year.

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accurate and less repeatable, across field surveyors of pika-relevant talus. Predictors were derived from 1-km resolution, daily DAYMET data (Thornton et al. 1997, 2000; hosted by NASA and Oak Ridge National Laboratory). DAYMET data reflect algorithms and software designed to interpolate and extrapolate from daily meteorological observations to create gridded (1 × 1 km) estimates of daily weather-related variables that include minimum and maximum temperature, precipitation, humidity, incident solar radiation, snow-water equivalent (a quantification of snowpack), and day-length. Whereas radiation is modeled as a function of sun-slope geometry and diurnal temperature range, humidity reflects the predicted daily-minimum and daily-average-daylight temperatures (Thornton et al. 2000). We used these output variables of DAYMET to derive each of our climatic predictors (Table 4), using a modified Thornthwaite-type water balance (following Lutz et al. 2010), and assuming a water-holding capacity of 50 mm in the water-balance model. Although additional temperature and water-balance variables are available, we only focused on predictors relevant to the behavioral, physiological, and forage-mediated mechanisms hypothesized in past research to directly or indirectly affect *O. princeps* (e.g., Beever et al. 2010, 2011; Erb et al. 2011; Beever et al. 2013). Sign of the coefficient (Table 4) refers to whether the predictor positively (i.e., directly) or negatively (i.e., inversely) explains persistence. Growing degree-days were estimated following McMaster and Wilhelm (1997). Each climatic predictor (described in Table 4 footnotes) represents the 34-year (1981–2014) average for that metric, spatially averaged across either all surveyed locations (at pika-extirpated sites) or all pika-occupied locations (at pika-extant sites) within the site. No spatial averaging was needed for Utah points; we just randomly selected 1 location from all the locations in that patch to use for analyses (see earlier text). Given the likely disparity across our pika-extirpated sites of the timing of when extirpations actually occurred (although exact dates of the extirpations are all unknown), we used the 1981–2014 time series as a standardized measure of aspects of prevailing climate recently experienced at each of our sites.

We performed multiple logistic regressions against each of our climatic variables in a 2-variable regression with talus-habitat area to assess the ability of area versus each aspect of climate to explain patterns of pika persistence within each region. Because several of our climatic predictors were correlated within 1 or more regions, we ran them in separate models to begin to investigate different mechanisms by which climate may act on pikas. For these regression analyses, each site (i.e., each row in Tables 1 or 2) constituted a statistical replicate in the Great Basin and in northeastern California. In contrast, each contiguous talus patch was treated as a replicate for Utah parks analyses (ZION and CEBR). The spatial extent encompassed by each site corresponded to the areal extent of each region (which affects how many nonoverlapping sites fit within the region) and to how conservative criteria for extirpation were. The Great Basin is by far the largest region (> 42 million ha for the minimum convex polygon around all sites), and we have used the most conservative criterion to assert site extirpation (i.e., all patches within the 3-km buffer had to be unoccupied) there. Our northeastern California region encompasses 5.72 million ha, and we used a less-demanding 1-km buffer within which all patches had to be unoccupied, to assert extirpation. On the other extreme, the Utah parks comprise only 62,391 ha, and all talus areas within ZION's 59,900 ha spanned far less than 5% of the park's area. Consequently, each replicate patch in Utah was considered unoccupied when no individuals were detected anywhere within the contiguous patch, which was distinguished from other patches by separation of ≥ 25 m of non-talus habitat. Given the differences among regions in the size of each replicate site, we could not join sites to perform cross-region analyses. Because our northeastern California region extends from the Sierra Nevada-Cascade mainland to the western edge of the Great Basin (defined as not connected to the mainland mountain chain by high-elevation habitat), we removed the 8 sites in the northeastern California region that occur in the Great Basin (see Table 2) for California analyses in Table 4.

Results

Patterns of Persistence and Distribution

Hydrographic Great Basin.—Locally comprehensive surveys at 9 sites (Table 1) suggest that *O. princeps* is apparently extirpated from 5 (Table 1). Adding our new sites to those previously reported equates to extirpation of pikas from all talus patches within 3 km of each of 15 of 34 (44.1%) sites across the Great Basin with historical (pre-1991) records (Fig. 2). Of the 25 sites surveyed initially during 1898–1990, 24% had suffered pika extirpation by 1999 and 40% by 2008 (Fig. 2), thus providing greater clarity in that region about the rate of site-wide extirpation through time. Additionally, relative to the low-elevation limit in surveys during 2003–2008 (see Methods and Appendix V of Beever et al. 2011), the lowest-elevation detection of pikas across the Great Basin moved upslope as much as 380 m within sites and moved > 15 m upslope within 5 of 16 sites. Within the protected Army Depot on and near Big Indian Mountain (Wassuk Range, Mineral County, Nevada—Beever et al. 2003), the lowest detection of pikas in 2012–2014 surveys occurred 392 m above the lowest old fecal pellets we detected. This restricted-access site constitutes our 1st effort to more comprehensively survey below the minimum elevation of pika occupancy that we have detected at this site since the historic records; such efforts allow us to retrospectively establish pika distributions in the decades before our surveys in 1994–1999.

Southern Utah.—We surveyed 515.5 50-m transects on 32 talus patches in ZION (including 360.5 in 2015), 58 transects on 7 patches within CEBR (including 35.5 in 2015), and 146 transects on 19 additional patches in areas around CEBR. Pikas are apparently extirpated from all patches from which they were known in both ZION (n = 1–3 patches at Lava Point; first reported by Stock 1970) and CEBR (n = 3 patches). In CEBR, pikas were detected at those 3 patches (with photographic or video evidence; C. Waters) each year during 2009–2012 inclusive, but not in 2014 or 2015 surveys. However, after 2014

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Table 4.—Results of 2-factor, multiple logistic regressions assessing the ability of talus-habitat area and each of 8 temperature and water-balance variables to explain American pika occupancy within each of the 3 regions evaluated. The test statistic (χ^2) reflects a Wald chi-squared test (estimate of the coefficient/SE)^2, testing whether the coefficient is significantly different from zero. ET = evapotranspiration; PET = potential evapotranspiration.

Climatic factor	Great Basin, 2014 and 2015 sites only (n = 22 sites)						Utah national parks (n = 82 patches)						Mainland portion of northeastern California (n = 21 sites)					
	Climate-factor results, in each model			Habitat-area results, in each model			Climate-factor results, in each model			Habitat-area results, in each model			Climate-factor results, in each model			Habitat-area results, in each model		
	χ^2	P value	Sign of coefficient	χ^2	P value	Sign of coefficient	χ^2	P value	Sign of coefficient	χ^2	P value	Sign of coefficient	χ^2	P value	Sign of coefficient	χ^2	P value	Sign of coefficient
Annual ET[a]	5.39	0.020	–[i]	0.19	0.66	+	12.08	<0.0001	–[i]	0.78	0.38	+	0.43	0.51	–[i]	3.48	0.062	+
Annual water deficit[b]	4.63	0.031	–	0.08	0.78	+	10.89	0.001	–	0.12	0.73	+	0.23	0.63	–	3.49	0.062	+
Annual precipitation[c]	0.64	0.426	+	0.04	0.85	+	15.27	<0.0001	+	0.04	0.85	+	0.48	0.49	–	2.23	0.135	+
Average temperature[d]	4.72	0.030	–	0.58	0.45	+	14.13	0.0002	–	0.03	0.86	+	1.19	0.27	–	3.59	0.058	+
Annual rain[e]	0.62	0.431	–[i]	0.02	0.88	–[i]	13.32	0.0003	–[i]	0.06	0.80	+	1.76	0.18	–[i]	2.97	0.085	+
Max. snowpack[f]	1.66	0.198	+	0.02	0.90	–[i]	15.36	<0.0001	+	0.00	0.97	+	0.17	0.68	+	3.50	0.062	+
Annual PET[g]	4.91	0.027	–	0.39	0.53	+	12.58	0.0004	–	0.38	0.54	+	0.32	0.57	–	3.51	0.061	+
Cumulative growing degree-days[h]	4.50	0.034	–	0.43	0.51	+	13.28	0.0003	–	0.02	0.90	+	1.03	0.31	–	3.58	0.059	+

[a] Annual ET is the sum of monthly actual evapotranspiration. Actual evapotranspiration is the amount of water transpired through vegetation and evaporated from soil. On a monthly basis, it can be limited by temperature, soil moisture storage, and precipitation inputs.
[b] Annual water deficit is the sum of monthly deficits, the difference between potential evapotranspiration and actual evapotranspiration.
[c] Annual precipitation is the sum of monthly precipitation in both frozen and unfrozen forms.
[d] Average temperature is the annual average of monthly temperature averages.
[e] Annual rain is the sum of monthly rainfall.
[f] Max. snowpack is the maximum snow-water equivalent regardless of month in which it occurs.
[g] Annual PET is the sum of monthly PET values estimated using the Hamon (1963) equation.
[h] Cumulative growing degree-days is an annual sum of heat units expressed as daily growing degree-days.
[i] The sign of the coefficient was opposite of our hypothesized directionality, given that *Ochotona princeps* typically is associated with cool, moist areas (Hafner 1993).

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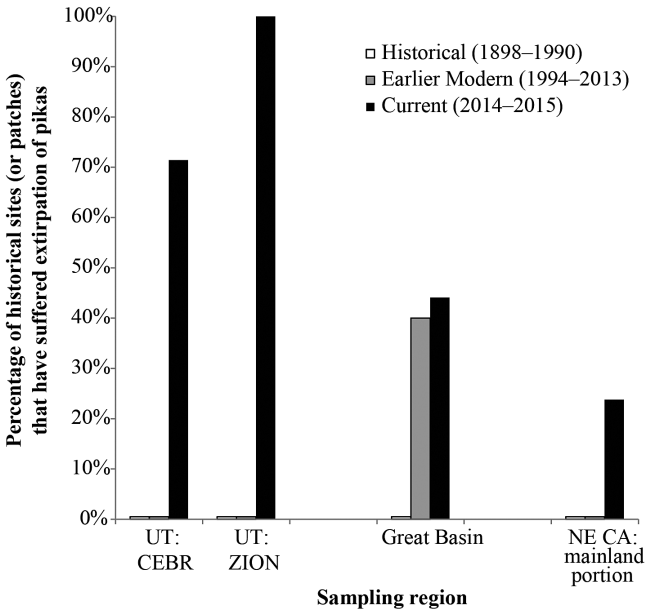

Fig. 2.—Summary of the percentage of sites with historical records of American pikas (*Ochotona princeps*) that had suffered extirpation by the end of the historical (1898–1990), earlier modern (1994–2013), and current (2014–2015) periods for CEBR, ZION, the hydrographic Great Basin, and northeastern California. There remains uncertainty for the dates at which pikas were extirpated from each site in northeastern California and from several sites in the Great Basin, as well as for patches with no historical records in Utah. Because of the scarcity of historical records of American pikas within CEBR, we used the percentage of patches in the monument with any pika pellets that had pika occupancy within 2014–2015, for that "current" estimate. CEBR = Cedar Breaks National Monument; ZION = Zion National Park; NE CA = northeastern California.

surveys, we identified 4 additional talus patches in this forested park that has few roads and trails, using CalTopo.com. Surveys in 2015 detected a total of 4 pika individuals: 2 at each of 2 of the 4 newly discovered talus patches within CEBR (Fig. 2). Inside CEBR, elevations of the 2 pika-occupied patches ranged from 3,074 to 3,102 m, whereas the 5 unoccupied patches ranged from 2,970 to 3,218 m. On adjacent Dixie National Forest land, the 12 pika-occupied patches spanned 2,702–3,371 m, whereas the 7 unoccupied patches ranged from 2,658 to 3,372 m. Pika density inside CEBR averaged 0.069 individuals per 50-m transect and averaged 0.363 individuals per 50-m transect on adjacent Dixie National Forest land. All 12 unoccupied patches contained old sign (haypiles, fecal pellets, or both) of pikas; the amount and distribution of sign suggested previous pika occupancy rather than simply exploratory use. Straight-line distances to the nearest other pika-occupied patch are 0.51 and 1.49 km from the CEBR pika-occupied patches, respectively.

In ZION, we failed to detect pikas at any of 7 talus patches around Lava Point, at which pikas were last reported in 2011 during pika surveys (C. Crow and K. Day, pers. obs.). We detected no evidence of current pika occupancy at any of the 41 talus patches we surveyed in ZION (Fig. 2), but we did not sample at 9 talus patches in 2 private inholdings. The 41 patches occurred in 5 areas of the Park and spanned elevations from 2,125 to 2,645 m. The 9 unsampled patches occurred at elevations 199–349 m below the highest-elevation patches we searched within ZION, and CalTopo.com imagery suggested that altogether they only contained 23.5 home ranges of talus habitat, 13 of which were in the 3 lowest-elevation patches. We detected evidence of previous pika occupancy (old pellets only) at 30 patches, which ranged from 2,132 to 2,645 m. The 11 patches with apparently no pellets ranged from 2,158 to 2,362 m.

Northeastern California.—Among the 29 locations of historical records of *O. princeps* that we sampled in 2014 and 2015, pikas have apparently been extirpated from 11 sites (37.9%; see Fig. 2). One additional low-elevation (1,463 m; see Table 2) site was inaccessible due to private land. Additionally, during 2013–2016 surveys across the east side of the Lassen National Forest (T. Rickman and E. A. Beever, pers. obs.), we documented loss of pikas from another 2 sites that they occupied as recently as 2012 and encountered only evidence of previous pika occupancy (Table 3) at 57 additional talus patches. Collectively, these results suggest that changes in *O. princeps* distribution in this region are widespread.

Relationship of Persistence to Variables Related to Temperature and Water Balance

Our logistic regression analyses suggest that both temperature-related and water-balance-related variables estimated from DAYMET strongly explained pika persistence at sites in the Great Basin and in Utah, but that talus area poorly ($\chi^2 < 0.80$, $P \geq 0.38$) predicted persistence in all models for those 2 regions (Table 4). In fact, Great Basin wide, extirpated sites had on average 1.15× more talus within 3 km than pika-extant sites. In the Sierra-Cascade portion of northeastern California, however, habitat area more strongly predicted pika persistence ($\chi^2 \geq 2.23$, $0.058 < P \leq 0.135$) than did the climatic predictor in all models, and no climatic predictor governed persistence ($0.18 < P < 0.69$; Table 4). The sign of the coefficient of all variables was the same across all 3 regions (negative for all variables except maximum snowpack, which was consistently positive), except for annual precipitation in northeastern California; however, the probability associated with each of our climatic variables varied between the Utah and Great Basin regions (Table 4). Each of our 8 aspects of climate strongly predicted occupancy in Utah, whereas only the 5 temperature-related metrics strongly predicted pika persistence in the Great Basin. Contrary to our hypothesized relationships, annual rainfall and annual evapotranspiration negatively predicted persistence of pikas in all 3 regions; the sign of coefficients for all other predictors was as we predicted, except for the above-mentioned effect of annual precipitation in northeastern California (Table 4). Within the Utah data, if ZION records were removed (i.e., if only CEBR locations were used), no variable predicted pika occupancy.

Discussion

Differing conservation status and differing controls on status and trends in mainland versus insular areas.—Our results illustrate that mainland and more insular areas differ not only in their

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trends in population persistence (with isolated areas exhibiting steeper declines) but also in the relative importance of climatic factors versus habitat extent in mediating those trends. Our finding of higher rates of extirpation in isolated areas compared to the Sierra Nevada and Rocky Mountain mainlands corroborates earlier research across the western United States. For example, whereas we report extirpation of pikas from 44.1% of all historical sites (15 of 34) in the hydrographic Great Basin, Stewart et al. (2015) document pika extirpation from only 10.9% of sites (5 of 46) in the Sierra Nevada and its eastern flank. In the northern Great Basin, extensive surveys of talus patches across Sheldon and Hart Mountain National Wildlife Refuges (Collins and Bauman 2012) found 12 of 32 sites currently occupied, 6 sites with only old sign, and 14 sites classified as "unoccupied or possibly extirpated." If future surveys find old pellets at one or more of these latter 14 sites, then the extirpation rate of 33.3% (12 of 18) of the recently suitable patches would increase accordingly. Millar and Westfall (2010) classified only 2% of their sites (6 of 329) in the Sierra Nevada where they detected any evidence of current or past pika occurrence as "old," but 50% of such sites (8 of 16) in the more isolated central Great Basin as "old." In a study of Rocky Mountain (mainland) sites, Erb et al. (2011) found pikas absent at only 5.8% of resurveyed sites (4 of 69), and subsequent surveys have detected pikas at 2 of those 4 sites (L. Erb, University of Colorado at Boulder, pers. comm.). Because our northeastern California study region spans from a portion of the Sierra Nevada-Cascades "mainland" chain all the way out into the western fringe of the insular Great Basin, this allowed us to test which subportion of this study region experienced a greater rate of extirpation. Although the mainland portion experienced sitewide extirpation of pikas from only 23.8% (5 of 21) of sites, the insular portion experienced a 75% loss (6 of 8 sites). Millar and Westfall (2010) reported *O. princeps* in the Sierra Nevada as low as 1,827 m, whereas the lower-elevation bound of pika occupancy within Great Basin historical pika sites has risen by as much as 661 m (mean ± 1 SE = 222.1 ± 51.8 m).

Although we found widespread evidence of distributional loss (local extirpations, upslope retractions, and encounter of only old sign; Table 3) in all 3 study regions in 2014 and 2015, aspects of temperature and water balance strongly explained extirpations among sites in both of the more insular regions (Utah and the hydrographic Great Basin) but not in the region that included parts of the Sierra Nevada-Cascade mainland. Although increases in growing degree-days would intuitively seem to benefit herbivores such as pikas that have high forage intake requirements and often live in areas with short growing seasons (Hafner 1994), growing degree-days was negatively associated with pika persistence in all 3 regions. Bell-shaped curves of niche theory and the "Goldilocks effect" of Jeffress et al. (2013) suggest, however, that above some level of degree-days, further increases would inevitably lead to declines in *O. princeps* abundance and distribution.

Local amount of field-tallied habitat poorly explained persistence in both the Great Basin and in Utah. This suggests that in these regions, climate is acting as an additional filter to constrain pika distribution, in that otherwise perfectly suitable talus remains unoccupied in these regions. In contrast, Stewart et al. (2015) found amount of remotely sensed talus habitat within a 1-km radius to be 1 of the 2 best predictors of persistence (along with average summer temperature), and extirpated sites in the northern Sierra Nevada had the smallest amount of local talus habitat among their sites (Stewart and Wright 2012). Similarly, areal extent of talus-like mine-tailing patches proved an important factor in extinction–recolonization dynamics of a metapopulation on the eastern flank of the Sierra Nevada (Moilanen et al. 1998). Our results (Table 4) further reinforce the importance of talus-habitat area, for pikas in the Sierra Nevada-Cascade mainland. Although all but 2 of our models had $0.05 < P \leq 0.06$ for the effect of habitat area, several authors (e.g., Taylor and Gerrodette 1993) have argued that in instances of potential ecological declines, investigators should consider assigning different importance to type I and type II errors (e.g., by adjusting alpha to $P \leq 0.10$). When we analyzed all 29 sites in northeastern California, which spans from the mainland to the western fringe of the Great Basin, we found "hybrid" results that reflect the region's biogeographic mix. Namely, in all 5 models that included an aspect of temperature (i.e., excluding annual precipitation, annual rain, and maximum snowpack), both habitat area and the climate factor predicted persistence ($P < 0.10$). Furthermore, likelihood ratio tests (which compare the full model against the model with that factor removed) for each of those 5 models suggested that both habitat area and the climate factor predicted persistence ($P < 0.05$).

Although we considered them separately, talus area and climatic factors may also interact in several ways that have important implications for Island Biogeography Theory. As climate isoclines generally rise up mountain ranges, over time: 1) previously continuous habitable areas become fragmented for climatically stenotopic species; 2) mountaintop island areas decrease; and 3) isolation from adjacent mountaintops effectively increases (e.g., Brown 1971; McDonald and Brown 1992). Brown (1971) and subsequent authors have considered the Great Basin as a nonequilibrium system, in that cooler periods during the Pleistocene facilitated dispersal among largely contiguous habitats across the Basin, but that subsequent warming has led to conditions where extirpations of mountaintop mammals are no longer being balanced by colonizations (in part due to the intervening valleys' warmth). Furthermore, although no North American montane mammal is more obligately tied to a specific, obvious habitat type than is *O. princeps*, changing climatic aspects such as interstitial temperature and climatic water balance can convert physically suitable habitat to being ecologically uninhabitable. Failure to incorporate such phenomena into biogeographic analyses in insular terrestrial areas could introduce significant error into analyses. A different approach to these challenges involves bioclimatic-niche modeling. Although bioclimatic-niche models account for climatic suitability, they typically do not include structural or biological requirements or constraints on habitat, nor do they index the microclimates that are used daily by species but are several orders of magnitude finer resolution than a single climate-modeling pixel (Potter et al. 2013).

Because the 2014 drought across the western United States may have exerted immediate and lagged effects on more

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continuously distributed populations through direct physiological and indirect mechanisms of stress, our results may simply reflect waning years of distribution or 1-year-lagged effects of it. However, at a majority of our extirpation sites, we found no evidence of even recent occupancy, but only evidence of occupancy further in the past (Table 3). Despite our rigor and conservative approach, we acknowledge that some sites considered pika-extirpated may contain pikas at low densities. For example, populations existing at low densities for several generations might evolve lower detectability, as the cost of vocalizations (i.e., risk of predation) may outweigh benefits of territorial defense. Relative to most other populations of *O. princeps* across western North America, several populations in northeastern California vocalize less frequently (E. A. Beever, pers. obs.). Forecasts of increasing frequency of drought and more generally, decreased precipitation and increasing water stress in ecosystems of the southwestern United States (e.g., Seager et al. 2007), may portend challenges for species such as pikas that are associated with mesic conditions (Hafner 1993).

Status versus trend information, to inform conservation?—Resurvey results such as ours and others from diverse geographic, jurisdictional, and topographic contexts (Erb et al. 2011; Stewart et al. 2015) underscore the need for more extensive sampling and monitoring, especially in northeastern California, where so many local losses have already occurred. Resurveys are valuable not only because of their (often) longer-term perspective on occupancy over time (with greater inference deriving from increasing numbers of resurvey events) but also because they remove the confounding effects of habitats that may never have been suitable by excluding them. On the other hand, historical surveys, even comprehensive and spatially extensive ones such as that of Hall (1946), were almost never designed probabilistically, and thus provide an incomplete picture of status. In our case, recent surveys have detected *O. princeps* at additional, previously unsurveyed, sites in the Great Basin not connected by high-elevation corridors to the Sierra Nevada (n = 2 sites by Millar et al. [2013], n = 14 sites by Collins and Bauman [2012]), some within < 10 km of extant and extirpated sites reported here. There are areas with talus habitat that have never been surveyed historically *for O. princeps* (Beever et al. 2008), and surveys in northwestern Nevada during 2015 hold some promise for identifying new occurrences and thus refining our understanding of the pika's distribution in the Basin (M. Jeffress, Nevada Division of Wildlife, pers. comm.). However, we expect few new discoveries in the central Great Basin, except in the Toiyabe Range. Furthermore, a historic record associated with "Adel" (Oregon, elevation 1,280 m; reported in Verts and Carraway 1998), although it had no field notes and was thus not included in our analyses, produced only old evidences and suggested another sitewide extirpation. Surveys, which spanned 4 days during 20–27 June 2016 and involved 174.5 50-m transects that spanned from 1,414 to 2,073 m on 14 talus patches, uncovered buried pellets at 4 locations (1,933–2,034 m), and an old haypile at another 4 locations (1,942–2,020 m). Surveys by the 4 data collectors extended up to the highest elevations of talus within 20 km of Adel, including to the north, south, and west of Adel. Along the more hospitable microclimates of Camas Creek (≥ 16.8 km away), we detected buried pellets and 1 old haypile at 3 locations, from 1,682 to 1,702 m elevation.

The localized range losses reported here corroborate the loss of pikas (as evidenced by copious amounts of buried or very old pellets, but no evidence of current occupancy) from dozens of patches elsewhere in the Sierra Nevada, Cascade Range, (less frequently) portions of the Greater Yellowstone Ecoregion, and other portions of *O. princeps*' geographic range (E. A. Beever, pers. obs.). However, many locations of pika detection in previously unsurveyed areas have been reported from the Sierra Nevada and its eastern spur ranges (Stewart and Wright 2012; Millar et al. 2013, 2014; Stewart et al. 2015) and from the major mountain chains of Utah (K. Asmus-Hersey, Utah Division of Wildlife, pers. comm.).

Conversely, without the longer-term perspective afforded by historical information, it is impossible to assess a species' trend in coarse-scale distribution—and depending on the nature of the historical surveys—or in fine-scale occupancy or abundance. Despite widespread occupancy and apparent resiliency to climatic forces in some regions (e.g., Millar and Westfall 2010; Manning and Hagar 2011), important information on fitness, persistence versus extirpation, colonization, microclimatic conditions, and historical baselines are frequently lacking to support robust inference on population status, trend, and niche width (e.g., Anthony 1928:476; Van Horne 1983). Collectively, conservation and management are best informed by understanding of both status and trend. Ideally, monitoring animals of conservation concern into the future will employ probabilistic designs, to allow strong inferences regarding both status and trend (e.g., via rotating-panel designs).

Water balance, temperature, and habitat area as possible drivers of distributional change among montane animals.—Although the pervasiveness and rapidity of contemporary climate change appear likely to have led to distributional changes in innumerable species, empirical demonstration of exactly how and why the changes occurred has proven elusive. In a recent worldwide meta-analysis of all species, out of 136 studies focusing explicitly on local extinctions associated with climate change, Cahill et al. (2013) identified only 7 studies that identified the proximate causes of the extinctions. Although high-elevation mountain ecosystems contain sharp climatic gradients as well as the majority of the world's most strongly protected areas (Joppa and Pfaff 2009; Sanderson et al. 2015) and ultimate sources of freshwater, the systems' isolation means that climate monitoring and species monitoring within mountains are relatively sparse, thus weakening the ability to identify the mechanisms by which climate acts on species distribution. Nonetheless, recent research has identified numerous types of microrefugia, within which microclimate is decoupled from the broader-scale climate, in mountainous ecosystems, including areas of cold-air pooling, local valley bottoms, gorges, north-facing aspects (in the northern hemisphere; south-facing, otherwise), and riparian corridors (Dobrowski 2010). Such microrefugia facilitate pika occupancy in the Columbia River Gorge near sea level (Varner and Dearing 2014b; Beever et al.

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2016), in Craters of the Moon National Monument in the Snake River Plain (Rodhouse et al. 2010), and in Lava Beds National Monument (Beever 2002; Ray et al. 2016) and likely at a few other of our low-elevation sites in northeastern California. By demonstrating the role that topo-edaphic factors play in moderating temperature and water availability, Dobrowski (2010) described how microclimates support subpopulations through unfavorable periods or in spatially isolated places, even as regional conditions of temperature and water availability change through time. Because mountains contain physiographically complex landscapes, it is important to use fine-resolution climate data and knowledge of topographic and edaphic modifiers to understand distributional responses of mammal species to climate.

Many of the climatic factors limiting distributions of species involve mechanisms related to climatic water balance (Dobrowski 2010). Although early efforts to understand responses of montane species to climate identified aspects of temperature as primary determinants of the pattern of occupancy or distributional change (e.g., Beever et al. 2003; Walther et al. 2005; Moritz et al. 2008), more recent research has identified precipitation (Erb et al. 2011) or aspects of water balance as also being critically important (Beever et al. 2013; Rapacciuolo et al. 2014). The seasonal interactions between precipitation and temperature that affect both physical and biological processes are simplified in the water-balance concept, because it estimates the simultaneous availability of energy and water that drive these processes (Stephenson 1998). In hydrologic applications, water balance has been used to describe riverine response to seasonal snow accumulation and water runoff (Gray and McCabe 2010). In ecological applications, it has been used to understand global patterns in biome distributions (Frank and Inouye 1994) and primary productivity (Goulden et al. 2012), as well as to identify apparent drivers of plant species distributions (e.g., Stephenson 1998; Lutz et al. 2010; Piedallu et al. 2013). In remote-sensing studies, water balance has been shown to be a better predictor of spatial and temporal patterns in primary productivity across broad areas than simple measures of temperature or precipitation (Campo-Bescós et al. 2013). Although aspects of water balance may affect montane mammals directly, indirectly, or both, water balance has only recently begun to be applied to investigation of distributional shifts in animals.

Paleoecological research illustrates that across 2 major geological epochs of the Quaternary, mammal species did not simply move upslope and northward, but instead exhibited a wide diversity of apparent distributional responses (Lyons 2003). Specifically, at transitions from the preglacial to the glacial period (~20,000 years ago) and from the glacial to the Holocene (~10,000 ± 500 years ago), species shifted their distribution in nearly all different azimuths, with varying distances from the previous range centroid, and with vast differences in the change of the size of the geographic range (Lyons 2003). Similarly, although many montane species are shifting their contemporary distributions upwards (especially at the lower-elevation range margin—Wilson and Gutiérrez 2011), responses will often be nuanced and context-specific (Jeffress et al. 2013). For example, although dominant plant species across 2,000 m of elevation in the Santa Rosa Mountains retained the same lower- and upper-elevation bounds, the relative abundance of individuals of each species declined towards the lower-elevation boundary but increased at all elevations above the earlier mean elevation. These changes produced an elevationally skewed distribution of abundance (Kelly and Goulden 2008). Rapacciuolo et al. (2014) reviewed a wide diversity of distributional responses among bird, butterfly, plant, and mammal species across California, including shifts in many populations and communities that defied expectations based solely on increased mean temperature. In particular, Tingley et al. (2012) found that downslope shifts in bird species occurred as frequently as upslope shifts and Crimmins et al. (2011) found that plant species shifted downslope more frequently than they shifted upslope (but see Stephenson and Das 2011). Furthermore, Rapacciuolo et al. (2014) reported that much of the mainland portion of our northeastern California study region actually cooled, received more precipitation, and experienced lower climatic water deficit during 1970–2009 compared to during 1900–1939. Such finer-scale trends in climate may have contributed to lower rates of, and importance of climatic factors in, pika extirpations in that region.

The importance of our work in this regard is that we have shown strong relationship of pikas in 2 different more insular regions to aspects of both temperature and water balance (consistent with Wilkening et al. 2011; Ray et al. 2012; and Beever et al. 2013), but no significant relationship to climate in the Sierra Nevada-Cascade mainland in northeastern California (consistent with findings of Stewart et al. 2015 that talus area strongly predicted pika persistence across California). The test statistics and sign of the relationships in all regions (Table 4), especially the counterintuitive result that annual rainfall at sites negatively rather than positively predicted persistence, suggest a particularly strong influence of temperature mediating extirpations, especially in the Great Basin region. The inability of annual precipitation to explain patterns of persistence in the Great Basin and northeastern California suggests that this variable mixes the vastly different climatic phenomena of winter snow and growing-season rain (and their associated mechanisms of influence on montane species) into a single heterogeneous variable. Further post hoc analyses using a derivative of the DAYMET data that crudely approximates whether water is limiting in a system—namely, whether (annual precipitation [P] − annual potential evapotranspiration [PET]) is greater than zero—suggest that water is generally not limiting across our sites, on an annual basis. However, this generalization belies the fact that the (P − PET) was < 0 in 24.8% of site-year combinations, among pika-extirpated locations. Collectively, our work reinforces the notion that further research is needed to ascertain the relative importance of chronic, acute, and very acute climate stressors on animals, as well as the importance of water balance across key time periods that may be limiting (such as before and after parturition or during driest months of the year). Our continuing research efforts in these regions involve

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radiocarbon-dating fecal pellets to understand when extirpated sites were last occupied (sensu Millar et al. 2013), comparing plant chemistry at pika-extirpated and pika-occupied sites, and use of microclimatic sensors to understand highly local conditions that can quantify types of acute and chronic temperature stress. Because we were unable to explicitly include edaphic factors in our modeling of water balance, we encourage this as an avenue for future research attention.

Conservation and management implications.—Investigation of possible mechanisms by which such distributional changes are occurring is critically important for informing conservation and management responses. This might include locating activities such as borrow pits and rock quarries to sites where pikas are already extirpated or where modeling clearly indicates that they are unlikely to persist. Alternatively, the atypical nature of some pika habitats in northeastern California suggests that they may be refugia for disjunct populations of other species (e.g., mosses, lichens, arthropods, bats, amphibians) associated with cool, moist conditions.

More fundamentally, such analyses indicate the types of climate-related wildlife losses that may increase in the coming decades, their rates, and the types of contexts where they may occur. Given how widely *O. princeps* has been heralded as an early warning indicator of faunal response in mountain ecosystems facing climate change (e.g., Krajick 2004; Holtcamp 2010), a geographically broad update on pika resurvey results is timely. Although widespread and comparatively rapid distributional changes have previously been reported in *O. princeps* from the hydrographic Great Basin, this paper identifies 2 other regions of relatively strong distributional change in *O. princeps*.

Losses of *O. princeps* may cause cascading changes in ecological systems due to its ecosystem engineering (nutrient redistribution, selective herbivory, seed dispersal) and trophic roles (due to the fact that so many species prey upon them—Aho et al. 1998). Because these losses have been occurring at many sites that contain hundreds of home ranges of physically suitable talus habitat, reserve-style management, or both, our results illustrate that contemporary climate change can cause distributional losses even without any physical habitat loss and even in protected areas. The frequency and magnitude of these distributional losses contrast strikingly with the density and occupancy of the species < 370 km away from the Great Basin at elevations near sea level in the Columbia River Gorge (Varner and Dearing 2014a, 2014b). This juxtaposition of status and trend suggests that climate does not act unilaterally across geographic ranges of species. Instead, burgeoning research on *O. princeps* has collectively shown the heterogeneity and nuance with which climate can act on the distribution of mountain-dwelling animals.

Acknowledgments

We thank K. Condon, M. Curran, J. French, A. Gill, C. Giordano, J. McFarland, K. Orlofsky, L. Pettinger, J. Roper, K. Taylor, and A. Whipple for fieldwork assistance. We thank A. Johnston, C. Millar, and J. L. Wilkening for critical comments on an earlier version of this manuscript and several anonymous reviewers for their input. We thank J. Stewart for providing estimates of talus area for 9 sites in northeastern California. Funding was provided by the Great Basin LCC and the U.S. Geological Survey. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government.

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Submitted 10 April 2015. Accepted 05 July 2016.

Associate Editor was Duke Rogers.

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