

Testing alternative models of climate-mediated extirpations

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Abstract. Biotic responses to climate change will vary among taxa and across latitudes, elevational gradients, and degrees of insularity. However, due to factors such as phenotypic plasticity, ecotypic variation, and evolved tolerance to thermal stress, it remains poorly understood whether losses should be greatest in populations experiencing the greatest climatic change or living in places where the prevailing climate is closest to the edge of the species' bioclimatic envelope (e.g., at the hottest, driest sites). Research on American pikas (*Ochotona princeps*) in montane areas of the Great Basin during 1994–1999 suggested that 20th-century population extirpations were predicted by a combination of biogeographic, anthropogenic, and especially climatic factors. Surveys during 2005–2007 documented additional extirpations and within-site shifts of pika distributions at remaining sites. To evaluate the evidence in support of alternative hypotheses involving effects of thermal stress on pikas, we placed temperature sensors at 156 locations within pika habitats in the vicinity of 25 sites with historical records of pikas in the Basin. We related these time series of sensor data to data on ambient temperature from weather stations within the Historical Climate Network. We then used these highly correlated relationships, combined with long-term data from the same weather stations, to hindcast temperatures within pika habitats from 1945 through 2006. To explain patterns of loss, we posited three alternative classes of direct thermal stress: (1) acute cold stress (number of days below a threshold temperature); (2) acute heat stress (number of days above a threshold temperature); and (3) chronic heat stress (average summer temperature). Climate change was defined as change in our thermal metrics between two 31-yr periods: 1945–1975 and 1976–2006. We found that patterns of persistence were well predicted by metrics of climate. Our best models suggest some effects of climate change; however, recent and long-term metrics of chronic heat stress and acute cold stress, neither previously recognized as sources of stress for pikas, were some of the best predictors of pika persistence. Results illustrate that extremely rapid distributional shifts can be explained by climatic influences and have implications for conservation topics such as reintroductions and early-warning indicators.

Key words: American pika; climate change; climate-induced stress; Great Basin, North America; information-theoretic analyses; niche conservatism; *Ochotona princeps*; physiological stress; population extinction.

INTRODUCTION

The abundance, distribution, and demography of animals are known to track climate-related variables over a broad range of spatial (Post and Forchhammer 2002) and temporal scales (Post and Stenseth 1999,

Walther et al. 2002, Martínez-Meyer et al. 2004, Parmesan 2006). Within mountainous terrain in particular, the distributional limits of biotas have long been known to be strongly controlled by climate (Merriam 1894, Grinnell 1917), which, in such terrain, reflects latitude, elevation, and other abiotic factors such as precipitation and temperature (Rickart 2001, Körner 2007).

The recent, global increase in temperature has been near the upper limit of previous predictions (Rahmstorf et al. 2007) and rivals or exceeds the rate of temperature change during any time in the last 20 000 years (Root and Schneider 2006). The magnitude of temperature increases during the 20th century varied spatially and temporally, being greater at higher latitudes, in the northern hemisphere, and at middle and higher elevations (Beniston 2003, Walther et al. 2005), especially in

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spring and late winter (Fig. 1; Abatzoglou and Redmond 2007).

The rate of these climatic changes may exceed the capacity of many species to evolve physiological and other adaptations to altered climate (Davis et al. 2005, Parmesan 2006, Barnosky and Kraatz 2007). If local adaptation is minimal and the bioclimatic niche of a species is fixed across its geographic range, then individuals should be physiologically stressed at sites near the climatic “edge” of this bioclimatic envelope. Under this hypothesis, extirpations should occur at sites where the prevailing climate is near the edge of the envelope, regardless of the magnitude of climate change. Field observations supporting this hypothesis include disproportionate losses of species from the lowest elevations (e.g., Walther et al. 2005, Wilson et al. 2005) and northward extensions (Parmesan et al. 1999, Thomas and Lennon 1999, Guralnick 2007) of species’ geographic ranges. Species in warming climates have tracked not only the recent northward migration of climatic isoclines, but also the seasonal (within-year) migration of climatically appropriate windows for critical life processes. Species have tracked these changes by breeding earlier (Beebe 1995, Réale et al. 2003), arriving earlier to springtime habitats (Bradley et al. 1999), or emerging earlier from hibernation (Inouye et al. 2000). Strikingly, however, studies have only rarely identified climate change as a primary driver of local extinction or extirpation (McLaughlin et al. 2002).

Alternatively, local adaptation to microclimate may be the norm, especially for species that are broadly distributed yet have relatively poor dispersal capabilities. Although the hyperdimensional “width” of a species’ bioclimatic niche may be fixed over ecological time, the location of the niche on a climatic continuum can slide over evolutionary time, due to local adaptation. Still, if the climate changes too rapidly or severely, the species may fail to adapt. Under this hypothesis, losses should be determined primarily by the magnitude of change in (rather than absolute values of) climatic conditions at each site. In support of this hypothesis, numerous animal taxa have been shown to exhibit rapid evolution in thermal tolerance (Good 1993, Skelly and Freidenburg 2000). This hypothesis is also supported by the high frequency (Lema 2008) of phenotypic plasticity, which may allow species to accommodate highly variable and physiologically stressful environments (Réale et al. 2003). Behavioral thermoregulation, e.g., in the duration and timing of an individual’s foraging bouts or aboveground activity, is a particularly relevant example of such plasticity. Porter and Gates (1969) used “climate space” models that incorporated radiation, air temperature, wind, and humidity to mechanistically describe the bioclimatic niche that species may occupy and suggested that individuals could vary their metabolic rate, water loss rate, fur or fat thickness, and diel periods of activity to accommodate climatic extremes. Ecotypic variation, especially in traits that modify the

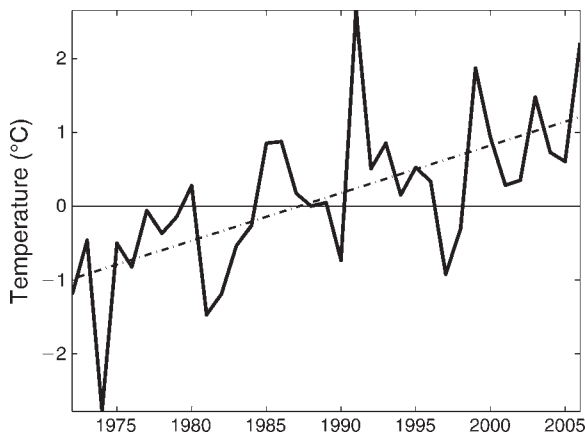


FIG. 1. February–May mean temperatures at 2438 m elevation, averaged across the Great Basin ecoregion in North America (37.5–45° N, 110–117.5° W), as derived from National Centers for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) data. Free-air temperatures on isobaric surfaces from the NCEP/NCAR reanalysis were areally averaged over the ecoregion and then linearly interpolated using temperature and geopotential height fields to estimate temperature on a fixed-height surface. The horizontal line represents the biologically important temperature above which snow melts, and the months (February–May) represent the important transition season for snowmelt.

influence of climate (e.g., body size and shape; Millien et al. 2006), is another type of local adaptation supporting this hypothesis.

American pikas (*Ochotona princeps*) are small (120–175 g) lagomorphs that inhabit taluses and talus-like structures (e.g., lava flows, mine tailings) in cool, higher-precipitation microhabitats across western North America (Smith and Weston 1990). This species is typically found in alpine habitats, yet does not hibernate. Populations in the Great Basin of western North America have been lost from a number of sites, during both prehistoric (Grayson 2005) and historical (Beever et al. 2003) periods. Several lines of evidence suggest that 20th-century losses were tied to thermal stress (Beever et al. 2003): pikas were lost from hotter and drier sites, from sites at lower elevation, and especially from sites lacking a thermal refuge (the best predictor of persistence was the maximum elevation of habitat available to the population).

Experimental research has shown that pikas are particularly vulnerable to acute heat stress. When denied access to cooler, sub-talus microclimates, individuals die if exposed to ambient temperatures as low as 25.5–29.4°C (MacArthur and Wang 1973, Smith 1974). Furthermore, analysis of location records for 2239 *O. princeps* museum specimens suggested that the species is a faithful indicator of cool microhabitats that receive relatively high precipitation (Hafner 1993).

In this research, we have sought to determine whether pika persistence in the Great Basin can be explained by climatic variables alone. We present new data on recent

population losses in the Basin and ask whether all losses from historical times through 2007 are best explained by recent climate change or by the prevailing climate at each site. For each site, these two alternatives were respectively defined as (1) change in climatic parameters between the two periods, 1945–1975 and 1976–2006, and (2) climatic parameters based on data recorded recently (2005–2006) or modeled over a long period (1945–2006).

Root and Schneider (2002) concluded in their review that relatively few studies have been able to establish climatic influence as the unequivocal driver of observed changes in a species' distribution, abundance, morphology, or phenology. More recently, several authors have strongly advocated for a mechanistic understanding of how climate change affects species (e.g., Walther et al. 2002, Root and Schneider 2006). Accordingly, we sought to ascertain which (if any) of three classes of thermal stress, chronic heat stress, acute heat stress, and acute cold stress, might best explain pika losses over the past century. In each case, we defined stressful climatic conditions in accordance with past research on the species (MacArthur and Wang 1973, 1974, Smith 1974, Hafner 1993). Each metric of stress was calculated from data on both the prevailing climate and the change in climate at each site. For example, we calculated a metric of acute-heat stress (the number of days above 28°C) for the entire period of 1945–2006, as well as the change in this metric between the periods of 1945–1975 and 1976–2006. We used an information-theoretic approach to compare support for these different mechanisms of thermal stress (including models with multiple variables) as predictors of pika persistence across 25 sites in the Great Basin. Our results suggest that climate stresses individuals either directly (e.g., by exceeding energy or physiological thresholds for water balance or upper lethal temperature) or indirectly via effects on their food supply, altered distribution of their predators, or increased susceptibility to pathogens (Porter et al. 2000).

MATERIALS AND METHODS

Study system

The hydrographic Great Basin of western North America, roughly as defined by Brussard et al. (1998), served as the study domain (see Fig. 1 map in Beever et al. 2003). Many of the Basin's mountain ranges exhibit a sharp topographic gradient, up to nearly 3000 m of relief, with consequent zonation in climate and vegetation. Because many species are isolated on "sky islands" at the tops of these mountains, the Basin has served as a prominent stage for biogeographical research (e.g., Brown 1971, Johnson 1975, Fleishman et al. 2001), development of climate change predictions (McDonald and Brown 1992), and theoretical critiques and refinements on this work (Skaggs and Boecklen 1996, Lawlor 1998, Grayson 2005, 2006). Only recently have ecologists recognized that the metapopulation dynamics and persistence of species within the Basin may be affected less by patch size and isolation than by factors such as

patch quality and climatic influence (Fleishman et al. 2002, Beever et al. 2003). Among the montane mammals analyzed in biogeographic treatments of the Basin, *O. princeps* is one of the most obligately montane (high-elevation) species (Rickart 2001, Grayson 2006). For the current analysis, we conducted research at 24 sites with historical records of *O. princeps* (Beever et al. 2003), plus one additional site where pikas were recently discovered (Beever et al. 2008). We compared recent presence/absence data (gathered during 1994–2007) with historical records of pika occurrence (dating back to 1898). Most of these historical records were generated by E. Raymond Hall, one of the foremost mammalogists of the 20th century. We used fine-resolution sampling of the species at each historical site; collectively, sites spanned an area of 38.2 million ha.

Multiple sets of independent data suggest a direct or indirect connection between climate and population biology of American pikas (*Ochotona princeps*) and suggest that the species is ideal for studying climate-related hypotheses regarding recent losses. The species occurs across 18° of latitude and >23° of longitude, ~5° of each within the Basin (Hall 1981). This broad distribution, combined with the species' relatively poor dispersal ability and consequent mountaintop isolation, has led to description of 36 subspecies across the species' range, six of which occur within our study region (Hall 1981). Taken together, these two facts mean that populations with divergent recent evolutionary histories experience unique climatic regimes. Furthermore, their relatively rich paleological record indicates that pikas have experienced range expansions and contractions over the past few millennia, in concert with glacial–interglacial cycles (Grayson 2005). Smith (1974) and MacArthur and Wang (1973) experimentally demonstrated pikas' vulnerability to heat stress. This vulnerability stems from the species' high body temperature (mean = 40.1°C), which is higher than that of any other North American lagomorph (Katzner et al. 1997) and very near the species' upper lethal temperature (mean = 43.1°C; MacArthur and Wang 1973, Smith 1974). This high mean body temperature reflects a high basal metabolic rate: 143% of that predicted by allometric models. The small difference between mean and lethal body temperatures reflects low thermal conductance, as low as 53% of the value predicted by *O. princeps*' body mass (MacArthur and Wang 1973).

American pikas are particularly appropriate for studies of climate-induced range shifts. They are locally abundant and highly detectable (Beever et al. 2008) and are found only in an easily identifiable habitat (taluses and boulder fields; Smith and Weston 1990, Hafner 1994). Furthermore, their relatively stable population sizes (Smith 1980, Southwick et al. 1986) further reduce the possibility that the species could remain undetected due to a temporary decline in population size. Stability of taluses and boulder fields, over ecological timescales, allows for the rare opportunity to investigate climatic

influences on biotas independently of habitat loss. Although pika dynamics may be affected by fine-scale habitat degradation (Beever et al. 2003), recent petitions to protect this species under U.S. state and federal laws cite climate change as the primary threat (e.g., Wolf et al. 2007).

Fieldwork

Following methods in Beever et al. (2003), we surveyed each of 25 historical-population sites during two periods: 1994–1999 (Beever et al. 2003) and 2005–2007. In brief, each site was surveyed for eight hours within talus habitat, during which time taluses within 3 km of the historical point location were sampled for evidences of pikas. Three kilometers represents an approximate upper limit of typical dispersal distances for *O. princeps*. To improve our effectiveness in locating specific patches of talus that were historically occupied, we consulted the field notes of historical collectors, when available (see Beever et al. 2008). Historical records of *O. princeps* in the Basin date from 1898 to 1956, plus one record from 1990 (cited in Lawlor 1998). During 1994–1999, E. A. Beever surveyed each of these sites at least once each during late June to August. Where no pikas were detected, sites were resurveyed one to three times during this period. Following a similar protocol during 2005–2007, all surveys of a given site were conducted on a similar Julian date. Site surveys were supplemented with four or more visits per site during April through November, both to increase confidence in absence data and to retrieve data from temperature sensors. Although surface activity of *O. princeps* varies appreciably throughout the year, behavior did not change noticeably during the <7 weeks during July and August in which our sampling of nearly all sites occurred. These times encompass the peak of above-talus activity of pikas during the year (Smith and Weston 1990).

Sampling involved walking line transects, partitioned into 50-m segments, along contours ~15 vertical meters apart, and recording locations of unequivocal evidence of the species (i.e., sighting, vocalization, or active hay pile) with a handheld GPS unit equipped with a wide-area augmentation system (WAAS; accuracy = 3–7 m). Because the species' surface activity can become crepuscular and even nocturnal at thermally stressful locations (Smith 1974), the sampling period at warmer (e.g., lower-latitude, lower-elevation) sites excluded midday and included one hour before sunrise and one hour after sunset. We used double sampling by independent observers within each segment to estimate the detectability of individuals. We also used several other sampling methods (see Beever et al. 2003) to increase our confidence in apparent extirpations. During 2000s sampling, we increased sampling density at sites of apparent extirpation; after the first visit, transects were positioned only 5–7 m apart. The elevational span of taluses sampled within sites was 441 ± 49 m (mean \pm SE, maximum = 872 m).

Quantification of climatic stress

We installed a network of temperature sensors (DS1921G Thermochron i-Buttons, Maxim Integrated Products, Sunnyvale, California, USA) at 156 locations across the Great Basin in late spring 2005. To approximate the conditions experienced by individual pikas better, most sensors were placed ~80 cm below the talus surface in talus patches exhibiting past or current evidence of pikas. Each sensor was placed in a thin waterproof PVC casing and attached to baling wire, which was wrapped around a small rock that was covered from direct sunlight; this entire apparatus was used to carefully thread each sensor into talus interstices. To facilitate data retrieval from sensors, we used GPS navigation with WAAS, written and pictorial descriptions of sensor location within the talus patch, and nontoxic paint to indicate sensor location. Sensor positions spanned up to 608 m of elevation (256 ± 32 m) and diverse aspects (chosen randomly from among those available) within sites. Temperature was recorded to the nearest 0.1°C every two hours during May–September 2005 and every four hours thereafter. The former frequency allowed us to characterize heat stress with higher resolution during the first year.

We considered certain temperatures to be directly stressful to pikas based on previous research. Our metric of acute heat stress was the number of days in which the maximum temperature was above 28°C. Above 28°C, pikas that have been prevented from behavioral thermoregulation (held in full sun, above the talus) have perished (Smith 1974). Our metric of chronic heat stress was the mean temperature (i.e., across all times of the day for recent climate; see *Modeling of past temperatures within sites* for hindcast estimates of this variable) during the hottest months of the year. Because pikas are small and do not hibernate, lack of snow can mean lack of insulation from harshly cold winter temperatures (Irving et al. 1955, Wunder 1992, Morrison and Hik 2008). Given that mountain snowpack has been declining across western North America since the mid-20th century (Mote et al. 2005), we also considered metrics of acute cold stress.

We focused on cold temperatures experienced during 1 January through 30 June of each year, for two reasons. First, adult survival in the other North American pika (*O. collaris*) appears linked to timing of spring snowmelt (Morrison and Hik 2007). Second, spring temperatures have witnessed greater change than have fall temperatures (Fig. 1; Abatzoglou and Redmond 2007), including at elevations occupied by pikas within the Great Basin (Fig. 1). Unfortunately, there are few data with which to estimate a temperature threshold for cold stress. Hafner (1993, 1994) concluded that *O. princeps* generally occurs where the ambient temperature remains below 0°C for more than 180 days per year, suggesting that any threshold for cold stress must lie below 0°C. However, when the ambient temperature is far below 0°C, the temperature underneath a snow pack may

remain close to 0°C, suggesting that the threshold for cold stress may be close to 0°C if pikas depend on snow cover for insulation. During a year of heavy snow cover, pikas at 3660 m in Colorado collected during winter had no brown adipose tissue (BAT), yet animals collected in a December with little snow cover had “a lot” of BAT (Wunder 1992). Brown adipose tissue is the major site of nonshivering thermogenesis, a process used only when the individual is exposed to temperatures below its lower critical temperature; consequently, BAT can indicate exposure to cold temperatures, if other confounding factors are controlled (Wunder 1992). A small data set based on marked individuals ($n = 9$) and temperatures measured just below the surface of the talus suggested that *O. princeps* was less likely to survive where temperatures dropped below -5°C (C. Ray, *unpublished data*). Therefore, we defined two thresholds of acute cold stress as the number of days on which the temperature just below the surface of the talus remained below 0°C or -5°C .

Modeling of past temperatures within sites

Calculating our metrics of climatic stress according to the prevailing climate at each site and determining the magnitude of change in each metric over time required long-term data on the climate at each site. The U.S. Historical Climate Network (HCN) represents a subset of National Weather Service Cooperative (COOP) weather stations that have been selected for completeness and longevity and have been adjusted to account for changes in instrument, station location, time of observation, and other factors that could confound long-term trends (Karl et al. 1990). We used daily data from six HCN stations in Nevada and Oregon for comparison with the data from the temperature sensors. For each of the 25 sites, we formed a site mean temperature from all below-talus sensors at the site. Daily maximum and minimum temperatures from the two-hourly or four-hourly sensor data were estimated using cubic-spline interpolations. Days when the temperature at a sensor fluctuated $<2^{\circ}\text{C}$ were judged to be affected by snow cover and were excluded from the regression analysis. These data from in situ sensors were compared with data on ambient temperatures from HCN stations within the study region. Each site's data set was highly correlated ($0.82 \leq r \leq 0.98$, $r_{\text{avg}} = 0.93$) with at least one HCN data set. For further modeling, each site was paired with an HCN station according to the highest correlation between site and station data sets. Each pair of data sets was then related via two linear regressions, one for daily maximum temperatures and one for daily minimum temperatures. These regression coefficients established using the recent climate data were used to generate a time series of modeled temperature maxima and minima for each day since 1 January 1945 for which the HCN station had data. We used the daily maximum temperatures to estimate acute heat stress (i.e., days above 28°C), the

daily minimum temperatures to estimate cold stress (i.e., days below -5°C and days below 0°C), and the mean of the estimated maximum and minimum temperatures within each day to estimate chronic heat stress (i.e., mean temperature during 1 June to 31 August). These metrics were then adjusted to correct for missing data from each HCN station (e.g., due to equipment malfunction). For example, if the number of days with minimum-temperature data were 4200 out of 5661, the modeled number of days below 0°C would be (the reported number of days below 0°C) \times (5661/4200). This approach is valid when missing values are randomly distributed throughout the time series; however, given that missing values constituted $<10\%$ of the time series from any weather station, severe nonrandomness would be required to noticeably affect results. The number 5661 in this example is the number of days in the first half of each year, over either 31-yr period ($=365.24 \text{ d/yr} \times 31 \text{ yr} \div 2$). Because this approach links temperatures observed within taluses on snow-free days with HCN values on those same days, these modeled temperatures essentially correspond to snow-free temperatures at the sensor location. Currently, there is no feasible way to deduce when the sensor locations would have been covered by snow historically.

We quantified the prevailing climate at each site in two ways: (1) as conditions measured by sensors within talus interstices during 2005–2006 (hereafter, “recent climate”); and (2) as the cumulative (e.g., days above 28°C) or average (e.g., summer temperature) conditions over 1945–2006 (“average climate”). Metrics of stress based on the average climate were first calculated within each period (1945–1975 and 1976–2006), then weighted by the number of missing values within each period, before being summed or averaged across periods.

To document changes in climate over time (“climate change”), two approaches are commonly used: linear trends and differences between the means over two periods. Linear trends in summer temperature (i.e., the grand mean of daily maximum and daily minimum temperatures, June through August) at HCN climate stations in the Great Basin range from -0.5 to $+2.5^{\circ}\text{C}$ over the 1920–2002 period, with a mean change of $+0.64^{\circ}\text{C}$. Estimates for our study area over the same period using PRISM data (Daly et al. 1994; resolution = 680–760 m) and Hadley Center Climatic Research Unit cells (5° of latitude \times 5° of longitude) suggested changes of $+0.4^{\circ}\text{C}$ and -0.1°C , respectively. To estimate mean climatic parameters, investigators commonly use ≥ 30 years of data, to moderate the effects of climatic anomalies (e.g., von Storch and Zwiers 1999). We quantified “climate change” as the magnitude of change in each stress metric between the periods 1945–1975 and 1976–2006.

Snow depth measurement (e.g., SNOTEL) sites are sparse in the Great Basin, especially historically; thus, hindcasting precipitation and related metrics at remote

sites would involve substantial error. Additionally, biological responses to temperature are better understood than are responses to precipitation (Root et al. 2003). For these reasons, we did not model variables related to precipitation. Instead, we compared duration of snow cover between presence and absence sites during 2005–2006. We assumed that a sensor was insulated by snow cover if it recorded a diel temperature variation $<2^{\circ}\text{C}$.

Auxiliary temperature data

At some sites only a portion of the talus patches were occupied by pikas in 2005–2007. In these mixed-occupancy sites, sensors were placed in both occupied and unoccupied patches. Only data from sensors in occupied patches were used to model site occupancy (e.g., for forming a site mean temperature). Furthermore, to indicate the relevance of our sensor network for other species, we also placed 19 sensors above the talus surface within six sites (three pika-occupied, three unoccupied) across the Great Basin. Each of these above-talus sensors was paired with and placed within 3 m of a nearby below-talus sensor. We found that above-talus temperature sensors correlated strongly with their paired below-talus counterparts ($r_{\text{avg}} = 0.83$).

Analyses

Sites with populations persisting through the 2000s sampling period, including mixed-occupancy sites, were designated “1” and extirpated sites were designated “0.” Persistence was modeled as a logistic function of stress metrics estimated from data on prevailing conditions (recent and average climates) or climate change. Each model included up to three predictor variables, all of a single type; e.g., predictors based on average climate did not occur in models with predictors based on either recent climate or climate change. Predictors that were correlated ($|r| > 0.65$), including the two metrics of cold stress (days below 0°C and days below -5°C), appeared only in separate models. We used corrected Akaike Information Criterion (AIC_c) to compare the strength of evidence in support of these different models, following Burnham and Anderson (2002).

RESULTS

Apparent extirpations

Of the six sites at which *O. princeps* was not detected in sampling during 1994–1999, none revealed pikas during subsequent surveys. In addition to these six extirpations, pikas were apparently extirpated from three more sites during 2000–2007. Patterns of loss evidenced in the 1990s and 2000s surveys were markedly different. For example, whereas five of the six earlier losses occurred at the northern tip of the Great Basin, all of the more recent extirpations have occurred in the southern portion of the Basin.

Detectability

At sites with pikas, once we were within the occupied talus during appropriate sampling times, time to first detection of pikas was only 0.2–11.3 min. During 2005–2007, double counts by independent observers suggested that detectability of individuals within sites was quite high, ranging from 85.0% to 100% within sites (average among sites = 95.9%) for the more-experienced observer and from 57.1% to 100% (average = 85.2%) for the less-experienced observer. Not surprisingly, counts by these two observers were highly correlated ($r = 0.991$, $N = 10$). In spite of our findings of high detectability of individuals (also see Beever et al. 2008), further visits would provide additional confidence to our categorizations of site occupancy.

One site (Cougar Peak) where the detected population was classified as “functionally extirpated” during the 1990s hosted a robust population in 2005. This discrepancy was likely due to insufficient sampling rather than increased density: during the 1990s, Cougar Peak was not visited during times of day optimal for observing pika activity.

Climatic variables and pika distribution

Temperatures beneath the talus correlated with ambient temperatures measured at HCN weather stations ($0.82 \leq r \leq 0.98$; $r_{\text{avg}} = 0.93$), even though sensors and stations were separated by large distances (mean = 61.1 km, range = 19–119 km). Temperature profiles based on sensor data indicated that all but three pika-extant (hereafter, “extant”) sites had continuous snow cover for more than two weeks at all or most (i.e., $>75\%$) of the sensors within the site. At these sites, snow persisted for up to 8.2 months above sensors. Two of the three exceptions exhibited the lowest density of pikas. In contrast, seven of nine pika-extirpated (hereafter, “extirpated”) sites never experienced snow cover continuously for more than two weeks during our period of data collection. One of the exceptions was the site of most recent extirpation. As expected, temperatures within talus interstices at extirpated sites surpassed 28°C more frequently than at extant sites, 10.74 times more frequently during 2005–2006 and an estimated 74.94 times more frequently during 1945–2006. Much of this difference, however, reflected very high values at one site. Because this site contained no remnant hay piles even in 1990s sampling, it is likely that this population was extirpated early in the 20th century. Summers were hotter at extirpated sites, during all time periods (mean difference = 3.3° – 4.7°C ; Table 1). Also as expected, temperatures within taluses during 2005–2006 dipped below -5°C less frequently at extant sites compared to extirpated sites (where temperatures reached as low as -22°C), apparently because sensors at extant sites were more likely to be insulated by snow cover during cold snaps (Table 1). This 17.2% difference in potential cold stress between extant and extirpated sites was even more pronounced (29.5% different) if the site of lowest pika

TABLE 1. Modeled and observed climate (mean \pm SE) at sites where the American pika (*Ochotona princeps*) remains extant or has become extirpated, within the hydrographic Great Basin of western North America.

Climate metric by time period	Pika extant sites ($N = 16$)	Pika extirpated sites ($N = 9$)
Days above 28°C		
Modeled		
1945–1975	1.7 \pm 1.2	109.2 \pm 96.1
1976–2006	1.4 \pm 0.7	120.4 \pm 99.1
Climate change	–0.3 \pm 0.6	11.3 \pm 9.6
Observed		
2005–2006	0.8 \pm 0.2	8.9 \pm 4.0
Mean summer temperature		
Modeled (1 Jun–31 Aug)		
1945–1975	12.55 \pm 0.63	15.99 \pm 0.84
1976–2006	12.74 \pm 0.63	16.04 \pm 0.85
Climate change	0.19 \pm 0.08	0.05 \pm 0.16
Observed (1 Jun–30 Sep)		
2005–2006	12.40 \pm 1.00	17.05 \pm 0.81
Days below 0°C		
Modeled (1 Jan–30 Jun)		
1945–1975	2449 \pm 250	2352 \pm 252
1976–2006	2244 \pm 244	2238 \pm 236
Climate change	–205 \pm 37	–115 \pm 36
Observed (1 Jan–31 Dec)		
2005–2006	169.7 \pm 10.1	141.5 \pm 7.5
Days below –5°C		
Modeled (1 Jan–30 Jun)		
1945–1975	872 \pm 117	1032 \pm 155
1976–2006	685 \pm 96	895 \pm 123
Climate change	–187 \pm 32	–137 \pm 39
Observed (1 Jan–31 Dec)		
2005–2006	21.2 \pm 5.9	25.6 \pm 8.4

Notes: “Days” refers to the total number of days in which the given threshold was exceeded during the given period. “Climate change” refers to the modeled value for years 1976–2006 minus the modeled value for years 1945–1975.

density (suggesting vulnerability to future extirpation) is considered functionally extirpated (also see *Discussion: Average climate, recent climate...*). Hindcasts also suggested greater frequency of acute cold at extirpated sites (Table 1).

Among our metrics of climate change, the one that differed most dramatically between extirpated and extant sites was estimated change in acute heat stress. Extirpated sites experienced a \sim 10% increase in estimated number of days above 28°C during 1976–2006 (relative to 1945–1975), whereas the number slightly decreased at sites where pikas have persisted. In contrast, change in mean summer temperature was negligible and indeed counter to what one would predict, if an increase in this metric of stress were to predict extirpation. For numbers of days below freezing and below –5°C, extirpated sites lost fewer days from 1945–1975 to 1976–2006 than did sites where pikas remained extant.

Climatic models of population persistence

Our best models, based on climatic variables alone, accounted for much of the variance in pika persistence, according to the relatively low plausibility of the null model. The best predictors were chronic heat stress (average summer temperature), acute cold stress (number of days below –5°C; also see *Discussion: Importance of climatic extremes*), and acute heat stress (Tables 2 and 3). The average of Akaike weights/model for the three metrics of chronic heat stress ($w_{\text{avg}} = 0.0394$ per model) indicated that such chronic stress best predicts patterns of extirpation, across all timescales investigated. Following chronic heat stress, acute heat stress ($w_{\text{avg}} = 0.0277$ per model) and cold stress based on days below –5°C ($w_{\text{avg}} = 0.0252$) far surpassed the predictive value of number of days below freezing ($w_{\text{avg}} = 0.0171$ per model; Table 3).

Except for days below freezing and some metrics of climate change, metrics of stress were all negatively

TABLE 2. Information-theoretic analyses of logistic-regression models that had substantial support (i.e., difference in corrected Akaike Information Criterion [ΔAIC_c] < 2), for predicting persistence of pikas from 25 sites in the Great Basin.

Model	$-2 \times \log(L)$	K	AIC_c	ΔAIC_c	Akaike weight	Evidence ratio ⁻¹
Mean summer temperature (2005–2006)	22.559	2	27.104	0.000	0.148	1.000
Days below –5°C (1945–2006) and mean summer temperature (1945–2006)	20.330	3	27.473	0.368	0.123	0.832
Days above 28°C (2005–2006)	23.337	2	27.883	0.779	0.100	0.677
Mean summer temperature (2005–2006) and days above 28°C (2005–2006)	20.774	3	27.916	0.812	0.099	0.666
Mean summer temperature (1945–2006)	23.954	2	28.500	1.396	0.074	0.498

Notes: The “Model” column lists predictor(s) of each candidate model. L is the likelihood of the fitted model. The AIC_c value of a model reflects the fit of the collected data to the model while penalizing for having unnecessary parameters. Models with the lowest AIC_c values are considered the plausible best within the set of proposed models. ΔAIC_c represents the difference between AIC_c of the model under consideration (model i) and the one with the lowest AIC_c value of all models, at the top of the table. The generalized Akaike weight (w_i) of each model indicates the strength of evidence that the selected best model is best; w_i ranges from 0 to 1 and provides an effective way to scale and interpret the Δ_i (Burnham and Anderson 2002). The evidence ratio is calculated as w_0/w_i , where w_0 is the generalized Akaike weight of the model with the lowest AIC_c value and w_i is the generalized Akaike weight of model i . The evidence ratio is a relative measure of the evidence in favor of the best model vs. model i ; we present the inverse of the evidence ratio. K represents the number of parameters estimated in each model (Burnham and Anderson 2002).

TABLE 3. Variable weights for the analysis in Table 2, across all models in the a priori set.

Predictor	Mean Akaike weight per model	Sign of effect
Recent mean summer temperature (°C)	0.0629	6–
Long-term mean summer temperature (°C)	0.0530	6–
Recent no. days above 28°C	0.0530	6–
Cumulative no. days below –5°C	0.0491	4–
Recent no. days below 0°C	0.0271	2–, 2 +
Cumulative no. days above 28°C	0.0263	6–
Recent no. days below –5°C	0.0252	3–, 1+
Cumulative no. days below 0°C	0.0207	3–, 1+
Change in no. days above 28°C	0.0037	6–
Change in no. days below 0°C	0.0034	4–
Change in mean summer temperature (°C)	0.0022	1–, 5+
Change in no. days below –5°C	0.0014	3–, 1+

Notes: For each predictor, the mean weight indicates the sum of the Akaike weights from all models in which the factor appeared, divided by the number of models in which it appeared. The sign is the coefficient of the variable and reflects that variable's effect on pika persistence. "Recent" refers to field-collected data from 2005–2006, "cumulative" and "long-term" refer to hindcasted data from 1945–2006, and "change" refers to [(1976–2006 estimate) – (1945–1975 estimate)]. The sign is the coefficient of the predictor variable and reflects that variable's effect on pika persistence; the numbers in that column reflect the number of models in which the coefficient was positive (+) or negative (–).

related to pika persistence (Table 2). In the case of metrics based on the recent climate or average climate, these negative relationships suggest that more stress decreases persistence or increases the likelihood of extirpation.

Across all models, metrics of recent climate were the best predictors of pika extirpation ($w_{\text{avg}} = 0.0452$ per model); among those metrics, chronic heat stress was the best predictor (Tables 2 and 3). Long-term, average-climate metrics garnered slightly less support ($w_{\text{avg}} = 0.0378$ per model). Climate change metrics were by far the poorest predictor of pika extirpation ($w_{\text{avg}} = 0.0004$ per model; Table 3). Models based on climate change generally garnered less support than the null model.

DISCUSSION

A large number of studies have predicted changes in distribution for many taxa and across a broad range of extents, as a result of continued warming temperatures (e.g., Dullinger et al. 2004, Thomas et al. 2004). To test these ecological forecasts, several authors have noted the need for high-resolution data sets that are extensive in time, elevation, and space (e.g., Moorcroft 2006, Parmesan 2006, Root and Schneider 2006). We present data on the changing distribution of the American pika from dates spanning over a century and from a broad distribution of sites in the Great Basin. These data, combined with spatially and temporally intensive data on microclimate, suggest previously unappreciated effects of temperature on the persistence of this species. Although we strategically placed temperature sensors in microhabitats used by our study organism (i.e., talus interstices), high correlation ($r_{\text{avg}} = 0.83$) between paired below-talus and above-talus sensors suggests the utility of these data for other species and questions. These data may be particularly useful given the relative paucity of high-resolution climatic data from physiographically

complex mountainous environments (Rickart 2001, Lundquist et al. 2003). Such data are needed not only for research and monitoring (Körner 2007, Sekercioglu et al. 2008), but also to address management issues in wilderness and other protected areas, which are located disproportionately in these areas (Scott et al. 1993), the same high-elevation areas that will likely experience some of the most dramatic shifts in climate (Pounds et al. 1999, Root et al. 2003).

Climate envelope models have become a favored approach for forecasting species response to predicted future warming, and hundreds of forecasts in the literature predict climate-related changes in distribution, demography, or trend for different taxa, guilds, and regions. Although sophistication of the assumptions and parameterization of such models has improved with time, many constraints still hamper their predictive accuracy (e.g., see Walther et al. 2002, Guisan and Thuiller 2005, and reviews by Berteaux et al. 2006, Hijmans and Graham 2006). Because of these constraints, and particularly because climate forecasts are intended to be accurate at spatial resolutions tens to hundreds of times coarser than the resolution of our data (Burns et al. 2003), we do not forecast distributional changes for pikas here.

Average climate, recent climate, and climate change as predictors of loss: ecological and evolutionary considerations

Species' geographical ranges are often bounded on different edges by different constraining factors. For example, a mid-elevation montane insect may be bounded at its lower-elevation edge by sympatric competitors or predators, yet be bounded by minimum temperatures at upper elevations. Similar divergence in range determinants occurs between species' northern and southern boundaries. Recent climate-related shifts

at both northern and southern boundaries (i.e., northward expansion and southern contraction) have been demonstrated for eight butterfly species (Parmesan et al. 1999), but southern retractions have surprisingly lagged behind northern expansions for many more taxa. However, given that the most-recent extirpations and lowest pika densities are occurring at the southern edge of the Great Basin, approximately the southern border of the species' geographic range, monitoring the southernmost populations of *O. princeps* may be warranted. Recent declines in abundance at lower elevations concomitant with sympatric increases in abundance at higher elevations have been observed for other species in the Great Basin (Beever et al. 2005), and lower-elevation losses have occurred in multiple taxa (e.g., Wilson et al. 2005). The ability of species to track climatic isotherms in the coming years depends on isolation and quality of their remaining habitats, dispersal abilities of species, normal population densities, frequency of longer-distance dispersal events, and effects of human infrastructure on patch connectivity. For montane species in particular, as species distributions track climates upslope, one or more physical parameters that covary with elevation (see Körner 2007) may further constrain distributional shifts. For example, high wind speeds that typically occur on mountaintops may make these areas unsuitable as recipient habitats.

Over longer (evolutionary) timescales, many authors have suggested that the niche of a species is little changed over time (i.e., exhibits niche conservatism; Peterson et al. 1999, Martínez-Meyer et al. 2004, Guralnick 2007), which justifies the use of niche-based species distribution models such as climate envelope models (Pearman et al. 2007). Local adaptation at range margins that would allow expansion of a species' distribution may be limited by several evolutionary processes (Bridle and Vines 2006). For example, niche shifts may be limited if selective gradients (e.g., climatic parameters) change abruptly on fine spatial and temporal scales, as is the case for *O. princeps* in the Great Basin, because the central population may be too small to furnish sufficiently high genetic variance to marginal areas (Bridle and Vines 2006). The relatively poor predictive power of climate change in our study, compared with the predictive power of the prevailing climate (Table 3), suggests a fixed-dimension climatic niche, especially with respect to metrics of heat stress (i.e., average summer temperature and number of days above 28°C). We predicted that chronic heat stress would be least likely, relative to our metrics of acute stress, to determine the climatic niche of this species. However, chronic heat stress was the strongest predictor of pika extirpation among metrics of stress based on the recent climate and the second strongest predictor among metrics based on the average climate (Table 3). An alternative explanation for the poor predictive ability of our climate-change metrics is that the magnitude of climate change at the HCN stations did not reflect

magnitudes of change in the microclimates experienced by pikas at our montane sites. Yet another explanation may be that pikas are responding to changes in climate that have occurred more recently than those reflected in our climate change metrics. This alternative is somewhat supported by the relatively strong predictive ability of stress metrics based on the recent climate as observed during 2005–2006.

To track changes from the colder Late Pleistocene to the warmer present, mountain-dwelling species shifted their distributions upslope, whereas flatland-dwelling species moved their southern range edge northward more than did montane species (Guralnick 2007). By examining evolutionary changes from mammalian fossil evidences at many hierarchical levels (from genes to species and higher taxonomic groups) and timescales (from decades to glacial–interglacial transitions), Barnosky and Kraatz (2007) concluded that current rates of warming are too fast to influence evolution significantly and will instead hasten extinctions. Similarly, Parmesan (2006) found that Pleistocene glacial–interglacial transitions, which represent temperature shifts 5–10 times that, observed during the 20th century, did not foster the appearance of new forms outside of the known variation for any species, nor result in major extinction or speciation events.

In contrast to the niche conservatism paradigm, one criticism of climate envelope models is that they assume that species cannot evolve in response to changing climate (Skelly et al. 2007). Evidences of niche shifts are known in many taxa and over many timescales (see reviews in Pearman et al. 2007, Skelly et al. 2007). Individual animals at hotter and drier portions of the species range possess physiological adaptations that include reduced thermal conductance, lower evaporative water loss, and higher heat tolerance (reviewed in Sekercioglu et al. 2008). Furthermore, phenotypic plasticity and ecotypic variation both provide additional observed mechanisms by which a species' niche can vary across the geographic range. In fact, the niche occupied by a species can vary regionally to the point at which there is complete absence of niche overlap at opposite edges of the geographic range, even when lack of overlap is driven largely by differences in abiotic conditions rather than by regional adaptation (Murphy and Lovett-Doust 2007). Our finding that climate change so poorly predicted pika losses may mean that pika populations have not locally adapted to these potentially stressful conditions or at least that absolute (e.g., physiological) constraints are more definitive determinants of their distribution.

Clearly, extirpations before 2005 could not be caused by future conditions (exemplified by our recent climate data collected during 2005–2006). We used recent climate as a proxy for prevailing conditions, which should approximate the bioclimatic niche of the species either in the present (given recent climate change) or over the long term (given no climate change). The fact

that stress metrics based on recent climate were the most explanatory, combined with the fact that these sites have experienced some climate change, suggests that climate change is having effects on the distribution of this species. The importance of recent climate conditions (Table 3) is consistent with not only the recency of many pika extirpations (five of the nine occurred within the past 15 years), but also with: (1) the fact that across the contiguous United States, all years since 1998 have had positive temperature anomalies relative to 1961–1990 (IPCC 2007); (2) strongly positive temperature anomalies in the Great Basin during 2002–2006; and (3) increased rate of upward shifts in alpine-plant distributions during 1985–2003 relative to 1905–1985 (Walther et al. 2005).

Furthermore, fieldwork by colleagues in 2008 at one site (Pinchot Creek) on the southern edge of the study area strongly suggests that the site is now functionally extirpated. In contrast to the one site (Cougar Peak) suspected to be functionally extirpated after just one visit in 1990s sampling, Pinchot Creek has been sampled by eight biologists on 18 days across four years since 2005. During this intensive sampling, never have more than two individuals been detected on any visit. Considering the site as “functionally extirpated” does not change: (1) the identity of either of the two top-ranked models; (2) the relative rank of the Akaike weight and weight/model of the two most-predictive variables; or (3) the relative rank of predictive values of recent-climate, average-climate, and climate change metrics.

American pikas as models for investigating extirpation, occupancy, and climate–distribution dynamics

Pikas seem to represent an excellent model to test extinction theory (McDonald and Brown 1992, Hafner 1994). They may be particularly vulnerable to local extinctions, particularly those induced by climate change, because of: their relatively poor dispersal capabilities, which appear especially poor at thermally stressful locations (Smith 1974); their obligate relationship to talus, which is patchily distributed elevationally and on several spatial scales; a high body temperature that averages only 3°C below the species’ upper lethal temperature combined with a thick layer of insulating fur, which effectively limits dissipation of metabolic heat (Smith 1974, Katzner et al. 1997); and low fecundity, relative to other lagomorphs (Smith and Weston 1990, Thomas et al. 2004). Our failure to detect *O. princeps* during multiple visits over a decade of resampling within a 3-km radius suggests genuine shifts in the species’ distribution rather than temporary movements.

Classical ecological theory, however, would predict that the small body size, short generation time, and shallow fluctuation in population density over time in *O. princeps* (Smith 1980, Southwick et al. 1986) should dictate that the species has relatively low extinction risk (Tuljapurkar 1980, Lewin 1989, Cardillo et al. 2006).

Given that their physical habitat (i.e., talus) has changed little in extent or configuration over ecological time-scales, continuing losses of pikas illustrate that wildlife–habitat relationships used to model future distributions will require supplementation with empirical verification of trend, at least for some species. Taking these facts together, American pikas provide an excellent example of the manner in which rapid climate change may impose a vastly different selective regime on extinction dynamics, across species. Even in the conservation literature, studies of population extinctions that are based on original field data are quite rare (Sarukhán 2006), yet are critical for informing not only conservation and management strategies, but also forecasted biotic responses to climate change.

Both paleontological (Graham et al. 1996, Grayson 2000) and contemporary results (Lawlor 1998, Kelt et al. 2005) suggest that extirpation dynamics may vary greatly across species, as a function of physiology, behavior, and other life history characteristics. Both forecasted (e.g., Thomas et al. 2004) and observed rates of biotic distributional response to climatic changes (Post and Stenseth 1999, but see Lyons 2003) are known to vary among broad taxonomic groups. Furthermore, responses to climate change will vary across seasons and across species’ geographical ranges (Kudo and Suzuki 2003, Murphy and Lovett-Doust 2007; review in Walther et al. 2002), and across sexes and age classes within species (Stenseth et al. 2002). Although we advocate employing mechanistic approaches for other species, our results should not be expected to apply directly to other species nor to other ecoregions.

Mechanistic effects of climate on montane biotas

Mechanistic understanding of biotic response to rapid climate change not only illuminates the manner in which biotas are being altered, but this understanding allows for more informed mitigation, management, and conservation strategies, in the face of continued climatic change. Forecasts grounded in cause–effect relationships rather than in conceptual relationships or unvalidated correlations seem likely to provide a more fruitful foundation upon which to refine understanding and predictive ability (Hallett et al. 2004, Berteaux et al. 2006). In addition to the direct thermal stresses that we have suggested here, other pathways by which montane biotas in particular may be affected are numerous, and they constitute additional or alternative explanations for patterns we observed. They include: altered food abundance and availability, with consequent effects on foraging; altered community structure (e.g., lost symbioses, changes in predator or competitor distributions; Rickart 2001, LaVal 2004); altered exposure or susceptibility to infectious diseases or parasites; and altered daily activity patterns, that likely have energy consequences. Additional, even more indirect mechanisms may contribute independently of or synergistically with our direct climate mechanisms. These include altered

precipitation, cover of snow and ice, stream flow, humidity, soil moisture, and incident energy (insolation); changes in fire regime (Westerling et al. 2006); increased frequency or intensity of drought (Breshears et al. 2005); introduction of exotic species such as cheatgrass (Grayson 2000); habitat fragmentation (Root and Schneider 2006); atmospheric or water-borne or terrestrial pollution (Loehle and Li 1996); forest dieback and associated erosion (Allen 2007); and intensified land use or habitat degradation, among others. Although losses of pikas have been accompanied by colonization of patches by other talus-dwelling species (E. Beever, *personal observation*), long-term sympatry of these species within our sites suggests that interspecific competition was not the primary driver of pika extirpations.

One indirect mechanism that seems particularly plausible, given the high metabolic requirements of pikas (Johnson and Maxell 1966), is climate-induced alteration of vegetation within and adjacent to taluses (Burns et al. 2003, but see Wilson et al. 2005). Field notes from collectors of the pika specimens from the early 20th century indicate that elevational distributions of some tree species have moved upslope at some sites in the Great Basin; unfortunately, however, no elevational data were taken on herbaceous species most important for pika foraging. We have detected differences in vegetation between occupied and unoccupied patches across the Great Basin and in Lava Beds National Monument (Wilkening 2007; C. Ray and E. Beever, *unpublished manuscript*). Although American pikas are generalist herbivores, they rely on metabolic water and collect and store vegetation preferentially based on characteristics of chemistry and nutrition (Dearing 1997). However, manipulative experiments have shown that pika foraging significantly alters composition of local vegetation (Huntly 1987); this complicates our ability to assert whether vegetation, pikas, or feedbacks of both are causing heterogeneities in distribution.

Understanding the influence of precipitation on pika persistence and distribution remains a challenge for further investigations. This uncertainty reflects the fact that understanding the hydrologic cycle and how precipitation may change at fine spatial resolutions remain two of the most limiting gaps in climate change science and forecasting (IPCC 2007). Interestingly, 21 of the original 25 historical records for pikas in the Great Basin occurred during a period (1915–1930s) in which snow water equivalent was likely declining across the western United States (Mote et al. 2005). Hafner (1993) found that extant pika populations within 50 geographically isolated patches across western North America occur primarily in regions experiencing >300 mm annual precipitation, in addition to experiencing other macroclimatic conditions that may affect water balance for pikas and plants on which they feed (e.g., <20 d/yr above 35°C). Although pikas rely exclusively on metabolic water for hydration, water stress may be

imposed on arid mountain-dwelling animals through altered rates of evapotranspiration, soil moisture, and forage quality (Epps et al. 2004), especially in areas that are hotter and drier than Great Basin mountaintops are currently. Using simulation modeling and bootstrapping, McLaughlin et al. (2002) found that extirpations of two populations of a patchily distributed butterfly were hastened by increasing variability in precipitation. Spatial and interannual variability in precipitation have also been shown to predict persistence in bighorn sheep of desert mountains, overall richness of smaller-bodied mammal species, and abundance of individual small-mammal species (e.g., Epps et al. 2004, Letnic et al. 2005).

Importance of climatic extremes

Ecologists have often struggled to quantify and detect effects of climatic anomalies on biotas, due in part to limited data. To detect these effects requires data: (1) with sufficiently high spatial and temporal resolution to characterize the environments experienced by individuals and (2) that describe species' minimum and maximum tolerances. Although we characterized temperatures every two to four hours in the very microhabitats typically used by pikas, we did not have historical temperature data at such high temporal resolution. Thus, we used days (rather than hours) above 28°C as our metric of acute heat stress, although hourly data would seem to be a more accurate predictor. Although pikas have been shown to perish quickly when experimentally subjected to high temperatures (MacArthur and Wang 1974, Smith 1974), our metric of acute heat stress was the poorest predictor of pika extirpations, across all temporal resolutions, if Pinchot Creek is functionally extirpated. This suggests that behavioral thermoregulation (i.e., timing above-talus activity to avoid hottest temperatures) is at least partly mitigating the importance of this demonstrated biophysical relationship. Temperatures recorded by sensors reflect both the air temperature and heat radiated by nearby talus rocks, mimicking the two external sources of heat that most strongly determine "operative" temperatures for *O. princeps* (Kearney and Porter 2004). In addition to the two data limitation challenges for quantifying biotic response to extreme events, other challenges include the facts that energetically challenging conditions may occur in different forms and at different times in each year, as well as across different years; be expressed immediately or after a delay of varying length; and can depend upon other interacting stressors on the individual (Hallett et al. 2004).

Our analyses of acute cold stress (i.e., number of days below -5°C), however, confirmed that (as predicted) pikas were extirpated at sites where microclimates were not only more frequently very cold (perhaps due to lack of snow cover), both historically and during 2005–2006, but also that pikas persisted at sites that lost more very cold days over the last 62 years (Table 1). We

hypothesized that although pikas appear to be adapted for cooler temperatures, very cold temperatures might prove stressful for a ~150-g homeotherm with high metabolic requirements. Because effects of cold stress on pikas had not been previously illustrated, we further explored the effects of extreme cold stress by replacing the number of days below -5°C with number of days below -10°C in our set of a priori models. This post hoc analysis resulted in strong support for extreme cold stress as a predictor: all plausible models ($\Delta\text{AIC}_c \leq 4$) included the (long-term) average of extreme cold stress, regardless of whether or not the Pinchot Creek site was considered functionally extirpated. Also, the number of days below -10°C averaged >2.5 times greater weight per model, across all predictor variables, than did any other climatic predictor.

More broadly speaking, annual (rather than our daily) maximum temperature, averaged over 48 years, was one of five environmental variables that collectively predicted 88% of the variance in mammal species density across North America (Badgley and Fox 2000). Parmesan (2006) reviewed five long-term studies in which extirpations occurred during extreme droughts and low-snowpack years; collectively, these extirpations occurred at lower elevations and latitudes, shifting distribution of extant populations northward and upward. At least for some taxa, extreme climate events can often be more relevant ecologically than fluctuations in mean climate (Stenseth et al. 2002, Sinclair et al. 2003). Given that extreme climate events are increasing in frequency (IPCC 2007), their influence on biotas may increase in coming years.

The issue of scale

Currently in the Great Basin, pika populations probably operate independently at scales smaller than entire mountain ranges, in contrast to other montane mammal species. From sampling allozymic patterns of 56 populations and comparing genetic similarity among samples of increasing geographic separation, Hafner and Sullivan (1995) concluded that *O. princeps* metapopulations are separated by 10–100 km. The current analysis is somewhat coarse in scale due to the current, relatively coarse resolution of modeled climatic data (~720 m) relative to the nearest-neighbor distances observed for pikas (14–32.6 m; Smith and Weston 1990). Our extensive sampling within sites likely encompasses most dispersal events associated with metapopulation dynamics, but does not include entire mountain ranges, the focus of much previous biogeographic work on montane mammals. Even for species as detectable as *O. princeps*, heterogeneity in distributions and vicariance histories suggest that determining presence/absence at the scale of mountain ranges may be overly ambitious if not accompanied by comprehensive sampling at appropriate times of day and season.

Predictive accuracy of ecological forecasts will depend upon not only our ability to quantify stochasticity in

climate but also upon multi-scale data across broad spatial and temporal extents. For example, VEMAP (Vegetation/Ecosystem Modeling and Analysis Project) models (55×35 km) used to forecast mammal species gains and losses in eight U.S. national parks (Burns et al. 2003) would not detect most of the site losses and within-site changes in occupancy we have observed. Similarly, characterizing occupancy within sites that are broader than most dispersal distances (as opposed to across entire mountain ranges) provides an earlier signal of distributional change, should any local extinctions occur. Multi-scale dynamics in complex ecological systems warn against overstatement of experiments that are temporally or spatially inappropriately designed (Walther 2007).

Caveats

Searches in late 2007 and early 2008 of databases of state Natural Heritage Programs, museums, and other locations (e.g., Global Biodiversity Information Facility, Mammal Networked Information System [MaNIS]) uncovered very few sites with evidence of pika presence in the Great Basin that were independent of our set. Although our results probably reflect extinction dynamics accurately within the Great Basin, because we have not systematically searched all taluses within this region, we acknowledge that other sites with pikas may exist. Our approach of revisiting historical sites in the Basin, rather than performing a traditional investigation of occupancy, provided us with a longer-term ecological perspective of extinction dynamics. Nonetheless, examining patterns of loss among sites of historical record would thus provide a biased indication of pikas' status and trend within the Basin, should there turn out to be a large number of as-yet unidentified pika populations.

CONCLUSION AND APPLICATIONS

The ethical considerations associated with climate-related manipulative experiments suggest that ecologists may never again be able to obtain the strength of inference obtained from work that provided the foundation for mechanistic understanding of biotic responses to climatic stress in *O. princeps* (MacArthur and Wang 1974, Smith 1974). In addition to the importance of acute-heat stress for pikas suggested by those experiments, our research suggests even greater influence on pika persistence in the Great Basin by chronic heat stress (namely, mean summer temperature) and by cold stress (namely, number of days below -10°C or -5°C). In contrast to classical biogeographical assumptions, our research provides further confirmation that faunas in alpine and subalpine habitats are not protected from further losses, simply by virtue of their relative inaccessibility.

Sites that depart from our models of extirpation may be interpreted as indicating departures of species distributions from equilibrium (Svenning and Skov

2004), reinforcing the idea that the realized climatic niche of a species may differ from its fundamental niche due to biotic interactions such as predation and competition, as well as vicariance histories. For example, Duffer Peak, where talus interstices are several degrees Celsius cooler than microclimates at many pika-extant sites, may be a candidate for assisted reintroductions, if the genetic and other consequences associated with such efforts (McLachlan et al. 2007) are addressed. In contrast, reintroductions to other pika-extirpated sites with talus habitat that is less thermally suitable would likely be in vain. In contrast to the clear recent climate vs. mean climate vs. climate change trichotomy that we presented earlier, species may have canalized, absolute responses to some climatic stressors such as mean summer temperature, but may be sensitive to change in other metrics. Given that rate of climatic change may be as or more important for biota than the magnitude or duration of change (Davis et al. 2005), the rate of future losses of pikas and other patchily distributed species may hinge critically on the rate of further atmospheric changes. Our results to date confirm that mammals can experience range adjustments within just a few decades (e.g., Burns et al. 2003), though responses will likely vary widely across species. Rates of loss in *O. princeps* suggest the species as an early-warning indicator of biotic response to altered climate.

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