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Understanding relationships among abundance, extirpation, and climate at ecoregional scales

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Abstract. Recent research on mountain-dwelling species has illustrated changes in species' distributional patterns in response to climate change. Abundance of a species will likely provide an earlier warning indicator of change than will occupancy, yet relationships between abundance and climatic factors have received less attention. We tested whether predictors of counts of American pikas (*Ochotona princeps*) during surveys from the Great Basin region in 1994–1999 and 2003–2008 differed between the two periods. Additionally, we tested whether various modeled aspects of ecohydrology better predicted relative density than did average annual precipitation, and whether risk of site-wide extirpation predicted subsequent population counts of pikas. We observed several patterns of change in pika abundance at range edges that likely constitute early warnings of distributional shifts. Predictors of pika abundance differed strongly between the survey periods, as did pika extirpation patterns previously reported from this region. Additionally, maximum snowpack and growing-season precipitation resulted in better-supported models than those using average annual precipitation, and constituted two of the top three predictors of pika density in the 2000s surveys (affecting pikas perhaps via vegetation). Unexpectedly, we found that extirpation risk positively predicted subsequent population size. Our results emphasize the need to clarify mechanisms underlying biotic responses to recent climate change at organism-relevant scales, to inform management and conservation strategies for species of concern.

Key words: American pika; climate change; ecohydrologic variables; hydrographic Great Basin; information-theoretic analyses; mechanisms of climate–species relationships; *Ochotona princeps*; talus habitat.

INTRODUCTION

Contemporary climate change is increasingly implicated in observed shifts in numerous ecological attributes and phenomena (Sekercioglu et al. 2008). Ecological research surrounding contemporary climate change has broadly evolved from demonstrating changes in climatic parameters, to detecting ecological changes through time consistent with observed climatic changes, to using mechanistic studies to quantitatively attribute ecological changes to climatic drivers, to addressing ecological changes through conservation and management (Root et al. 2003, Loss et al. 2011). Although rarely implemented, explicit incorporation of mechanistic processes is a prerequisite for informing most management responses to climate change. Despite increasing prominence of climatic predictors in ecological research, evidence continues to mount that climate will typically act in concert with many other factors to affect ecological systems.

Compared to modeling trends of occurrence, there has been relatively less effort documenting climatic drivers of changes in abundance within species over time (see Nielsen et al. 2005, Myers et al. 2009). Geographical patterns of abundance provide the foundation for studying numerous issues in ecology, including the causes of species' range limits, population dynamics, gene flow within populations, and explanations for macroecological patterns (Sagarin et al. 2006). In particular, demographic and abundance data are useful for understanding exactly *how* species are being affected (i.e., mechanisms) by climate. Abundance data provide earlier indication of change than do occupancy data (because declines typically precede absence), and linear regression has greater power than logistic regression, with equal sample sizes. Although density of organisms is not always indicative of habitat quality for species (van Horne 1983), relative abundance or carrying capacity may be indicative of the vulnerability of populations to extinction (Pimm et al. 1988, Lande 1993, Caughley 1994). In contrast, however, simulations suggest that population sizes can be relatively insensitive to deteriorating environmental conditions, such that

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population sizes can sometimes be similar or even larger than those before environmental decline began, until a precipitous population decline to extinction occurs (Abrams 2002). Seeking to bridge the gap between range-wide extinction and abundance, Ceballos and Ehrlich (2002) examined patterns of population loss in 173 declining mammal species from six continents and found losses to be greatest in areas of high human density or extensive anthropogenic land use. These seminal works and related research underscore the need for further investigation of the relationship between, and geographic patterns in, population abundance and extinction risk, particularly in regard to climate change.

The biogeographic isolation of the highest-elevation habitats limits resilience of mountaintop species to contemporary climate change (e.g., Sekercioglu et al. 2008) and makes mountaintops key areas for investigations of extinction risk. Furthermore, protected areas are disproportionately located at higher elevations, and the sharp topographic and vegetative gradients of mountain ecosystems facilitate high beta and gamma diversity.

Our study objectives were to: (1) identify patterns of change in population abundance of American pikas relative to elevation, the species' local lower elevation boundary, or site latitude that were observed during 1994–2008 (and therefore may identify early-warning indicators of occupancy changes); (2) quantitatively compare the predictors of pika abundance (i.e., counts) at sites of historic records across the hydrographic Great Basin between the late 1990s and late 2000s, using the same model set; (3) assess whether incorporation of ecohydrologic variables improves our ability to predict relative density; (4) compare predictors of pika abundance and extirpation from the same temporal and spatial domains; and (5) determine the statistical relationship between probability of persistence and subsequent abundance of pikas (*Ochotona princeps*; see Appendix A).

METHODS

Study area and design

Our research area was the hydrographic Great Basin, USA (Appendix B), except that we excluded spur ranges of the Sierra Nevada and Rocky Mountains (Beever et al. 2010). These "mainland" ranges have dramatically different biogeographic histories, high-elevation habitat area, climates, and land-use histories from interior ranges of the basin, and early investigations of these mainlands (Millar and Westfall 2010, Erb et al. 2011) suggest that their pika population trends have accordingly differed from those in the basin. The mountaintop "islands" of the basin have been used as a model system for testing classical ecological theory for over four decades with montane mammals, birds, butterflies, conifers, and other taxa (e.g., Brown 1971). Our 25 study sites comprise all records of *O. princeps* with specimen evidence and precise locational information

prior to our large-scale sampling effort initiated in 1994. This region, one of North America's best sampled during the early 20th century, constitutes the southern extent of the species' geographic range at the range of longitude that our study area spanned. Since 1994, we have defined a site as all talus patches within a 3-km radius from the historical-record location, which we pinpointed using historical field notes.

Study organism

Pikas have exhibited marked increases in rates of site-wide extirpation and upslope retraction across the hydrographic Great Basin, thereby spurring research on the species in other portions of its distribution (e.g., Erb et al. 2011). Acute heat stress (when individuals are prevented from behavioral thermoregulation) can cause death in *O. princeps* in less than 6 h, and multiple investigations strongly suggest that the species' distribution is shaped by climatic factors, at numerous scales (e.g., Smith 1974, Beever et al. 2010, 2011, Millar and Westfall 2010, Erb et al. 2011). The species often exhibits interannually stable population sizes (e.g., average annual population fluctuations <30%; Southwick et al. 1986), detectability frequently above 90%, and numerous other attributes to make it a model study organism for investigating numerous ecological paradigms (e.g., island biogeography theory, source-sink, metapopulations). In spite of this, we are unaware of any ecoregional-scale, climate-related investigation of abundance of *O. princeps*. In fact, lack of information on population abundance and trend throughout most of the species' range was a primary reason that *O. princeps* was not listed under the U.S. Endangered Species Act, in a 2010 decision (Crist 2010). In terms of relevant life-history characteristics, *O. princeps* exhibits across its geographic range nearest-neighbor distances between haypiles from 14–32.6 m. Adult females have 2 litters/yr with a postpartum estrus; conception of the first litter typically occurs 30 d before snowmelt, and its parturition in May to mid-June. Average litter size varies from 2.34 to 3.68 young throughout the species' range. Haypile building begins in the summer, and continues until late fall; haypiles are individually defended and serve as winter energy sources (Smith and Weston 1990).

Field sampling

Pikas were surveyed at all historical (1898–1956) sites during 1994–1999 and again during 2003–2008. Sampling involved walking successive 50-m transects, along elevational contours of most talus patches and vertical walks up the middle of narrow (≤ 5 m wide) patches. To quantify and assess detectability of individuals, we performed independent-observer, double counts on each 50-m transect (Buckland et al. 2004). Observers consulted each other after each transect to determine how many animals were detected on each transect and their apparent location; detectability was calculated for each observer as a function of the number of individuals

detected by both observers, and the number of individuals detected by the other observer (Caughley 1974). Microclimates were measured with 204 remote temperature recorders (Thermochron iButtons, Maxim, Sunnyvale, California, USA) placed in talus interstices. Further details on the sampling protocol can be found in Appendix A and in Beever et al. (2003, 2010, 2011).

Environmental variables

We determined pika-equivalent elevation (a linear combination of site latitude and longitude; see Table 1), average annual precipitation, nonnative grazing presence before each survey period, grazing intensity (total ungulate scat), and latitude for each site as in Beever et al. (2003). We defined the amount of local talus habitat as the number of home ranges of talus having pika-appropriate rock diameters (0.2–1.0 m) within each site (sensu Beever et al. 2011). We have found this method to be the most precise, repeatable (E. A. Beever, *unpublished data*) method to quantify habitat extent that accounts for the species' avoidance of areas with diameters outside that range, a consideration not yet accounted for by any remote-sensing product. We defined the number of very cold (below -5°C) days, average summer temperature, and number of hot (above 28°C) days per Beever et al. (2010), and MaxElevR (residual of the linear regression of maximum elevation of local talus habitat on site latitude) following Beever et al. (2011). All these variables are defined in greater detail in Table 1 and Appendix C.

We derived four biologically relevant aspects of the climatic water balance to better identify mechanisms that may be associated with patterns of pika abundance in this ecoregion, which is the driest portion of the species' geographic range. In previous studies, site-wide losses occurred at driest sites (in terms of PRISM-estimated total annual precipitation), both in this study region (Beever et al. 2011) and in the Rocky Mountains (Erb et al. 2011). Vexingly, however, information-theoretic analyses with multiple predictors suggested that long-term average annual precipitation was the poorest predictor of the pattern of persistence from historical records to 2008 in this region (Table 1b of Beever et al. [2011]). Variables were derived from 30-year normals for actual evapotranspiration (AET), climatic water-deficit, snow-water equivalent (SWE), and growing-season precipitation (GS_PPT; June–September, inclusive) for the period 1971–2000. Metrics of climatic water-balance were calculated using PRISM climate data (PRISM Climate Group, *available online*)⁷ and a climatic water-balance model (sensu Lutz et al. 2010) that operates on a monthly time step and accounts for atmospheric demand (potential evapotranspiration) and soil water storage, and includes the effect of temperature and radiation on snow hydrology via a

TABLE 1. Variable weights for five different predictors of abundance of American pikas (*Ochotona princeps*) at sites across the hydrographic Great Basin, western USA, in surveys during (a) 1994–1999 and (b) 2003–2008.

Predictor	No. models	w_i	w_i/model
a) 1990s surveys, $n = 19$ sites			
Grazed?	7	0.751	0.107
Pika-Equiv. Elev	9	0.723	0.080
PPT	9	0.362	0.040
GrazIntensity	5	0.102	0.020
Amt of Habitat	9	0.169	0.019
b) 2000s surveys, $n = 16$ sites			
PPT	9	0.826	0.092
GrazIntensity	5	0.287	0.057
Pika-Equiv. Elev	9	0.425	0.047
Amt of Habitat	9	0.137	0.015
Grazed?	7	0.091	0.013

Notes: The sum of weights across all models for a given variable is shown with w_i . The full model suite appears in Appendix C. Variables are listed in order of decreasing average variable weight (i.e., variable weight/number of models in which that variable appears). Abbreviations are: PPT, average annual precipitation received at the site centroid during 1961–1990 or 1971–2000, estimated using PRISM data; Pika-Equiv. Elev. is the pika-equivalent elevation, i.e., the minimum elevation of *O. princeps* populations throughout the geographic range, given site latitude and longitude (Hafner 1993); Grazed? indicates whether significant grazing by nonnative ungulates occurred at or near taluses for more than half the period leading up to the survey; GrazIntensity indicates number of cattle and horse defecations within 1 m of the survey path walked for 8 hr, within each site; and Amt (Amount) of Habitat indicates the number of 20-m-diameter home ranges of talus having pika-appropriate rock diameters (0.2–1.0 m) within each site.

snowmelt model. Details on the development of the water balance model, associated R code, and validation are presented in supplementary material to Dobrowski et al. (2013). Relative to key life-history events of pikas, we hypothesized that maximum SWE might affect pikas by either: (1) mediating for how long into the hotter season free water would be available, or (2) mediating likelihood of acute cold stress during coldest seasons (due to lack of insulation). Analogously, we hypothesized that GS_PPT or deficit might affect animals directly via water stress, or GS_PPT or AET might act through indirect mechanisms (e.g., forage quality).

Analyses

We used an information-theoretic framework to evaluate a suite of 20 competing a priori models (developed before the 1990s surveys) with plausible combinations of five variables predicting pika abundance (Appendices D and E). Because Beever et al. (2003, 2010, 2011) have already explored predictors of site-wide extirpations of *O. princeps* in this region, we sought here to avoid confounding extirpation with our index of population size. Accordingly, we omitted unoccupied sites (putative extirpations) from the analysis (i.e., six of the original 25 sites for the 1990s surveys, and an additional three sites for the 2000s surveys). Because of clear overdispersion in pika abundance

⁷ <http://www.prismclimate.org>

values, we used QAIC_c (quasi-AIC corrected for small N) as the information criterion to compare the evidence in support of our competing models (Burnham and Anderson 2002). We tested and compared the fit of quasi-Poisson and negative-binomial models by plotting the estimated variance-mean relationship based on the full model with the average squared residuals against the fitted values (e.g., Appendix F), per Ver Hoef and Boveng (2007). For both the 1990s and 2000s data, the quasi-Poisson model clearly provided superior fit. We did not have microclimate data from one site (Long Canyon); thus, we used the linear-regression relationship among all sites with each of the microclimatic variables' best predictor to impute those values. We also ran analyses without that site included, but this did not affect results appreciably. For analysis of relative pika densities in the 2000s surveys (objective 3 in the *Introduction*), we added a site with microclimatic data from Hays Canyon where pikas were recently discovered, to further assess the sensitivity of our relatively small-sample-size data set to site additions, following Beever et al. (2011). For this analysis of relative densities, quartile-quartile and leverage plots suggested that linear-regression modeling was appropriate. Thus, we compared models using AIC_c. We considered models with ΔAIC_c or $\Delta\text{QAIC}_c < 2$ to have substantial support, and models with $2 < \Delta\text{AIC}_c$ or $\Delta\text{QAIC}_c < 4$ to have considerable support (Burnham and Anderson 2002).

To address objective 2, we used the same set of models predicting the number of individuals detected by E. A. Beever in either of the 1990s or 2000s surveys, and compared the top models, variable weights (summed and average weight per model), and model-averaged coefficients. Using insights gained from the 1990s surveys and resultant analyses, we also created an updated model suite with which we sought to better predict patterns of density in the 2000s surveys (objective 3). With this, we investigated the evidence in support of alternative mechanisms underlying *O. princeps* density by including parallel models that alternatively replaced total annual precipitation (which mixes cold-season snow with warm-season rain) with each of the four derived ecohydrologic variables. For this analysis, we tallied number of 50-m transects surveyed on talus for pikas per site in the 2000s surveys, and divided the number of individuals detected by EAB by the number of transects along which we sampled for pikas for 8 h, within each site; we analyzed this quotient using linear regression. For objective 4, we compared average variable weights from b) with models of pika extirpation pertaining to time up until the end of each of the two survey periods (i.e., until 1999, and during 2000–2008), among the same 25 sites. For objective 5, we arcsine-transformed the probability of pika persistence at each site (weighted P[occ]; Table 2 of Beever et al. 2011) and regressed it against population abundance (counts) in the 2000s surveys using least-squares linear regression. All analyses were performed in R, version 2.13.1 or version 2.13.2 (R Development Core Team 2011).

RESULTS

Early-warning indications of distributional change

We observed four patterns of climatic influence on pika abundance across the Great Basin. First, at three different sites in the northern portion of the basin, we observed fewer pikas in the 2000s than in the 1990s at the lower elevation boundary (i.e., hotter range edge) of pika occupancy, without any change in the elevation of that boundary, similar to that observed by others (e.g., Kelly and Goulden 2008). Second, at two sites in the southern portion of our study area, we observed upslope retraction from the lower elevation boundary on south-facing slopes, while animals on north-facing slopes persisted at that minimum elevation. Our sensor data from across the region indicate that southern aspects are predictably the warmest, in most contexts (except, e.g., in instances of shading or cold-air pooling). Third, we observed a marked increase in the average elevation of detections (up to 120 m) from 1994 to 2008, within some sites (different from the three northern-basin sites mentioned earlier in this paragraph) at which the lower elevation boundary remained unchanged. Finally, the \log_{10} of the ratio (number of animals detected in the 2000s sampling : number detected in the 1990s sampling) was strongly and positively predicted by latitude (i.e., greatest declines at southernmost sites; linear regression $F_{1,17} = 6.9$, $P = 0.018$).

Detectability

Double counts, performed in 50-m segments at 10 sites during 2005–2007 by E. A. Beever and one less-experienced observer, suggested that detectability of individuals within sites averaged 95.9% across sites for the author. His counts were thus used for the 1990s vs. the 2000s analyses of abundance. Results also illustrated significant repeatability of counts at each site between paired observers ($r = 0.991$) and by E. A. Beever between time periods; more details appear in Appendix A.

Quantifying predictors of pika abundance

Information-theoretic analyses of *O. princeps* abundance in the 1990s and 2000s surveys with the same model suite indicated shifting influence of predictor variables between time periods (Table 1a, b). When ranking predictors by average variable weight (w_i /number of models with variable i), the top-ranked predictor of pika abundance in the 1990s surveys was the worst predictor in the 2000s surveys. No predictor had the same rank among the five predictors in both periods, and the total change in rank positions was nearly maximized (10 out of 12 possible rank changes). Changes in importance of ungulate grazing for pika abundance between the two periods were somewhat equivocal, as the presence of grazing during and before surveys went from most to least predictive, while effect of grazing intensity went from fourth to second most predictive (Table 1a, b). Amount of physically appro-

TABLE 2. Linear-regression results from analyses of relative density of *O. princeps* at sites in the 2000s surveys, including models with substantial ($AIC_c < 2$) and considerable ($2 < AIC_c < 4$) support, plus the null model.

Model	AIC_c	ΔAIC_c	K	Akaike weight	Cumulative weight	Model r^2
Maximum SWE + latitude	126.13	0.00	4	0.301	0.301	0.601
GS precipitation + latitude	128.15	2.02	4	0.110	0.411	0.551
AvgSummT + latitude	128.78	2.65	4	0.080	0.491	0.534
Maximum SWE	128.96	2.83	3	0.073	0.564	0.438
Latitude	129.34	3.21	3	0.061	0.625	0.425
Maximum SWE + MaxElevR + latitude	129.39	3.25	5	0.059	0.684	0.606
Null	136.17	10.04	2	0.002	0.994	

Notes: Variables are defined in the *Environmental variables* section of the *Methods*. K is the number of model parameters. Abbreviations are: SWE, snow-water equivalent; GS, growing season; AvgSummT, average summer temperature; and MaxElevR, residual of the linear regression of maximum elevation of local talus habitat on site latitude.

priate talus habitat within a site was the worst or second worst predictor of pika abundance, in both periods. Total annual precipitation increased in importance from the 1990s to the 2000s surveys, and its variable weight (summed, or weight per model) was nearly twice as high as that of any other predictor in the latter surveys (Table 1a, b). Re-analyzing the 1990s data with only the 16 sites of the 2000s surveys did not affect the rankings of any of the predictor variables' average weights.

When looking at ranks of plausible models of *O. princeps* abundance in both periods, no models with substantial support ($\Delta AIC_c < 2$) were common to both periods, and only one model (precipitation alone) occurred in both periods among the 11 models with $\Delta AIC_c < 4$ (Appendix E). Comparing estimates of model-averaged coefficients from both periods across models with $\Delta AIC_c < 4$, averages for two variables (annual precipitation, grazing presence) changed sign between periods, and magnitudes of the coefficients all differed dramatically (Appendix G).

Predicting abundance in the 2000s surveys with updated model suite

Our updated model suite effectively predicted patterns of *O. princeps* density in the 2000s surveys, as >82% of models ranked above the null model. Average annual precipitation did not appear in any of the most plausible

models, but maximum SWE or growing-season precipitation appeared in four of the six top models (Table 2). Only latitude was more pervasive (in five of the six top models); however, it appeared in four to five times more models than each of these ecohydrologic variables. Variable weights (summed, and weight per model) reflected a similar pattern, as both maximum SWE and growing-season precipitation (as well as two other variables) better predicted population size than did average annual precipitation (Table 3). The top six ranked models and the five variables with highest variable weight per model were unchanged across analyses using different versions of Long Canyon imputed values and exclusion of the Hays Canyon site.

Comparing predictors of abundance and extirpations of pikas from the same temporal and spatial domains

Average variable weights (i.e., w_i /number of models) from original a priori model sets used to explain results from both the 1990s and 2000s surveys suggested that presence of nonnative grazing at sites remained the second poorest predictor (among five variables) of persistence in both periods, but for abundance it went from best predictor in the 1990s to worst predictor in the 2000s surveys (Appendices H and I vs. Table 1a, b). However, the measure of grazing intensity nearly tripled its average variable weight in predicting abundance from

TABLE 3. Variable weights, average variable weights, and sign of the coefficient of predictor variables from the analyses in Table 2.

Variable	Variable weight	Weight per model	Sign of variable coefficients
Maximum SWE	0.471	0.0941	positive
Latitude	0.802	0.0501	positive
GS precipitation	0.159	0.0396	positive
AvgSummT	0.117	0.0195	negative
Average annual precipitation	0.064	0.0160	positive
Residual of maximum local-habitat elevation on latitude	0.150	0.0107	mixed
Grazed in most years before 2000s sampling?	0.034	0.0085	negative
Days below -5°C	0.033	0.0082	negative
Water deficit	0.040	0.0079	negative
Days above 28°C	0.018	0.0058	positive
Actual evapotranspiration	0.028	0.0056	mixed

Note: See Table 2 for clarification of the variables and abbreviations.

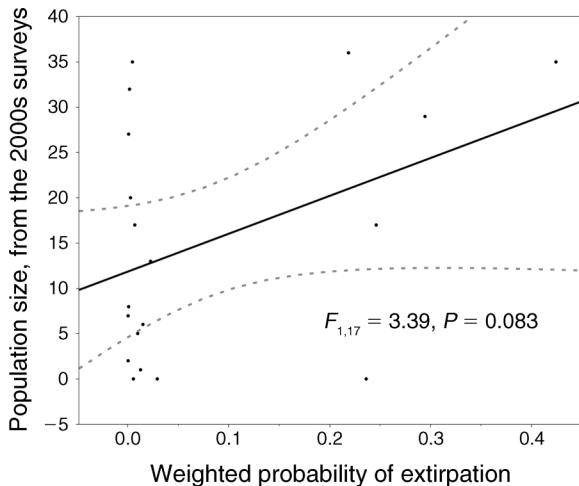


FIG. 1. Relationship between the probability of future site extinction, given model-averaged results from extirpations that occurred through the surveys from 1994–1999, and the number of American pika (*Ochotona princeps*) individuals detected within each site during surveys done in 2003–2008. Shown are the least-squares linear-regression line (solid) and the 95% confidence-interval lines (dashed). Untransformed probabilities are graphed, for visually more intuitive representation of relationship; for regression with arcsine-transformed independent-variable values, test results were $F_{1,17} = 2.46$, $P = 0.135$.

the 1990s to 2000s surveys (Table 1a, b). Whereas the mountain range-wide amount of talus habitat fell from most predictive of extirpations in the 1990s to the third most predictive in the 2000s surveys, amount of talus within 3 km was the poorest or nearly poorest predictor of pika abundance in both survey periods (Appendix I vs. Table 1a, b). Additionally, we used several identical predictors in analyses seeking to explain patterns across sites of the Great Basin observed in the 2000s surveys in either abundance or persistence, using an updated model suite (Table 3 vs. Appendix C). Only one predictor exhibited similar average model weights and relative ranking among predictors for both pika abundance and persistence: presence of ungulate grazing, which was only moderately predictive. In contrast, several predictors differed in their strength of apparent influence on pika abundance vs. persistence in the 2000s surveys: latitude and average summer temperature (higher importance for relative density, in both cases), as well as high-elevation refuge within sites and number of very cold days (higher importance for persistence, in both cases; Table 3 vs. Appendix C). However, maximum SWE and number of very cold days are tightly linked conceptually and empirically ($r = -0.782$, in our data set); each ranked highly, in each analysis.

Assessing the relationship between abundance and probability of extirpation

Model-averaged probabilities of site-wide extirpation, given the six extirpations observed through the 1990s surveys, did not inversely predict number of pikas

detected in the 2000s surveys at the 19 remaining sites. Instead, they tended to positively predict abundance (i.e., counts), and nearly significantly so (linear regression $F_{1,17} = 2.46$, $P = 0.135$; Fig. 1). These probabilities exhibited no relationship with *O. princeps* abundance in the 1990s surveys ($F_{1,17} = 0.01$, $P = 0.93$).

DISCUSSION

Understanding the relationship between population size and extinction, as well as the factors driving patterns and trends in abundance within species, remain fundamental challenges for ecology (Nielsen et al. 2005). This first relationship may be mediated through any number of mechanisms related to habitat suitability, landscape context, or both (Larson et al. 2004). Although abundance can be a more noisy indicator of ecological change and be strongly affected by detectability, its greater sensitivity to environmental perturbations is often considered advantageous in monitoring (Noss 1990). Abundance is more sensitive than occupancy, given that all individuals must be gone to detect a change in occupancy. We have used abundance data from survey periods dating to 1994 for *O. princeps* across ~40 million ha of the Great Basin, western USA, to quantitatively assess the relationship between abundance and extinction risk.

Changing determinants of pika abundance between the 1990s and 2000s surveys

Ranks of predictor variables changed substantially between the two survey periods, as was evidenced in analyses of extirpation (Beever et al. 2011). Using fossil assemblages, McGill et al. (2005) similarly found that degree of change in small-mammal communities of North America can vary with the temporal, taxonomic, and geographic scales of investigation. Arguably the most remarkable result of our analyses, however, was the one predictor of abundance whose importance remained constant (and low): amount of field-verified habitat within each site (Table 1). Further substantiating this, the numbers of animals detected in the 2000s surveys were poorly correlated ($r = -0.12$) to the number of 50-m transects surveyed per site. Although these results run counter to the truism that animals need habitat (especially for territorial species living obligately in easily quantifiable habitats such as talus), ecologists know that “habitat” encompasses far more than physically suitable habitat. Important other characteristics include tolerable thermal and chemical environments, and densities of predators and competitors, among other factors. Consequently, wildlife–habitat relationships for predicting trends in abundance or distribution must now move beyond static depictions of habitat or vegetation types.

Updated model suite, and relationships between drivers of abundance and extinction

Markedly increased importance of annual precipitation for predicting abundance from the 1990s to the

2000s surveys reaffirmed our interest in examining alternative mechanisms by which precipitation may affect *O. princeps* abundance. Maximum SWE, the best predictor of relative density in the 2000s surveys, echoed the importance of days below -5°C in extirpations basin-wide from historical records through 2007 (Appendix J) or of days below -10°C (a relevant threshold of acute-cold stress) in extirpations after 1999 (Appendix C). Strong support for growing-season precipitation echoes (1) findings (Appendices J and K) that mean summer temperature was the best predictor of basin-wide patterns of pika extirpation through 2007 (because these two variables exhibited the second-highest correlation [-0.828] among any pair of our predictors), (2) increase in importance of average daily maximum temperatures in August from least (before the 1990s surveys) to second most predictive of recent extirpations (Appendix H), and (3) importance of subsurface water presence in predicting pika occupancy in the southern Rockies (Erb et al. 2011). All of these variables (i.e., growing-season precipitation through subsurface water presence) reflect physiological or related stresses during summer. Though one might expect greater importance of precipitation on population dynamics in this drier portion of the species' range (Appendix L) than elsewhere, we encourage comparable analyses in regions such as the southern Rocky Mountains (Erb et al. 2011), Sierra Nevada (Millar and Westfall 2010), and along the length of the Columbia River Gorge (Simpson 2009). Although pikas experimentally caged above in situ talus patches overheat and expire quickly at climatically more marginal sites (e.g., Smith 1974), the frequency of very hot days at sites across the basin not only had the lowest (summed) variable weight in Table 3 (i.e., most poorly predicted density), but the sign of its coefficient suggested a direct (rather than indirect) relationship. Maximum SWE and growing-season precipitation better predicted relative density than did average summer temperature. This suggests that temperature and precipitation may influence species synergistically, such as indirectly, through forage quantity or quality (Wilkening et al. 2011). To further investigate this empirically, we regressed a site-wide estimate of total aboveground gross annual productivity (Goward et al. 1985) during 2003–2007 against either (1), number of pikas detected per site in the 2000s surveys or (2) pika relative density (i.e., number of pikas detected per 50-m transect). The integrated area under the growing-season NDVI (normalized difference vegetation index) curve illustrated that mean productivity strongly predicted abundance among all sites ($F_{1,24} = 12.78$, $P = 0.0015$), and also among pika-detected sites only ($F_{1,15} = 6.75$, $P = 0.02$). Even more convincingly, mean productivity predicted relative density of pikas across all sites ($F_{1,24} = 17.74$, $P = 0.0003$), and also among pika-detected sites only ($F_{1,15} = 11.51$, $P = 0.004$). Mechanistic

understanding will be best achieved, however, when broad-extent, fine-sampling-resolution results such as ours can also be linked with demographic data on survivorship and fecundity, physiological condition, and disease. Ideally, all of these data will be collected at comparable resolutions, which was our case except for the ecohydrologic variables.

Relationships between extirpation and abundance

Our finding that higher modeled probabilities of site-wide extirpation tended to predict higher (rather than lower) abundance of *O. princeps* in the 2000s surveys may reflect different factors governing dynamics between the 1990s and 2000s (sensu Beever et al. 2011). It could also reflect nonlinearities or lags in population size, “sink” habitats, or importance of rare extreme climate events (van Horne 1983, Abrams 2002). Lags or nonlinearities in population size seem unlikely to produce the observed relationship, however, given that probabilities derived from extinctions that had occurred up to 1999 had no relationship to *O. princeps* abundance at remaining occupied sites in the 1990s surveys.

For the relationships between extirpation and abundance that we have examined as well as other such ecological relationships, understanding the (1) mechanisms underlying relationships and their trends, (2) life-history strategies and species traits associated with abundance shifts, (3) climatic and geographic contexts where such shifts are and are not happening, and (4) synergies of climate with other system drivers, will likely remain frontiers of ecological research for decades to come.

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SUPPLEMENTAL MATERIAL

Appendix A

Archive methods and results providing further detail on *Ochotona princeps*, field-sampling procedures, how we quantified relative abundance and density, predictor variables, and estimation of productivity, as well as results on detectability and summaries of abundance and density data ([Ecological Archives E094-141-A1](#)).

Appendix B

Topographic illustration of the study region and the sites used in analyses of pika population size or relative density ([Ecological Archives E094-141-A2](#)).

Appendix C

Information on individual predictors and top models for pika persistence to the present (i.e., as observed at the end of the 2000s surveys) since the end of the 1990s surveys ([Ecological Archives E094-141-A3](#)).

Appendix D

Full list of models used to understand which combination of factors best predicted number of animals detected within each site in the 1990s and 2000s surveys of pikas across the hydrographic Great Basin ([Ecological Archives E094-141-A4](#)).

Appendix E

Top-ranked models for information-theoretic analyses of pika abundance reported in Table 1 ([Ecological Archives E094-141-A5](#)).

Appendix F

Example of a diagnostic plot suggested by Ver Hoef and Boveng (2007) to evaluate use of a quasi-Poisson vs. negative-binomial model ([Ecological Archives E094-141-A6](#)).

Appendix G

Comparison of model-averaged coefficients of pika abundance in the 1990s vs. the 2000s surveys, using the identical model suite ([Ecological Archives E094-141-A7](#)).

Appendix H

Ranks of average variable weight per model of *O. princeps* persistence, for each of two time periods in the hydrographic Great Basin, western USA, 1898–2008 ([Ecological Archives E094-141-A8](#)).

Appendix I

Comparison of variable weights, average Akaike weight per model, number of models in which the variable had positive and negative coefficients, and coefficient of variation across the fitted coefficients of the variable for each predictor of pika persistence at sites across the hydrographic Great Basin, for each of two periods ([Ecological Archives E094-141-A9](#)).

Appendix J

Information-theoretic analyses of logistic-regression models that had substantial support, for predicting persistence of pikas at 25 sites in the Great Basin, USA, from historic records (1898–1956) through the end of the 2000s surveys ([Ecological Archives E094-141-A10](#)).

Appendix K

Variable weights for the analysis in Appendix J, across all models in the a priori set ([Ecological Archives E094-141-A11](#)).

Appendix L

Photographs of a portion of each of two study sites, central Nevada, USA ([Ecological Archives E094-141-A12](#)).