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Reports

On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*)

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Abstract. Alpine species are among those most threatened by climatic shifts due to their physiological and geographic constraints. The American pika (*Ochotona princeps*), a small mammal found in mountainous, rocky habitats throughout much of western North America, has experienced recent population extirpations in the Great Basin linked to climatic drivers. It remains unclear whether these patterns of climate-related loss extend to other portions of the species' range. We investigated the distribution of the American pika and the climatic processes shaping this distribution within the Southern Rocky Mountain region. Results from a survey of 69 sites historically occupied by pikas indicate that only four populations have been extirpated within this region over the past few decades. Despite relatively few extirpations, low annual precipitation is implicated as a limiting factor for pika persistence in the Southern Rockies. Extirpations occurred only at sites that were consistently dry over the last century. While there was no climate change signal in our results, these data provide valuable insight into the potential future effects of climate change on *O. princeps* throughout its range.

Key words: *alpine; climatic change; distribution;* Ochotona princeps; *pika; Southern Rockies.*

Introduction

Climate change is affecting alpine communities worldwide (Hughes 2003, Krajick 2004). Empirical evidence from alpine plants in Europe (Lenoir et al. 2008) and alpine mammals in western North America (Moritz et al. 2008) clearly shows range retraction in many species as a response to climate change, generally due to an upslope shift in their lower elevational limits. However, few studies have demonstrated local extinctions at lower elevations, and fewer still have investigated specific climatic drivers that may lead to local extinction.

One species for which population extirpations have been documented is the American pika, *Ochotona princeps*. The American pika is a small, herbivorous lagomorph that resides primarily in talus (rocky debris) found in mountain ranges and high plateaus of western North America. Pikas worldwide benefit from metabolic and behavioral adaptations allowing them to survive cold winters without hibernating (Li et al. 2001, Sheafor 2003). However, because their resting body temperature is only a few degrees below lethal body temperature (Li et al. 2001), pikas are sensitive to temperature extremes. This sensitivity, coupled with high habitat specificity and low vagility in contemporary climates (Smith and Weston 1990), suggests that climate change could contribute to extirpation of pika populations.

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American pikas have become a bellwether species for alpine taxa in peril (Krajick 2004), partly because they are conspicuous, charismatic denizens of alpine communities, and partly because population declines have been attributed to climatic changes (Beever et al. 2003, 2010, Grayson 2005). Distributional shifts and population extirpations in the Great Basin and Sierra Nevada have been linked to recent climatic trends (Beever et al. 2003, 2010, Moritz et al. 2008) as well as climate change over the last glacial-interglacial period (Grayson 2005).

As evidenced by the recent decision not to protect this species under the Endangered Species Act, it remains unclear exactly how climate change is affecting the American pika across its full geographic range (Crist 2010). Although pika populations have been lost from fragmented, lower-elevation habitats in the Great Basin (Beever et al. 2003, 2010), it is unknown whether local extinctions are occurring in more contiguous habitats where populations are more likely to be rescued through dispersal. The Southern Rocky Mountains support some of the southernmost populations of the American pika, and represent the largest, most continuous region of habitat occupied by the species, including great heterogeneity in elevation and vegetation. This region is also climatically heterogeneous, and the intensity of climate change—experienced thus far and projected in future—varies greatly across the region (Mote et al. 2005, Knowles et al. 2006).

Here we analyze change in the distribution of the American pika throughout the Southern Rocky Mountains to assess the generality of a climate-mediated range

shift in this species. This study also improves the spatial extent and resolution of data on the current range of this species and its climatic drivers. Though naturalists recorded pika populations in the Rocky Mountains as early as 1872, the current regional distribution of the species is unknown. Here we examined whether the distribution of pikas in the Southern Rockies has changed in the last century by documenting where pikas were found prior to 1980 and surveying a subset of these locations in 2008. We sought to explain the persistence pattern seen in this region by surveying potential covariates of extirpation, including landscape characteristics (e.g., elevation), microhabitat features (e.g., talus properties), and climatic trends. We used these covariates to construct and evaluate alternative models of pika persistence within an information theoretic framework.

Methods

Study area and design.—Our research was conducted at 69 sites historically occupied by pikas in the Southern Rocky Mountains of southern Wyoming, Colorado, and New Mexico (41°30′ to 35°20′ N and 104°54′ to 108°17′ W; Fig. 1). Historically occupied sites were defined as those with documented pika presence prior to 1980, after which anthropogenic climate change became prominent in many datasets (IPCC 2007). Nearly 800 historical records of pikas were found in the region, gleaned from georeferenced museum specimens (from GBIF data portal *online*),[4] individual museum records (Denver Museum of Natural History and University of Colorado Museum of Natural History), and literature sources. Our 69 sites were selected based on geographic accuracy; selected sites had a mean georeferenced radius location error estimate of 1.3 km and maximum error of 3 km. Sites varied in elevation from 2703 to 4340 m and dates of historical records range from 1872 to 1979. The most common vegetation communities consisted of alpine forbs and grasses, but communities dominated by willow (*Salix* spp.), conifers, or aspen (*Populus tremuloides*) were also relatively common.

Climate data.—Local climate data for each site were compiled for the years 1908–2007. The climatic data necessary for site-specific climate calculations were obtained from PRISM, which provides these grid-based estimates at a 4 km^2 resolution over the time scales in question (PRISM climate calculations *available online*).[5] As with any interpolated data, particularly in a mountainous region, PRISM estimates may not be accurate for the exact coordinates of our historical records. However, because the precision of our historical records averaged over 1 km in radius and individual pikas can disperse over 2 km (Tapper 1973) we feel PRISM data were at an appropriate scale for this analysis. In a post-hoc analysis to account for fine-scale effects of solar gain within PRISM grid cells, we estimated insolation at each site as sin(mean slope) × cos(mean aspect), similar to Martinuzzi et al. (2009).

Resurveys.—Crews visited 69 sites in the summer of 2008 to determine current pika occupancy. Resurveys were comprised of searches for fresh pika sign: detection of individuals by sight and sound and fresh pika food stores ("haypiles"). Any one of these signs was considered evidence of current occupancy. Due to the difficulty of determining scat age, scat was not used as evidence for current pika occupancy. If visited early in the season (July), sites lacking fresh sign were revisited in fall (October or November) to verify site status. Where no fresh sign was found, exhaustive searches were conducted in all talus within the precision estimate for each georeferenced location, to a maximum distance of 3 km in all directions from the estimated historical coordinates. A minimum of 0.5 person-hours per hectare was spent searching talus for pika sign at each of these extirpation sites. In addition to pika occupancy data, we collected data on suspected drivers of pika persistence at a site, including microhabitat variables.

Analysis.—Using maximum likelihood estimates and an information-theoretic approach for model assessment, we compared models of pika persistence incorporating elevation, maximum summer temperature, annual precipitation, and site characteristics with potential climate-buffering effects such as rock type, talus depth, porosity of individual rocks, and evidence of persistent soil moisture beneath the talus. Talus depth was estimated visually at the deepest crevice found at a site, and rocks were defined as porous or not based on the presence of natural holes and pits in their surfaces. Visible or audible running water or pools under the talus and riparian vegetation at the base of the talus slope were all considered evidence of persistent sub-talus moisture.

The models explored in this study (Table 1) represent hypotheses derived from previous literature in other portions of the species' range, suggesting temperature and precipitation (Beever et al. 2003, 2010, Millar and Westfall 2010, Wilkening et al. 2011) as strong predictors of pika occupancy and persistence. Our hypotheses were also influenced by the results of Millar and Westfall (2010), Hafner (1994), and Smith (1974), suggesting talus properties provide climate-buffering effects for pikas. Elevation was included as a covariate because it often varies with a suite of environmental variables. We did not explore effects of latitude, as we felt this variable was redundant with climatic data used to test more specific hypotheses. Models represented the following hypotheses: pika persistence is related to (H1) the severity of changes in temperature and precipitation since initial pika detection (pikas persist in locations where the least change in climate has occurred); (H2) prevailing climatic conditions (pikas persist where the dominant climate over the last century was relatively wet and cool); (H3) variation in climatic trends over the last

[4] ⟨http://data.gbif.org⟩
[5] ⟨http://www.prismclimate.org⟩

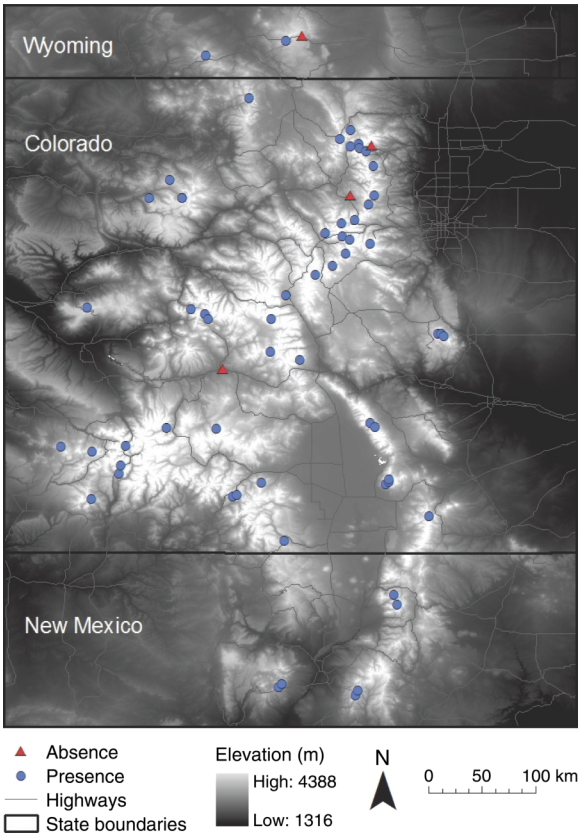

FIG. 1. Map of 69 sites historically occupied by the American pika (*Ochotona princeps*), differentiated by recent occupancy status in 2008 (blue circles, occupied; red triangles, unoccupied).

century (pikas persist where they have been exposed to the least climatic variability); (H4) habitat quality (pikas persist in locations with the deepest talus, most porous/insulating rock, and/or where water or ice persist under the talus); (H5) elevation (pikas persist at higher elevation locations).

Thirty models with three or fewer uncorrelated ($|r| < 0.5$) predictor variables were evaluated using the program PRESENCE (MacKenzie et al. 2002), allowing us to incorporate detection probability into our models. This study and others have found the probability of detecting this species to be quite high (>0.90; Beever et al. 2010, Rodhouse et al. 2010). Given this high detectability, we report the results of traditional logistic models, but results were identical in PRESENCE. Model fit was evaluated using Nagelkerke's max-rescaled R^2 (R^2_N), which provides a measure of the proportion of variance explained through logistic regression (Nagelkerke 1992).

RESULTS

The results of our pika surveys indicate that local population extirpations have been relatively few in the Southern Rockies: only four of 69 sites lacked recent sign of *O. princeps* in 2008 (Fig. 1). Despite the low number of extirpations recorded, analyses of these data indicate that the pattern of extirpation was not random. The model that best explained persistence ($R^2_N = 0.68$) included mean precipitation (average annual precipitation from 1908 to 2007) and decline in precipitation (the difference, in mm, in average annual precipitation for the period 1908–1979 vs. 1980–2007). A similar model with additional effects of persistent moisture under the talus (positively associated with pika occupancy) obtained similar support ($\Delta AIC_c = 0.94$; $R^2_N = 0.72$). These two top models have been averaged for depiction in Fig. 2. A full list of models with $\Delta AIC_c < 4$ can be found in Table 2.

In the Southern Rockies, climatic factors, rather than landscape or most microhabitat variables, appear to be the most influential in driving pika population extirpations. While our four extirpation sites were all roughly south- to southwest-facing (170° to 258°), a post hoc analysis of insolation indicated that this factor was not influential in pika extirpation. This result, combined with the fact that nearly half of our sites ($n = 31$ of 69) were roughly south facing, suggests that aspect is not predictive of American pika distribution in this region. Models incorporating elevation, talus depth, and rock porosity were not supported by the persistence pattern found. Our four extirpation sites ranged from 2703 to 3393 m (mean = 3116 m) in elevation and from 0.5 to >1.5 m in maximum talus depth. The talus at all four extirpation sites, along with 57 additional sites, was not comprised of porous rock. Vegetation type varied among sites, but reflected the dry nature of these locations: all extirpations occurred at locations dominated by montane grasses, shrubs, evergreens, or aspens, rather than forbs or riparian vegetation.

Pika populations have been extirpated from among the driest pika habitats in this region (Fig. 3a). Climate at our 69 sites varied dramatically, with average maximum summer (June–August) temperatures for the period 1908–2007 ranging 13.4–22.9°C and mean annual precipitation ranging 461–1407 mm for the same period. The mean annual precipitation across all sites between 1908 and 2007 was 884 mm (sd = 184 mm; range = 461–1407 mm), while the mean across extirpation sites was 593 mm (sd = 137 mm; range = 461–717 mm), a significant difference (Welch's t test for populations with unequal variance, $t = 4.06$; df = 3.66; $P = 0.02$). Extirpation sites have also shown relatively little change in mean annual precipitation since 1980 (Fig. 3b). In addition, extirpation sites are among the 47 sites apparently lacking a sub-talus water source. These results support our hypotheses H2 (prevailing climatic conditions) and H4 (habitat quality). While change in climate (H1) was influential for pika persistence, the trend was opposite our expectation: pikas were extirpated from sites that did not experience climatic change. Hypotheses represented by models incorporating aver-

TABLE 1. Alternative hypotheses and candidate model covariates.

Hypothesis: pika persistence is related to	Covariates used in constructing candidate models
The severity of changes in temperature and precipitation since initial pika detection	change in mean annual precipitation (1908–1979 vs. 1980–2007); change in maximum annual summer (June–August) temperature averaged over 1908–1979 vs. 1980–2007
Prevailing climatic conditions	mean annual precipitation (1908–2007); maximum annual summer (June–August) temperature averaged over 1908–2007
Variation in climatic trends over the last century	coefficient of variation in annual precipitation (1908–2007); coefficient of variation in maximum annual summer (June–August) temperature (1908–2007)
Elevation	average elevation of talus habitat found at a site
Habitat quality (as a climatic buffer)	each climatic variable above; talus depth; porosity of rock substrate; presence of water under talus

Note: Each candidate model contained one to three covariates.

age maximum summer temperatures, change in summer maximum temperatures, and variation in both summer maximum and mean annual precipitation were not supported by the persistence pattern found. Since 1980, maximum summer temperatures at our study locations have averaged 0.48°C warmer than they were from 1908 to 1979. Changes in maximum temperature varied widely among sites (−1.2°C to +2.5°C), as did changes in annual precipitation (−80 mm to +203 mm, −8.0% to +24.1%). The overall trend in this region appears to be toward an increase in annual precipitation: across all sites, precipitation has increased an average of 46mm (+5.6%).

DISCUSSION

In this study, we investigated landscape, microhabitat, and climate characteristics as possible drivers of population extirpation for *O. princeps*. Determination of these factors is particularly important in light of the recent consideration of this species for protection under the Endangered Species Act (ESA). The species was not listed under the ESA, in part because it remains unclear whether the patterns of climate-related loss observed in the Great Basin extend to other portions of the species' range. This study serves to narrow this knowledge gap and improve our understanding of pika distribution and the factors determining this pattern.

In the Great Basin, sub-talus high mean summer temperatures and low minimum winter temperatures were implicated as drivers of population extirpation (Beever et al. 2010). Millar and Westfall (2010) examined Sierra Nevada talus slopes and found that warmer, drier sites were less likely to support current pika populations than cooler, wetter sites. Here, we consider whether such patterns are consistent with results from the eastern portion of the species' range.

Extant pika populations in the Southern Rockies are experiencing substantial climatic change. Maximum summer temperatures are highly heterogeneous, but indicate a notable warming trend. Despite these changes in summer temperature, we did not find an effect of temperature on pika persistence in our study area.

While a recent impact of temperature on *O. princeps* populations does not appear universal throughout the species' range, an apparent impact of precipitation is more consistent. Our results indicate that water, in the form of precipitation and sub-surface moisture, is the primary driver of pika persistence patterns in our study region. Not only were the four extirpation sites among the driest of our sites, but they also lacked sub-talus water sources, a trend corroborated in the Sierra Nevada, where Millar and Westfall (2010) found a strong relationship between pika sign and high precipitation as well as sub-talus ice and water reserves. If present, these water sources could buffer pikas and the plant communities on which they depend from the effects of low precipitation.

If low precipitation drives extirpation in the Southern Rockies, one might expect populations experiencing a decrease in annual precipitation due to modern climate change to be more prone to extirpation. Thus far, however, this is not the case. Extirpation sites have experienced relatively little change in precipitation between the periods 1908–1979 and 1980–2007. The fact that sites experiencing decreasing precipitation

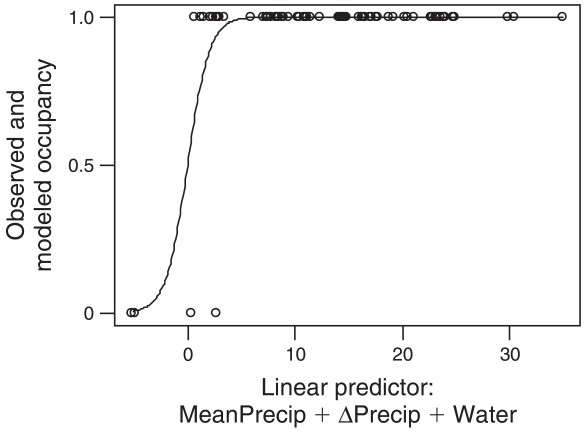

FIG. 2. Pika persistence (occupancy proportion) as observed (open circles) and as predicted (line) by a logistic function of local mean precipitation (MeanPrecip; mm), change in precipitation (ΔPrecip; mm), and presence of sub-talus water (Water).

TABLE 2. Results of logistic regression modeling.

Model	AIC_c	ΔAIC_c	Number of parameters	−2log-likelihood	Akaike weight	R^2_N
Mean precip, Δprecip	17.70	0	3	11.33	0.49	0.68
Mean precip, Δprecip, sub-talus water	18.64	0.94	4	10.01	0.35	0.72
Mean precip	21.04	3.34	2	16.86	0.08	0.50
Mean max temp, porous	21.23	3.53	3	14.86	0.08	0.57
Constant (null)	30.61	12.91	1	30.55	0.00	

Notes: Only models with $\Delta AIC_c < 4$ and the null model are shown. Definitions of variables: Mean precip, average annual precipitation, 1908–2007; Δprecip, difference between mean annual precipitation for 1908–1979 and 1980–2007; sub-talus water, presence of water under talus; mean max temp, mean of maximum June–August temperatures for 1908–2007; porous, porosity of individual rocks. R^2_N is Nagelkerke's max-rescaled R^2.

continue to support pikas may seem contradictory with the finding that populations at dry sites are more prone to extirpation. However, the sites that have decreased in precipitation since 1980 were among the wettest locations previously (pre-1980: mean = 968 mm vs. mean = 849 mm at sites increasing in precipitation; $P = 0.04$, $t = 2.25$, df = 18.95). Consequently, these 13 drying sites did not differ from the 56 remaining sites in mean post-1980 precipitation (950 mm/yr and 910 mm/yr, respectively; $P = 0.46$, $t = 0.76$, df = 20.15). It will be important to monitor these locations in the coming years and decades, as continued drying trends could place the pika populations at these sites at risk for future extirpation.

Although our documented extirpation sites represent the driest of the sites surveyed, pikas were detected in these locations in the past century. What, then, has changed? These extirpation locations may be marginal pika habitats. As such, these sites have likely always housed "sink" populations, requiring immigration from adjacent populations in order to maintain populations of their own (Pulliam 1988). We propose that these current extirpation sites likely support populations only when climatic conditions facilitate recolonization by individuals dispersing from adjacent sites. Local climate histories show that each of the four extirpation sites experienced a year in which annual precipitation exceeded the site's upper 99% CI for this variable just 1–4 years before the site's historical record of pika presence. This evidence suggests that dispersal may be facilitated by anomalously high precipitation conditions.

Our data indicate that precipitation is a driver of pika distribution in the Southern Rockies, but why are dry sites unable to sustain pika populations? The mechanism driving the trends we have found could be explained by several possible scenarios, including (1) low-precipitation sites do not provide adequate vegetation moisture content to sustain pika populations (Morrison and Hik 2007, 2008); (2) low-precipitation sites do not provide adequate snowpack insulation to buffer pikas from subzero temperatures (Beever et al. 2010); (3) a combined effect of plant water content and winter insulation. While Beever et al. (2010) did not investigate precipitation directly, they hypothesized that if sufficient snow cover is present during extreme cold events, pika populations are buffered from these events by the insulating properties of snow cover. Our results may support this hypothesis, given that our extirpation sites, which exhibited persistently low precipitation, may also lack sufficient snow cover. Our extirpation sites also lacked sub-talus water, a likely correlate of both low snow cover and reduced moisture in local vegetation. Thus, the potential mechanisms proposed are difficult to tease apart with current data. More detailed analyses of plant water content, sub-talus temperatures, and pika survival are needed to fully examine this question.

Conclusions.—Pikas in the Southern Rocky Mountains have not experienced the severe declines in site occupancy seen in the Great Basin. While these results suggest cause for optimism concerning the current status of the pika, the future of the species remains uncertain.

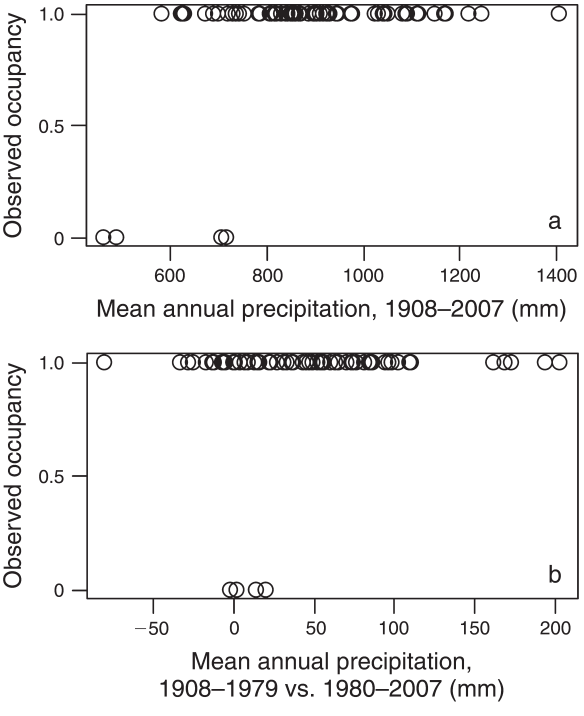

FIG. 3. Occupancy in 2008 vs. (a) mean annual precipitation (1908–2007) and (b) change in mean annual precipitation (comparing 1908–1979 and 1980–2007) for 69 sites historically occupied by pikas.

Our data, combined with evidence from other regions within the species' range (Beever et al. 2010, Millar and Westfall 2010), indicate that the American pika's distribution is limited by climatic factors: populations in areas with chronically low precipitation and lacking sub-talus water sources have been extirpated, supporting previous observations that these dry habitats are marginal for this species (Hafner 1993, 1994). Though the Rocky Mountains provide habitats that are higher in elevation and more contiguous than those in the Great Basin, as the severity of climate change increases in the American West, population extirpations may become more frequent throughout the species' range. Projected declines in snowpack throughout the western United States (Mote et al. 2005) suggest that apparently stable pika populations in regions such as the Southern Rockies may soon be facing drier conditions. Further monitoring of both pika populations and climatic trends should be conducted throughout the range of *O. princeps* to facilitate a range-wide analysis of trends in and threats to this species. Such an exercise would not only provide a better understanding of threats to the species, but may also aid managers in identifying extant pika populations that are at greatest risk of future extirpation.

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