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ORIGINAL ARTICLE

Revisiting the past to foretell the future: summer temperature and habitat area predict pika extirpations in California

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ABSTRACT

Aim The American pika (*Ochotona princeps*) appears to have experienced climate-mediated upslope range contraction in the Great Basin of North America, but this result has not yet been extended to other portions of the pika's range. Our goals were: first, to determine the environmental parameters that most influence current pika distribution within California; second, to infer whether these constraints explain extirpations that have occurred in California; third, to predict future extirpations; and fourth, to advance methods for assessing the degree to which pikas and other climate-sensitive mammals are threatened by climate change.

Location Historical pika record locations in California, USA, spanning four degrees of latitude and longitude, from Mount Shasta to the southern Sierra Nevada.

Methods We identified 67 precise historical pika record locations and surveyed them exhaustively, over multiple years, to determine whether pika populations persist at those sites. We used an information theoretic approach and logistic regression to model current pika occupancy as a function of 16 environmental variables, tested our best-performing model as a predictor of historical occupancy, and then used our model to predict future pika occupancy given anticipated climate change.

Results Pikas no longer occurred at 10 of 67 (15%) historical sites in California. The best predictors of occupancy were average summer temperature and talus habitat area within a 1-km radius. A logistic model fitted to this relationship correctly predicted current occupancy at 94% of sites and correctly hindcasted past occupancy at 93% of sites, suggesting that the model has strong temporal transferability. Depending on the future climate scenario, our model projects that by 2070 pikas will be extirpated from 39% to 88% of these historical sites in California.

Main conclusions Our simple species distribution model for pikas performs remarkably well for both current and historical periods. Pika distribution appears to be governed primarily by behavioural restrictions mediated by summer temperature and by the configuration of talus habitat available to pikas locally. Pikas, and other montane species in the western USA, may be subjected to above-average exposure to climate change because summer temperature is projected to rise more than annual temperature.

Keywords

Climate change, global warming, historical resurvey, metapopulation, *Ochotona princeps*, pika, range shift, species distribution modelling, talus.

INTRODUCTION

Rapid anthropogenic climate change is projected to emerge as a leading threat to global biodiversity conservation in the 21st century (Thomas *et al.*, 2004; Loarie *et al.*, 2008). The fingerprint of climate change is already apparent in natural communities in the form of range shifts, advanced phenology, and genetic changes (Parmesan, 2006). Predicting the fate of particular species in the face of climate change is complex because the processes that limit species distributions

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and control abundances can shift over time or from one geographical region to another (Hijmans & Graham, 2006; Dobrowski *et al.*, 2011; Santos *et al.*, 2014). To make accurate predictions, it is necessary to show that species distribution models (SDMs) are transferable both temporally and geographically (Tuanmu *et al.*, 2011; Blois *et al.*, 2013).

Mountain systems have inherent physical properties that both increase and decrease vulnerability of species to climate change. On the one hand, because climate gradients are relatively steep in complex topographic environments, montane species may be able to track their climate envelope by dispersing relatively short distances upslope (Loarie *et al.*, 2009), or by exploiting topographic heterogeneity such as by shifting slope aspects. On the other hand, geographical isolation and unique environmental adaptations may make montane species especially vulnerable to warming (La Sorte & Jetz, 2010). As climate change forces range contractions, species may effectively be 'pushed off' the tops of mountains by warming climate (Thuiller *et al.*, 2005).

The American pika, *Ochotona princeps* (Richardson, 1828), a small (120–180 g), saxicolous lagomorph, has emerged as a model organism for examining the effects of climate change on montane species (Smith & Weston, 1990; Krijack, 2004; Beever *et al.*, 2011). American pikas (henceforth referred to as pikas) may be especially vulnerable to climate warming because their lower elevational limit, at least in the southern part of their range, is relatively high with respect to other mammal species (McDonald & Brown, 1992; Moritz *et al.*, 2008). In the Great Basin, pikas appear to be experiencing accelerating upslope range contraction in concert with regional warming (Beever *et al.*, 2011). Further, SDM studies predict that pikas could suffer drastic range collapse and regional extinction across their range in western North America during the 21st century (Galbreath *et al.*, 2009; Calkins *et al.*, 2012). Because of this vulnerability, the species was petitioned for protection under the United States and California Endangered Species Acts (Wolf *et al.*, 2007a,b). Despite acknowledging that climate change is expected to cause continued range loss, both petitions were denied on the basis that presently available scientific evidence does not indicate pikas are currently experiencing or will experience range-wide extinction within the foreseeable future. In their responses, both management agencies highlighted the need for more information on the degree to which pikas are threatened by climate change (United States Fish & Wildlife Service, 2010; California Department of Fish & Wildlife, 2013).

Adaptations that allow pikas to survive in cold alpine climates make them poorly suited to warming temperatures. Low thermal conductance and high resting metabolic rate aid pikas in avoiding hypothermia during cold winters under the snow but make them vulnerable to hyperthermia in the summer (MacArthur & Wang, 1973; Smith, 1974). A key vulnerability is that their upper lethal body temperature is 3 °C above their resting body temperature (MacArthur & Wang, 1973; Smith & Weston, 1990). Thus, summer temperature may restrict pika distribution. To avoid acute heat stress during high temperatures, pikas thermoregulate behaviourally by reducing their foraging activity and spending more time in the cool interstices of talus fields where they reside (Smith, 1974). In contrast to many non-lagomorph small montane species, pikas do not hibernate or accumulate fat stores. Instead, during the summer they cache vegetation in haypiles on which they subsist during the winter (Smith & Weston, 1990). Reduced foraging and caching may result in reduced energy intake, reproduction, and survival (Smith, 1974). This same mechanism of range limitation – reduced foraging as a result of behavioural thermoregulation to avoid unsuitable temperatures – has been proposed as a common limitation for other montane mammals (Morelli *et al.*, 2012) and animal species as a whole (Pörtner, 2002). Resurvey results in the Great Basin support summer temperature as a top predictor of pika extirpations, but this result has not previously been generalized to other portions of the pika's range (Moritz *et al.*, 2008; Beever *et al.*, 2011; Erb *et al.*, 2011; Stewart & Wright, 2012).

We used historical resurvey data from across the pika's range in California to assess causes of pika extirpation, to infer whether climate change has led to upslope range contraction in California, and to build an SDM for projecting future occupancy. Two previous studies collected resurvey data on pikas within subregions of California, but both datasets suffered from small sample size and limited statistical power (Moritz *et al.*, 2008; Stewart & Wright, 2012). We fitted a logistic model to current occupancy patterns, tested the model's ability to hindcast known past occupancy based on past climate, and used the model to forecast future pika distribution. This study advances previous projections of future pika distribution (Galbreath *et al.*, 2009; Calkins *et al.*, 2012) in four respects. First, in contrast to previous approaches, which used 'pseudo-absences' from random locations across the landscape, our model is parameterized with verified, high-quality absence data. Second, we test our model for temporal transferability using historical occurrence data. Third, our model tests and incorporates a non-climate environmental variable (habitat area) into projections of future pika distribution. Finally, we use the most recent future climate projections from the Intergovernmental Panel on Climate Change (IPCC 5; Taylor *et al.*, 2012). While our study focuses on the American pika, our methods and conclusions should be generalizable to other montane species, as we discuss below.

MATERIALS AND METHODS

Field methods and historical data

We identified 67 historically recorded pika locations across the pika's range in California from the 19th and 20th centuries, and resurveyed them to determine whether pikas have persisted at those sites. Our field methods were comparable to those of Stewart & Wright (2012) in the northern Sierra Nevada, with minor modifications. We surveyed each site until we had either detected pikas, or until we had completed an exhaustive search of all pika habitat within a 1-km radius of the historical location. If pikas or current-year pika sign were detected at a site, the site was scored as occupied. In addition to pika sightings or calls, haypiles or pika scat (sign) were considered recent evidence if they contained green hues from undecomposed chlorophyll. As a final measure, we listened for pika calls during morning and evening hours, when pikas are most active at hotter sites (Smith, 1974). We also searched for and collected older ‘relict’ pika faecal pellets to confirm past occupancy. Pika faecal pellets often persist for a decades after extirpation with gradual decline in size and change in colour (Nichols, 2010; see Appendix S1 in Supporting Information). We used a 1-km survey radius because it is large enough to detect large-scale metapopulation extirpations. Given the density of pika habitat in our region, exhaustive resurveys of a 1-km radius required up to 5 days of search effort.

We aggregated data from six resurvey teams working in different regions of California (led by coauthors of this study). We endeavoured to include all reliable and spatially precise historical record locations that had been resurveyed prior to 2012. To obtain historical records, we queried biodiversity databases (accessed April 2011; Arctos: http://arctos.database.museum; CNDDB: http://www.dfg.ca.gov/biogeodata/cnddb; GBIF: http://www.gbif.org/; and MaNIS: http://manisnet.org/), read field notes, visited offline museums, contacted professional networks, and searched the literature. Records accompanied by a voucher specimen or observed by an experienced researcher (e.g. Joseph Grinnell, Annie Alexander; Museum of Vertebrate Zoology, UC Berkeley) were considered reliable. Records were considered sufficiently precise only if all plausible interpretations of the historical description fit within a 1-km search radius (Appendix S1).

The 67 records we resurveyed spanned the majority of the pika’s geographical and elevational range in the state. Records extended over more than four degrees of latitude and longitude, from the slopes of Mount Shasta in the north to the John Muir Wilderness in the south, and to the White Mountains in the east (Fig. 1, Appendix S1). The records covered an elevational range from the lowest known pika population in California (1380 m) to the high slopes of the southern Sierra (3940 m). Spatial uncertainty associated with historical records ranged from nil (detailed field notes accompanied by historical photographs; Appendix S1) to 1 km (e.g. museum skin with specimen tag specifying ‘east side of Pyramid Peak’) with a median precision of 0.4 km. The original observation year for records ranged from 1897 to 2000 (median = 1927), resurveys were conducted during 2004–2012 (median = 2010), and the interval between the historical observation and resurvey ranged from 12 to 109 years (median = 83). While 12 years may seem a relatively short interval for historical resurvey, our results indicate it has been sufficiently long for populations to become extirpated.

Pikas are highly detectable, based largely upon their frequent calls and copious and persistent faecal pellets. Previous studies indicate consistently high detection probability within discrete talus patches (> 90%) after 15–30 person-minutes (person-min) of search effort (Beever *et al.*, 2010; Rodhouse *et al.*, 2010; Erb *et al.*, 2011; Jeffress *et al.*, 2013). Extended to multiple talus patches within the 1-km radius, detection probability would approach certainty if three or more patches were occupied. We took several measures to maximize our confidence in observed extirpations. Depending on the amount of habitat, our search effort at extirpated sites ranged from 5 to 56 person-hours searching all talus (median = 11 person-hours) and 7 to 90 hours on site and within hearing distance of pika habitat (median = 24 person-hours). All sites where pikas were not initially detected during the first year were surveyed exhaustively in a subsequent year.

Analytical methods and predictor variables

We modelled pika persistence as a function of 16 environmental variables – 2 habitat, 2 elevation, and 12 climate variables – that capture the most biologically significant processes for pikas, as supported by a mechanistic hypothesis and/or by previously published literature (Appendix S2). These predictor variables were combined into 58 biologically informed *a priori* combinations and tested for predictive power. The 12 climate predictor variables were extracted from 270-m resolution grids, representing 10-year (2001–2010) average climate surfaces from the California Basin Characterization Model (Daly *et al.*, 1994; Flint & Flint, 2012; Thorne *et al.*, 2012). Given that pikas can escape acute heat stress through behavioural thermoregulation and that they attain a maximum age of 7 years (Smith & Weston, 1990), we expected that full demographic collapse and extinction of a local metapopulation would typically be the result of multiple-year chronic climate effects as opposed to single-year acute effects. Climate variables included seasonal and annual temperature, precipitation, snowfall, snowpack depth, snowpack duration, climate water deficit (a drought index), and actual evapotranspiration (a vegetation productivity index). Elevation was included as a high spatial-resolution proxy for coarser resolution climate variables. Absolute elevation was extracted from 10-m resolution digital elevation models. Pika-equivalent elevation was calculated as the difference between absolute elevation and latitude–longitude calculated minimum elevation for pikas (Hafner, 1993). Values for each climate and elevation variable were extracted for the most suitable location within each site boundary (e.g. minimum average temperature within 1-km radius site, maximum elevation, maximum average precipitation, etc.). For each site, talus habitat was hand-delineated into a GIS layer using the best available aerial imagery (*c.* 3 person-hours spent on talus delineation per site) and total talus area and

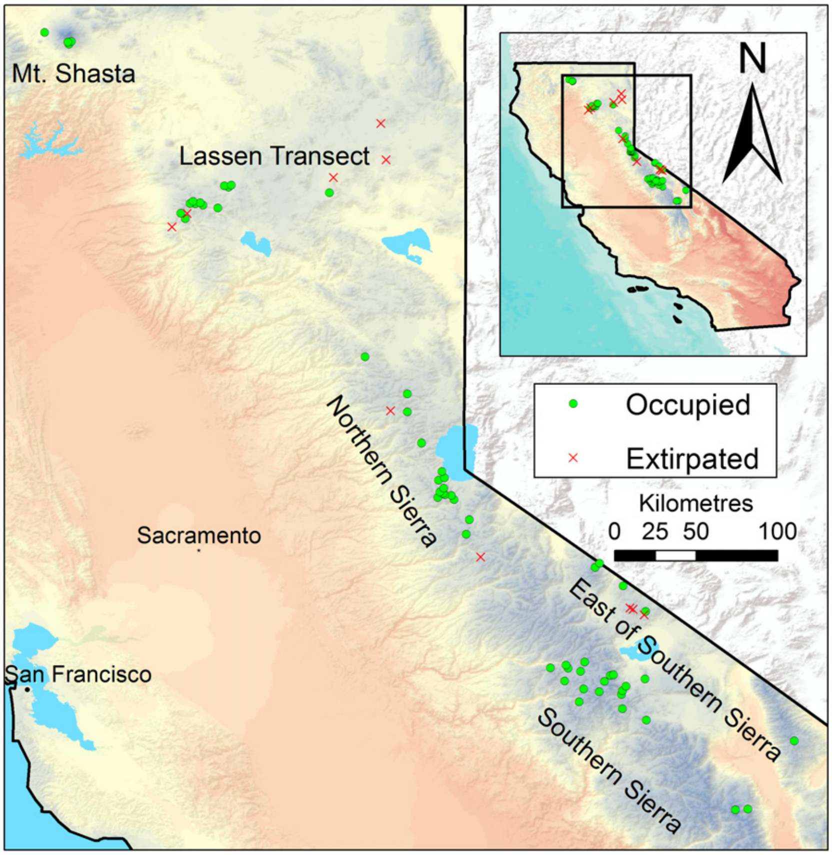

Figure 1 Location and current occupancy status of 67 historical American pika (*Ochotona princeps*) sites in California. Background is coloured by average summer temperature.

perimeter within the 1-km radius site boundary was calculated. Talus perimeter was included in addition to talus area because pikas may preferentially use edge habitat for access to forage (Moilanen *et al.*, 1998; Millar, 2011; Jeffress *et al.*, 2013). Two sites with anthropogenic pika habitat (ore dumps), where aerial talus mapping was not possible, were delineated on the ground.

We evaluated the performance of the *a priori* models (Appendix S2) using logistic regression and multi-model inference techniques (Burnham & Anderson, 2002). Highly correlated variables ($|r| > 0.7$) and variables that attempted to measure similar causal mechanisms were not included in the same model (e.g. temperature and elevation were not included in the same model). To avoid over-fitting we restricted all models to a maximum of five events per variable (Vittinghoff & McCulloch, 2007). With a total of 10 extirpations ('events') in our data, this translated to no more than two predictor variables per model. To test whether our results were robust to imperfect detection, we performed simulations in which we iteratively reclassified one of 10 extirpated sites as occupied and evaluated the performance of our 58 *a priori* models. In addition to internal model evaluation we evaluated model performance using spatial and temporal cross-validation (Fielding & Bell, 1997; Wenger & Olden, 2012). First, we evaluated model performance in the current period using 10,000 iterations of randomly partitioned training (80%) and evaluation (20%) data (i.e. spatially distinct, temporally equivalent data; Kohavi, 1995). Next, we tested temporal transferability by training the model with the full set of current data and evaluating model performance using the full set of historical data (i.e. spatially equivalent, temporally distinct data; e.g. Boyce *et al.*, 2002; Araújo *et al.*, 2005; Moritz *et al.*, 2008; Smith *et al.*, 2013). Finally, we tested model transferability using data partitions that were both temporally and spatially distinct (Kharouba *et al.*, 2009) – iteratively training the model with current data from 80% of sites and evaluating the model with historical data from the remaining 20% of sites.

We projected pika occupancy for both historical and future climate conditions using the best-performing logistic model trained on current occupancy patterns. Sites with ≥ 50% predicted probability of occupancy were classified as occupied, and sites below this threshold were classified as unoccupied. We assumed no change in the amount of talus habitat at sites from the historical to future periods (1897–2070). Historical climate for a given time period was calculated using the delta method and a 10-year running average of statewide deviations from current (2001–2010) climate (Abatzoglou *et al.*, 2009; CCT 1895–2012). Downscaled Coupled Model Intercomparison Project Phase 5 (CMIP5, 2011) future climate change scenario surfaces, i.e. prepared for the IPCC's 5th assessment report (Taylor *et al.*, 2012), were obtained from the WorldClim database (30 arc-second resolution, *c.* 800 m grid cells; Hijmans *et al.*, 2005), and further downscaled to 270 m to match current climate data resolution and baseline (delta method). We projected pika distribution during 2070 using one low emission and one high emission representative concentration pathway (RCP 4.5, 'low,' and RCP 8.5, 'high') combined with a low sensitivity (NASA Goddard Institute for Space Sciences model GISS-E2-R), high sensitivity (Atmosphere and Ocean Research Institute, University of Tokyo, National Institute for Environmental Studies, and Japan Agency for Marine-Earth Science and Technology model MIROC-ESM) and ensemble mean general circulation model (mean of 17 GCMs), for a total of six future climate scenarios (Taylor *et al.*, 2012).

RESULTS

Overall, 57 historically occupied sites were currently occupied by pikas (85%) and 10 sites were extirpated (15%). The average elevation of currently occupied sites (2800 m) was 500 m higher than the average elevation of extirpated sites (2300 m) (one-sided *t*-test, $P = 0.009$). We found old pika faeces, but no fresh sign, at all 10 extirpated sites, confirming previous site occupancy. Detection of old faeces was relatively easy at extirpated sites (median = 13, range = 5–59 person-min). Of the 10 extirpated sites, five occurred in the Lassen Transect, two occurred in the northern Sierra, and three occurred in the Bodie Hills (Fig. 1). For most occupied sites (81%) pika detection was easy, with pikas detected within 30 person-min (median = 5 person-min) and in the first talus patch surveyed. Pika detection was more difficult at nine of the occupied sites (median = 65 person-min, range 34–582 person-min). Five occupied sites where pikas were not detected during partial resurvey of the 1-km radius in the first year were discovered to be occupied during complete survey of the 1-km radius in a subsequent year. Occupied and extirpated sites did not differ statistically in year of their historical observation (median 1926 vs. 1931, respectively).

The best-performing model, talus area + mean summer temperature, received considerably greater support than the next best-performing model (difference in corrected Akaike's information criterion, $\Delta\mathrm{AIC_c} = 2.39$), 69% of the Akaike weight (w_i) for all *a priori* models [area under the receiver operating characteristic curve (AUC) = 0.98; Table 1], and correctly classified current occupancy at 94% of sites (63/67; Fig. 2). The model performed nearly as well when cross-validated using partitioned, spatially distinct training and evaluation data [AUC = 0.95, 95% confidence interval, CI, (0.67, 1.00); percentage correctly predicted = 93%, 95% CI (77%, 100%)]. Relative support for the best model was more pronounced when models with climate-proxy variables (e.g. elevation) were excluded in order to extrapolate pika occupancy under past and future climate conditions ($\Delta\mathrm{AIC_c} = 7.41$, $w_i = 0.96$). In simulations designed to test model robustness to imperfect detection probability, where one extirpated site was iteratively reclassified as occupied, the best-performing model (talus area + mean summer temperature) received the highest support in 9 of 10 simulations. In the remaining simulation, talus area + mean summer temperature had the second highest support, and talus perimeter + mean summer temperature received the highest support.

As a test for temporal transferability, we applied the best model to historical site temperature data to hindcast past occupancy at historical record locations. When evaluated against temporally distinct and spatially equivalent data, the model correctly hindcasted past occupancy during the year of the original observation at 93% of sites (62/67). When evaluated against temporally and spatially distinct data, the model correctly hindcasted 92% of sites, 95% CI (77%, 100%).

Projecting to the future, our best-performing model predicted progressive site extirpations as summer temperatures warm. By 2070, overall extirpation at the 67 historical sites is projected to range from 39% to 88%, depending on the emissions pathway and the GCM used (Fig. 3, Appendix S2). Under ensemble mean GCM climate scenarios, the model projects that 51% to 75% of sites will no longer be occupied by pikas for the low and high emissions scenarios, respectively (RCP 4.5 and RCP 8.5). Extirpations at the historical localities are projected to be most pronounced in the northern Sierra (north of 38.5° latitude), the Lassen Transect, and the ranges east of the southern Sierra, where pikas were projected to disappear from 44% to 100% of these historical sites in these regions by 2070, over all future climate scenarios. However, even for the worst-case future climate scenario considered (MIROC-ESM, RCP 8.5), pikas are projected to persist through 2070 at some historical sites (at least 12% overall). Taking into account range-wide (i.e. beyond historical site) temperature projections (Rogelj *et al.*, 2012), persistence past 2070 appears most likely in the high peaks of the Southern Sierra, the White Mountains, and Mount Shasta.

DISCUSSION

Two variables, talus area and mean summer temperature, did a very good job at separating sites where pikas are extant from sites where pikas have become extirpated since documented historical presence. Our best model, which incorporates these variables, strongly outperformed all other candidate models (Table 1), and correctly predicted current occupancy at 94% of sites (Fig. 2). The model performed nearly as well in a test of transferability through time – correctly predicting past occupancy at 93% of sites. This level of performance through historical time is high relative to models applied to other species, including other montane small mammals (Smith *et al.*, 2013), butterflies (Kharouba *et al.*, 2009), and plant species (Dobrowski *et al.*, 2011).

These same two variables, summer temperature and talus area, have strong mechanistic support, and have been repeatedly identified as the best predictors of pika occupancy elsewhere in the pika's range, suggesting that our best-performing model may also be geographically transferable. Calkins *et al.* (2012) used Maxent (Phillips & Dudík, 2008)

Table 1 Performance and statistics of top models ($\Delta AIC_c \leq 10$) fitted to explain recent American pika (*Ochotona princeps*) persistence or extirpation relative to historical presence in California, USA; and of variables included in top models.

Model	ΔAIC_c	AUC	R^2	w_i	Predictor	w_j	w_j/model	Sign	CV
TalArea + **SumT**	0	0.98	0.79	0.69	**SumT**	0.7	0.078	–	0.432
TalArea + ElevEq	2.39	0.97	0.76	0.21	ElevEq	0.213	0.071	+	0.416
TalArea + Elev	4.57	0.97	0.72	0.07	TalArea	0.983	0.066	+	0.365
TalArea + **AnnT**	7.41	0.94	0.68	0.02	Elev	0.07	0.012	+	0.413
TalPerim + **SumT**	8.02	0.95	0.67	0.01	**AnnT**	0.017	0.006	–	0.439
TalPerim + ElevEq	9.92	0.94	0.64	0	TalPerim	0.017	0.001	+	0.343
Null Model	35.81	0.5	0	0					

Left hand columns: models are listed in order of their difference from the best-performing model in corrected Akaike's information criterion (ΔAIC_c). Climate predictors appear in bold. Column headings denote the area under the receiver operating characteristic curve (AUC), Nagelkerke's max-scaled coefficient of determination (R^2), and Akaike weights among all *a priori* models (w_i). Right hand columns: column headings denote Akaike weights among all 58 *a prior* models (w_j), Akaike weights per model (w_j/model), the sign of fitted variable coefficients (Sign), and the coefficient of variation across all fitted coefficient values (CV). Variables are listed in order of decreasing weight per model. Coefficient signs (indicating a positive or negative relationship with occupancy) were consistent in all models and for all variables. Variable abbreviations are as follows: SumT, summer temperature; TalArea, talus area; ElevEq, pika-equivalent elevation; AnnT, annual temperature; Elev, elevation; TalPerim, talus perimeter. More information on variable definitions can be found in the text and in Appendix S2.

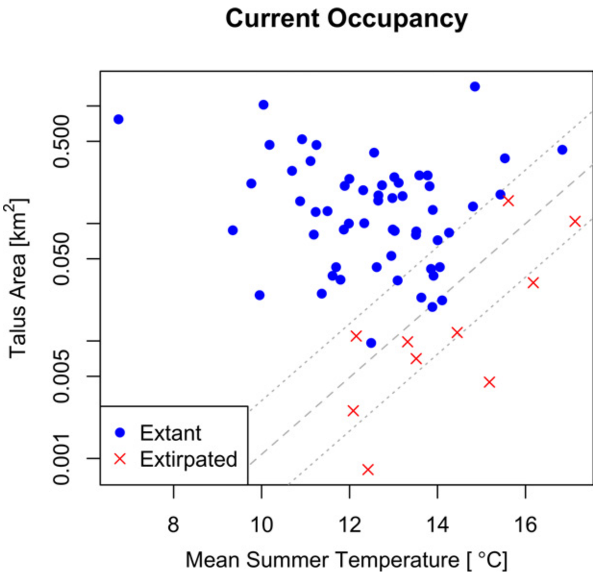

Figure 2 Current status of American pika (*Ochotona princeps*) occupancy at 67 historical pika record locations in California plotted against the best predictor variables, talus area and mean summer temperature. The central dashed grey line represents a 50% probability of occupancy as modelled by logistic regression, while the outer dashed lines represent 95% and 5% probability of occupancy.

and stepwise variable selection to identify mean summer temperature from a candidate set of 19 bioclimatic variables as the best predictor of pika distribution across the contiguous western USA. Two historical resurvey studies in the Great Basin indicated that mean summer temperature was the strongest limiting factor for pikas (Beever *et al.*, 2010, 2011). As a mechanistic hypothesis, mean summer temperature is supported as a factor limiting foraging as a result of behavioural thermoregulation. This mechanism is reinforced by knowledge of the pika's natural history (Smith & Weston, 1990), behavioural observations of reduced activity during high ambient temperatures (MacArthur & Wang, 1974; Smith, 1974), and physiological studies indicating very limited ability to dissipate heat and avoid hyperthermia (MacArthur & Wang, 1973). Mean summer temperature appears to regulate viability of low-elevation populations because it closely reflects conditions during crepuscular hours. The importance of crepuscular temperature to low-elevation sites is evidenced by the observed transition from diurnal activity at cold sites, to more-restricted crepuscular activity at warm sites, and ultimately to extirpation at the warmest sites (Smith, 1974; J.A.E.S., pers. obs.). Finally, temperature is supported as a limiting constraint by the palaeontological record of upslope range retreat by pikas since the Last Glacial Maximum (Grayson, 2005).

Talus area – the amount of habitat available to pikas locally – has also been previously identified as a factor affecting population and metapopulation dynamics (MacArthur & Wilson, 1967; Moilanen *et al.*, 1998) and has been documented in other pika extirpation studies in the Great Basin (Beever *et al.*, 2003, 2011) and in a subset of the California records (Stewart & Wright, 2012). Given that pikas preferentially use talus-edge habitat, with access to vegetation on which they feed (Moilanen *et al.*, 1998; Millar, 2011; Jeffress *et al.*, 2013), it is interesting that, in this study, talus area emerged as a better predictor of pika occupancy than talus perimeter. Talus area may be a more relevant measure of habitat availability because vegetation is often present in small patches within talus fields that are not reflected in talus perimeter measurements. Low talus area within a 1-km radius is generally indicative both of small habitat islands and poor connectivity between talus patches. Increased temperatures may compound poor habitat connectivity by impeding the survival of dispersing pikas (Smith, 1974). The precise mechanism behind the apparent relationship between talus area and site persistence is not known, but reasonable hypotheses include the following: (1) larger populations are less vulnerable to stochastic extinction (MacArthur & Wilson, 1967); (2) sites

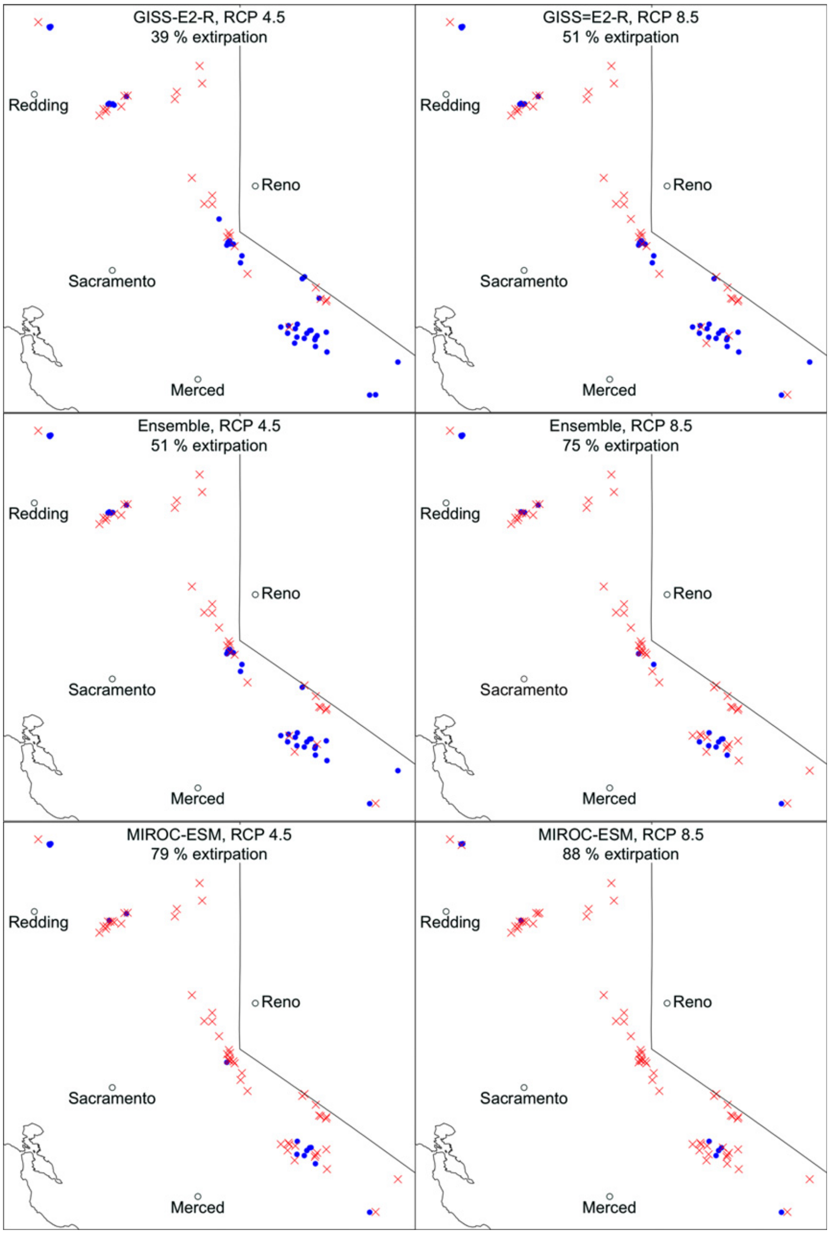

Figure 3 Predicted American pika (*Ochotona princeps*) occupancy status mapped at historical sites in California for 2070 under six future climate scenarios. Blue circles denote occupied sites while red crosses denote extirpated sites. Climate change scenarios (six panels) combine two representative concentration pathways, RCP, (low emission: RCP 4.5, high emission: RCP 8.5) with a low sensitivity general circulation model, GCM, (GISS-E2-R), a high sensitivity GCM (MIROC-ESM), and the ensemble mean of 17 GCMs. See also Appendices S2 & S3.

with more talus have better connectivity with higher elevation talus patches; and (3) sites with more habitat available are more likely to contain refugial areas with more suitable mesoclimate (Millar & Westfall, 2010).

In this analysis, we used a conservative criterion – complete absence of any current-year pika sign within a 1-km radius – to score sites as occupied or extirpated. We adopted this definition to differentiate landscape-level extirpations (on which this study focuses) from patch-scale metapopulation fluctuations, and to accommodate inclusion of records with moderately precise record descriptions. It is important to note that this definition glosses over interesting dynamics within sites. Four of our occupied sites appeared, anecdotally, to be sink habitats, i.e. sites that receive dispersers from nearby source patches and that do not currently sustain reproducing populations (Holt, 1985). At these sites, old pika faeces were widespread, but evidence of current occupancy was scant (≤ 2 individuals observed in any year), and search effort necessary for first detection of current occupancy was high (median = 356 person-min. searching talus). Two of these sites may have been very recently re-extirpated, as fresh pika sign was observed (green pellets and haypiles), but extensive late-summer surveys during morning and evening hours did not result in direct detection (sightings or hearing calls). At another site, a total of three pikas were observed during three years of extensive search effort, but no individual talus patch was ever occupied for two consecutive years. At the fourth site, we observed evidence of only two pikas (one direct sighting) and evidence of current occupancy had retreated upslope by *c.* 300 m elevation from the historical record. We suggest that juvenile pikas are able to disperse to these sites from nearby higher elevation habitat, but are not able to re-establish self-sustaining populations. Although we treated these sites as occupied in our analysis, our qualitative conclusions (i.e. talus area and summer temperature was the most informative model) are robust to treating these sites as either occupied or extirpated. Using our best-performing model, the probability of occupancy at our sink habitat sites was significantly lower than at occupied sites (one-sided Wilcoxon test, $P = 0.020$) and significantly higher than at extirpated sites (one-sided Wilcoxon test, $P = 0.012$).

Our results, coupled with the documented *c.* 1 °C increases in California-wide summer temperature over the past century (California Climate Tracker, 1895–2012; Abatzoglou *et al.*, 2009), strongly suggest that pikas have experienced climate-mediated range contraction in California over the past century. Because historical absence data for pikas is limited, definitive conclusions are not possible at this point. An alternative hypothesis is that all extirpations are the temporary result of normal metapopulation dynamics, and that the statistical relationship between temperature and pika extirpation (which has now been documented in both California and the Great Basin) exists because of more tenuous demographic conditions and higher turnover in patch occupancy near the lower boundary of the pika's elevation range, although not caused by temperature. Under the 'no climate effect hypothesis' we would expect that, in the intervening years since the historical era, an equivalent number of historical sites would have been colonized as were extirpated. As we were only able to identify one site where pikas were observed to be historically absent (recorded by Joseph Grinnell; still not occupied by pikas) we are not able to draw conclusions about recolonization. However, we observed apparently unsuccessful recolonization (e.g. dispersal followed by mortality) at four low-elevation 'sink-habitat' sites that are marginal in temperature and talus conditions, suggesting that previously occupied low-elevation sites have become unsuitable.

Using future temperature projections for 2070, and our statistical model of extirpation in relation to summer temperature and habitat area, we projected extensive (39%) to dramatic (88%) extirpation among our sites (Fig. 3, Appendix S2 & S3). Appendix S3 presents a graphical animation of the model results projecting pika occupancy through time as climate change becomes more severe: sites 'march' towards higher temperatures and eventually pass out of the threshold of pika viability.

We offer three important caveats to these projections. First, historical sites are not a random sample of the pika's entire distribution throughout California, and thus our projections are not interpretable as a range-wide estimate of range contraction but apply only to these historical sites. A critical step in applying our model to broader scales will be mapping talus distribution for entire regions. GIS algorithms that accurately automate talus mapping would represent an invaluable contribution towards this effort. Second, the performance and transferability of SDMs is dependent on the models taking into account the full range of important climate and non-climate environmental variables (Duncan *et al.*, 2009). Our small number of events (10 extirpations) limits our statistical ability to estimate parameters for more than two predictor variables in a model. While it appears that summer temperature and talus area are two of the most important limiting factors to pika distribution, other variables and variable interactions (e.g. hydrology) undoubtedly also play a role (Beever *et al.*, 2010; Erb *et al.*, 2011; Jeffress *et al.*, 2013). Third, for sites with high talus area (i.e. upper quartile), our dataset lacks extirpations, and thus model projection must extrapolate the temperature threshold for presence–absence at these sites (Fig. 2). For the highest talus area sites, the resulting projection predicts that pikas will persist through summer temperatures above the range of temperatures that pikas currently inhabit throughout their range (VertNet pika records 1970–present, $n = 1852$). We therefore suspect our model, uncritically applied, may underestimate extirpation at sites with high talus area.

That the American pika's distribution is tied to mean summer temperature does not bode well for the future of the species, especially because there is a near-consensus among climate models (16 of 17 GCMs) that summer temperature will warm by more than mean annual temperatures in the western USA (IPCC 5; Taylor *et al.*, 2012). This trend is also apparent in the historical instrumental record for California (California Climate Tracker, 1895–2012; Abatzoglou *et al.*, 2009). For sites in this study, summer temperature is projected to rise by 0.9 °C more on average than annual temperature (RCP 8.5, 2070). This may indicate that in the western USA, pikas and other species that are primarily active during the summer (e.g. most high-elevation species) will have higher seasonal exposure to climate change. Our results should therefore be a call for greater monitoring of high-elevation species throughout the western USA.

Our projection of particularly drastic, imminent, extirpation in northern California and east of the southern Sierra is concordant with two previous SDM projections (Galbreath *et al.*, 2009; Calkins *et al.*, 2012) which used presence-only data. Because pikas are already restricted to the highest elevations throughout much of these regions, climate change is poised to push their lower elevational limit higher than the range of available habitat in many areas. In contrast, most GCMs predict that temperatures in the highest peaks of the southern Sierra (Rogelj *et al.*, 2012) will remain suitable for pikas through the end of the 21st century. Two other notable 'sky islands' in California, where pikas could become restricted to the highest elevations by the end of the century, are Mount Shasta and the White Mountains.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Field methods and site locations.
Appendix S2 Predictor variables, candidate models, and model results.
Appendix S3 Animation of projected future fate of pika at 67 sites in California, USA.

BIOSKETCH

Joseph Stewart is a graduate student researcher at the University of California Santa Cruz and a Scientific Aide at the California Department of Fish and Wildlife. His research focuses on biodiversity conservation and climate change, with recent focus on the American pika, high-elevation communities, and the blunt-nosed leopard lizard (*Gambelia sila*). He grew up spending time each summer backpacking in California's Sierra Nevada Mountains with his father. He recently completed a M.S. degree at the University of Nevada Reno.

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