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Factors influencing distributional shifts and abundance at the range core of a climate-sensitive mammal

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Abstract

Species are frequently responding to contemporary climate change by shifting to higher elevations and poleward to track suitable climate space. However, depending on local conditions and species' sensitivity, the nature of these shifts can be highly variable and difficult to predict. Here, we examine how the American pika (*Ochotona princeps*), a philopatric, montane lagomorph, responds to climatic gradients at three spatial scales. Using mixed-effects modeling in an information-theoretic approach, we evaluated a priori model suites regarding predictors of site occupancy, relative abundance, and elevational-range retraction across 760 talus patches, nested within 64 watersheds across the Northern Rocky Mountains of North America, during 2017–2020. The top environmental predictors differed across these response metrics. Warmer temperatures in summer and winter were associated with lower occupancy, lower relative abundances, and greater elevational retraction across watersheds. Occupancy was also strongly influenced by habitat patch size, but only when combined with climate metrics such as actual evapotranspiration. Using a second analytical approach, acute heat stress and summer precipitation best explained retraction residuals (i.e., the relative extent of retraction given the original elevational range of occupancy). Despite the study domain occurring near the species' geographic-range center, where populations might have higher abundances and be at lower risk of climate-related stress, 33.9% of patches showed evidence of recent extirpations. Pika-extirpated sites averaged 1.44°C warmer in summer than did occupied sites. Additionally, the minimum elevation of pika occupancy has retracted upslope in 69% of watersheds (mean: 281 m). Our results emphasize the nuance associated with evaluating species' range dynamics in response to climate gradients, variability, and temperature exceedances, especially in regions where species occupy gradients of conditions that may constitute multiple range edges. Furthermore, this study highlights the importance of evaluating diverse drivers across response metrics to improve the predictive accuracy of widely used, correlative models.

KEYWORDS
abundance, American pika, climate change, escalator-to-extinction, occupancy, *Ochotona princeps*, range retraction

1 | INTRODUCTION

Globally, climate change has caused increases in seasonal and annual temperatures, decreases in snowpack, longer growing seasons, and increases in the intensity and frequency of temperature and precipitation-related extremes, among numerous other changes (IPCC, 2013; Mote et al., 2018). Species' climate change–driven responses can manifest in many forms, including shifts in phenology (e.g. Bartomeus et al., 2011), morphology (Hoy et al., 2018), physiology (Van de Ven et al., 2019), genetics (Rubidge et al., 2012), behavior (Beever et al., 2017), and distributions (Chen et al., 2011). Species generally have two strategies for adapting to climate change: persist in place or shift in space (Thurman et al., 2020). However, the directionality and degree to which species can shift in space is highly variable, differing considerably within and across species, space, time, and bioclimatic gradients (Freeman et al., 2018; Fritz et al., 2009; Moritz et al., 2008; Rapacciuolo et al., 2014; Tingley et al., 2012). Bioclimatic gradients represent multidimensional range limits; for example, montane species usually have lower, upper, latitudinal, and longitudinal range edges that may shift due to climate change. Montane species' capacities to spatially track optimal conditions can be constrained by a reduction in habitable area as species approach mountain peaks (a mountain-island effect), frequently leaving them vulnerable to climate change and constrained to persisting in place (Freeman et al., 2018). The Rocky Mountains of North America, for example, have a mean elevation of 1,844 m, yet land area decreases nearly exponentially at elevations above 2,080 m (Elsen & Tingley, 2015).

Examining changes in abundance and occupancy along bioclimatic gradients can inform forecasts of the rate and direction of range shifts, for example, by identifying whether distributions are "leaning" upslope (i.e., when species' upper and lower elevational limits remain constant through time, but most individuals within the span occur at increasingly higher elevations; Breshears et al., 2008; Lenoir & Svenning, 2015) or where changes will be of greater versus lesser magnitude. Although occupancy and abundance reflect similar aspects of species–environment relationships, they can be reflective of different processes. Site occupancy is believed to more strongly represent overall habitat suitability, whereas abundance reflects habitat quality (Mortelliti et al., 2010; Thomas et al., 2010, but see Van Horne, 1983). Moreover, abundance generally represents shorter-term conditions (i.e., seasonal and between-year changes) affecting the growth rates of populations, whereas site occupancy may more closely reflect prevailing conditions that act across broader temporal scales such as longer-term environmental changes that influence dispersal and associated recolonization (e.g. Schulz et al., 2019). Rapid and stochastic changes can also immediately influence population abundance without noticeable or immediate impacts to occupancy (Johnston et al., 2019; Rattenbury et al., 2018). This dichotomy underscores the importance of identifying climatic influences on both species' abundances and occupancy, as they may differentially influence range shifts. Comparing results of such paired analyses is one of the more robust means of assessing species–climate interactions through space and time, yet it is rare in the literature (Dibner et al., 2017; Schulz et al., 2019).

Species are responding not only to both short- and long-term changes in climatic conditions but also to extreme events operating within seasons. Anthropogenic climate change has markedly increased the variability and frequency of such events that often have abrupt and idiosyncratic impacts on species (Harris et al., 2018). Biological responses to climatic extremes are challenging to quantify in modeling, but their ecological relevance remains critical and is broadly under-investigated for vertebrates. The effects of extreme events (e.g., heatwaves, severe droughts, high rainfall) can stress individuals beyond their physiological tolerances (Riddell et al., 2019), leaving "fingerprints" on population vital rates, and ultimately species' distributions (e.g. Greenville et al., 2012; Hale et al., 2016; Prugh et al., 2018). For example, Campbell et al. (2012) demonstrated that climatic variability can have significant effects on survival rates and recruitment and can affect different life stages in opposing ways within a species depending on the timing, severity, and duration of the event(s). Thus, understanding the effects of changes in climatic means, variability, and extremes is important for accurately predicting distributional shifts and long-term viability (Forcada et al., 2005; Johnson et al., 2005). Given the various climate-related processes and underlying mechanisms that influence range dynamics, identifying the most influential factors correlated with distributional shifts at biologically relevant spatial and temporal scales remains a priority in ecology because universal patterns and responses rarely exist across taxa.

Here, we test how populations of the American pika (*Ochotona princeps*), a montane lagomorph, are responding to contemporary global change near their geographic range centroid by identifying the factors most strongly affecting patterns of site occupancy, abundance, and elevational-range retraction (hereafter "retraction"). Although true elevational-range centers are difficult to identify for many species, we systematically surveyed the full elevational extent of habitat across this region to test whether gradients associated with interior range edges (sensu Ray et al., 2016; Mehlman, 1997) show evidence of strong species–climate relationships. We test the importance of diel maxima and minima, seasonal means, thresholds (i.e., exceedances), and inter-annual variability, as well as local habitat characteristics. We used a priori model suites with an information-theoretic approach. Our models reflect a variety of environmental stressors, addressing both summer and winter conditions. These seasonal effects pertain to specific, hypothesized mechanisms tied to life-history characteristics (e.g., chronic heat stress in summer causing direct mortality), as opposed to using annual measures that may obscure identification of these intra-annual dynamics.

We sought to (1) evaluate whether changes in site occupancy have occurred region-wide; (2) compare the dominant factors governing occupancy and abundance, to compare whether the same factors influence both responses; (3) evaluate the climatic variables influencing the amount of retraction within watersheds; and (4) summarize which combinations of climatic and/or non-climatic factors best predict the patterns of pika occupancy, abundance, and retraction. Our approach to quantifying retraction is novel with respect to both the extent of our survey efforts (64 replicated watersheds across multiple mountain ranges) and the analytical approach used to characterize retraction. We examined retraction not only as absolute change in minimum elevation but also as the residual of the regression of retraction against historical minimum elevation of occupancy (i.e., relative extent of retraction, given the historical low-elevation boundary). Overall, we predicted that range retraction and declines in occupancy would be modest in the range core relative to peripheral edges within this species' geographic range because range-core environments typically have lower severity and frequency of extreme climatic events than do edges (Rehm et al., 2015). However, we predicted that lower elevations (representing local trailing edges) of our watersheds may have experienced greater local extinctions than other portions of the watersheds.

2 | MATERIALS AND METHODS

2.1 | Model species

American pikas (*O. princeps*) are small (125–200 g), ellipsoid-shaped lagomorphs that are considered habitat specialists, occupying broken-rock habitats that passively aid in thermal buffering (Millar et al., 2015; Varner et al., 2015). This montane species' range spans from northern New Mexico and southern California, USA, north to central Alberta and British Columbia in Canada (Figure 1). Importantly, the extent and spatial arrangement of this habitat changes very little through ecological time, thus eliminating habitat alteration as a confounding factor of change over time. This species is ideal for examining questions related to metapopulation and patch dynamics (e.g. Moilanen, 1999) because of its high detectability in field surveys (~92–95.9%, Beever et al., 2011; Ray et al., 2016; Rodhouse et al., 2010), philopatry to individual territories (Smith & Weston, 1990) and because its evidence (fecal pellets, urine stains, and old haypiles, table 3 of Beever et al., 2016) persist in talus interstices for years to centuries (Millar et al., 2014; Stewart et al., 2017). American pikas are also cold-adapted but, because they do not hibernate, can be exposed to changes in climatic averages and extremes in winter (e.g. Beever et al., 2011). For example, patterns of pika occupancy across four mountain ranges spanning a precipitation gradient across the northern United States were positively associated with colder winter temperatures (Thompson, 2017), and Hanley (2019) found pika occupancy to be positively associated with winter precipitation. Furthermore, Johnston et al. (2019) found drastic declines in pika abundances the year following a snow drought, which led to a functionally colder winter (i.e., less snowpack reduced thermal buffering from

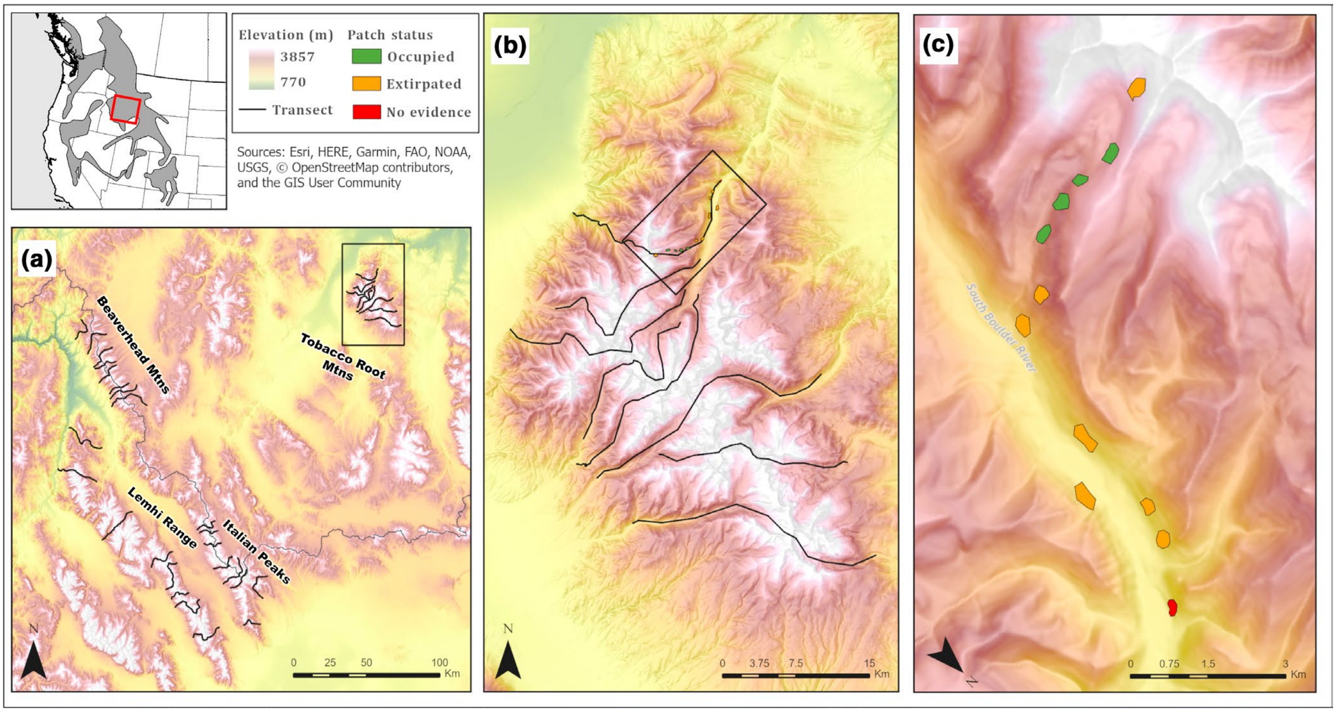

FIGURE 1 Map of the study region within the Northern Rocky Mountains of North America, illustrating the hierarchically nested design of the study. The small inset in the upper left corner is the geographic range map (from IUCN, 2011) of the American pika in western North America. (a) The four mountain ranges that we surveyed, which generally spanned a gradient of relatively warm and dry in the southwest to colder and wetter in the northeast. Each line represents a latitudinal transect pair connecting two watersheds, one on the east and one on the west of ridgelines. (b) Finer-scale depiction of transects within a single mountain range. (c) Example of a single watershed (half-transect) that was surveyed in the Tobacco Root Mountains, MT, with each patch outlined as a polygon and filled with the occupancy status.

fluctuating above-snow temperatures). This relationship between warmer winter conditions and cold stress may seem paradoxical; however, recent investigations of other species that occupy similar habitats as pikas, yellow-bellied marmots (*Marmota flaviventris*) and hoary marmots (*Marmota caligata*), have documented declines in population size and over-winter survival in response to lower snowpack since both species require sufficient snow for thermal insulation while hibernating (Cordes et al., 2020; Johnston et al., 2021). Such investigations exemplify how cold-adapted species like pikas are excellent indicator species for both quantifying the direct and indirect effects of climate change and illustrating sensitivity to short-term weather conditions (but see Smith & Millar, 2018, who used site occupancy as a proxy for over-winter survival at $n = 37$ patches).

2.2 | Study area

Surveys of pika occupancy and abundance were conducted in four mountain ranges, spanning 2.3 million hectares at the center of the species' geographic range, in the Northern Rocky Mountains (USA) of western North America (Figure 1) from 2017 to 2020. The annual mean monthly minimum and maximum temperatures in the region have increased ~1.7°C and 0.3°C, respectively, since 1895 (Halofsky, 2018). From 1951 to 2010, the number of annual growing degree-days increased from 194 to 206, whereas frost days declined from 171 to 159 (Whitlock et al., 2017). However, there have been no significant changes in annual precipitation during this period (Whitlock et al., 2017).

2.3 | Study design

Across this region and globally, warm, dry conditions prevalent at lower elevations are generally expected to shift toward higher elevations in the future. Conversely, cooler, wetter conditions occurring at the higher elevations illustrate what conditions were like at the lower elevations in the recent past. Using these gradients of climatic conditions, we delineated elevational transects within watersheds to quantify range retractions to assess where populations are presently and where they used to be (based on evidence of historical occupancy). Although methods for quantifying occupancy and abundance have long been fine-tuned in ecology, methods for detecting and measuring upslope range shifts or retractions are less standardized (Sexton et al., 2009). Although short-term or fine-scale, single-transect studies are robust and informative for many questions, they likely under- or overestimate broader-scale patterns (e.g. Brusca et al., 2013; Freeman et al., 2018; Moritz et al., 2008; Whittaker & Tribe, 1996). For example, the amount of retraction for a given species may be biased by the length and elevational span of a transect and by the geographic spread of sampling points. Therefore, we implemented high replication of transects ($n = 64$) and varying elevational spans within transects.

2.4 | Field methods

We conducted limited surveys in 2017 to test and refine field methods. We then field-surveyed talus patches for unequivocal evidence of current and historical pika occupancy from June through September in 2018 and 2019. We considered a patch occupied when ≥1 pika was detected by auditory and/or visual observation or when we found fresh haypile(s) containing ≥10 pieces of fresh, green vegetation (i.e., pika food caches with chlorophyll present, following Jeffress et al., 2013; to distinguish them from haypiles constructed in past years that can persist for decades). Talus patches (12 per watershed) were separated by at least 40 m (although ≥100 m, in most all cases) of nontalus habitat, which is >1.65 times longer than the average diameter of a pika home range (Smith & Weston, 1990). Although dispersal can occur over 40 m, adult pikas are individually territorial and rarely disperse (Peacock, 1997) and are unlikely to use two patches separated by 40+ m of non-talus habitat. These patches were composed of rocks 0.2–1 m in diameter.

Watersheds ($n = 64$ total, 16 per mountain range) were latitudinally paired and separated along ridgelines by ≥1 km, with one on the west side of the ridgeline and one on the east (Figure 1). All watersheds and patches were chosen using remotely sensed Landsat and Copernicus satellite imagery on Caltopo.com prior to fieldwork. Paired watersheds were always surveyed in random order within ranges, and both watersheds in each pair were surveyed on or near the same date to minimize confounding environmental factors. Eight watersheds surveyed in 2018 were partially resurveyed in 2020 to examine possible inter-annual changes in range-limit elevations (see Results). Field surveys indicated that eight patches were unsuitable for pika occupancy (i.e., lacking interstices) and were not included in analyses.

To maximize pika detections, we adapted patch-survey methods from previous research on this species (e.g. Beever et al., 2011). Briefly, these methods involve walking 50-m-long transects along elevational contours, spaced 15 m in elevation apart, typically covering the entire talus patch to determine occupancy status and relative abundance. To further increase the detectability of pikas, we initially walked narrow contours (<5 m elevational spacing) until we detected old evidence (which is typically easier to detect) and then current pika occupancy. We use the term "relative abundance" because we neither censused the entirety of all pika-occupied patches (some of which may have had >100 individuals) nor empirically assessed detectability, as detectability has been repeatedly reported to be >0.90 when surveys occur during optimal times of the day and season (e.g. Ray et al., 2016).

Surveys occurred shortly after sunrise and before sunset each day, avoiding the warmest hours (12:00–16:00) unless there was full cloud coverage (Beever et al., 2011). Although we used numerous techniques to reduce the likelihood of false negatives (i.e., considering a patch unoccupied when it is actually occupied), such as extending the search period and revisiting the patch on the return to the start of the transect, it is possible that a small fraction of the sites we deemed “apparently extirpated” were in fact pika-occupied. Another study in this region surveyed 41 patches using independent double observers and found that occupancy status was identical between observers for all 41 patches, further providing high confidence in determining patch-occupancy status (Thompson, 2017).

We estimated talus-patch size as the number of 20-m-diameter circles of pika-suitable talus, following Beever et al. (2011). Vegetation cover (e.g., moss, lichen, grass, or forb cover) was measured *in situ* via ocular estimation of each type of cover within a 12-m radius (aided with a laser rangefinder [accuracy ±0.1 m] to locate points 12.0 m from the pika evidence "center" in each cardinal direction), to index forage available to each individual pika, as they are a central-place-foraging species (Beever et al., 2008). Additionally, we determined current grazing status near each patch by determining whether cattle defecations were present within 50 m of the patch perimeter.

2.5 | Climate data

For each patch, we characterized the climate with metrics of temperature, precipitation, and vapor pressure deficit (VPD) using PRISM (Parameter-elevation Relationships on Independent Slopes Model; version AN81d gridded data at approximately 800-m resolution) daily values (Daly et al., 2008). We also obtained gridded, water-balance data from the National Park Service at 1-km resolution for actual evapotranspiration (AET), moisture deficit, and soil water storage, as described in Lutz et al. (2010) for July 1 – August 31 because this is the driest period of the year. Lastly, we obtained gridded snow-water-equivalent data from the National Weather Service's SNOw Data Assimilation System (SNODAS) at 1-km spatial resolution.

We used predictors from these datasets to create an a priori model set to represent mechanisms we hypothesized would be important to pikas in this region. For each predictor in the abundance analysis, we include 1-year- and 2-year-lagged conditions to test the near-term, temporal scale at which populations are most strongly responding (consistent with the lifespan of this species). For each predictor in the occupancy and retraction analyses, we included 10-year means and 10-year variances to test whether the species is responding more strongly to prevailing mean conditions or to climatic variability. The 10-year metrics were calculated as the means and standard deviations of annual means (or totals) across the 10 years prior to the survey year. All analyses on climate and water-balance data were done in Python v3.7 and R v3.4.1 using packages *dplyr* (Wickham et al., 2020), *gtools* (Warnes et al., 2020), *lubridate* (Grolemund & Wickham, 2011), *ncdf4* (Pierce, 2019), *purrr* (Henry & Wickham, 2020), *raster* (Hijmans, 2020), *rgdal* (Bivand et al., 2020), *rwrfhydro* (McCreight et al., 2015), and *tidyverse* (Wickham et al., 2018). All variables and their derivations (e.g., acute heat stress), including the hypothesized mechanisms that may influence distributional-range responses, are detailed in Table S1.

2.6 | Occupancy and relative abundance

To evaluate the influence of climatic conditions and identify the best predictor(s) of patch occupancy, we used generalized linear mixed-effect models (R package *lme4*, Bates et al., 2015) with a binomial distribution and logit link that included combinations of the prevailing climate of the site and local habitat characteristics as predictor variables (Table S2). For relative abundance, defined as the number of individual pikas detected per 50 m surveyed *sensu* Beever et al. (2013), we again used linear mixed-effect models that included the prevailing climate of the site with 1- versus 2-year lags, as well as habitat characteristics as predictors (Table S3). For relative abundance, we only included the subset of patches that included one or more pikas (n = 479) to more clearly discriminate between the factors influencing abundance versus occupancy. In both analyses, we used mountain range as a random effect and the climate and habitat variables as fixed effects. We removed patches at which we detected no pika evidence (n = 24) because we assumed that they had not been suitable for pika occupancy for the past several decades to centuries.

We first tested whether the 10-year mean conditions or the 10-year variance conditions better predicted occupancy; an identical approach was used for comparing 1-year versus 2-year lags in the abundance analyses. We used only the better-performing temporal scale for all final analyses, which was determined by evaluating AIC scores of all model pairs (i.e., same model structure with either climatic means or variances, or 1-year- or 2-year-lagged conditions). For all four response variables, we selected the temporal (for occupancy [10-year mean vs. 10-year variance] and abundance [1- vs. 2-year-lagged predictors] analyses) or spatial (for retraction analyses: watershed-wide vs. lowest-elevation patch) metric whose models ranked higher in most pairs. For both occupancy and abundance model suites, we evaluated additive models, as well as models with interactions. Variables were not combined within models if they were highly correlated (r > 0.75; e.g. Johnston et al., 2019). Additionally, we included all corresponding univariate models. All variables were scaled using z-score standardization, with a mean of 0 and standard error of 1. We evaluated model fit and parsimony using Akaike's information criterion (Burnham & Anderson, 2002) and also evaluated fit using both marginal and conditional coefficients of determination (R^2).

2.7 | Range retraction

We evaluated range retraction in two ways. First, we analyzed the raw magnitude of retraction (Table S4), which is the difference in elevation between the lowest patch containing evidence of historical occupancy and the lowest elevation of a currently occupied patch (≥1 individual). We also evaluated a second measure to optimize comparisons of retraction across watersheds and mountain ranges. We created this measure to reflect our assumption that watersheds where talus habitats extend lower would likely experience greater amounts of retraction than watersheds having talus at higher minimum elevations. Residual retraction was calculated as the watershed-specific residual from a linear model of the elevational distance retracted regressed against historical minimum elevation of evidence (Table S5). More positive residuals indicate greater retraction than expected for a given historical minimum elevation and, conversely, negative residuals indicate less retraction than expected.

We tested the influence of climatic conditions on range retraction using a 27-model subset from the occupancy model suite. From our initial a priori model set, we removed models where predictors were too highly correlated ($r > 0.75$) in our watershed-retraction data set ($n = 64$ watersheds). Each of these models was tested at four scales over the prior 10-year time span: (1) lowest-elevation patch's 10-year-mean conditions, (2) lowest-elevation patch's interannual variability, (3) watershed-wide mean conditions, and (4) watershed-wide interannual variability. Lowest-elevation-patch conditions were calculated as the 10 years' prior (to sampling) conditions of the lowest patch in the watershed (i.e., a proxy of climatic harshness at the trailing-edge patch that was currently or historically occupied, excluding no-evidence patches). For the watershed-wide conditions, we calculated the predictor variables as the average conditions across all 12 patches within the watershed.

In total, 108 models were assessed in two steps. To narrow down this model suite, we evaluated AIC model results to determine whether the lowest-elevation-patch conditions or the watershed-mean conditions performed better in explaining retraction. This comparison narrowed the model suite from 108 to 54 models of the best-performing spatial scale. Next, we tested the importance of mean climatic conditions versus variability in climatic conditions using the same pairwise AIC comparison. This reduced the final model suite to 28 models, including the null. This final model suite was used for the analysis of both raw retraction and the retraction residuals.

2.8 | Variable, climate-class, and seasonal importance

Following methods from Kittle et al. (2008), we determined the relative importance of predictor variables for each of the response variables (occupancy, abundance, and retraction) by dividing the total variable weights by the number of models containing each variable, $w_{i\text{-}avg}$ (Table 2; Table S6). This method has been applied elsewhere (e.g., Beever et al., 2010; Johnston et al., 2019; Stewart et al., 2015) and allows for the comparison of variable importance when variables are unequally represented across models. We also grouped variables into what we termed "climate classes," $w_{cc\text{-}avg}$, by the categories of temperature, precipitation, ecologically available water, and "other" (i.e., nonclimatic variables). We summed the climate class variable weights and divided the cumulative weight of each category by the number of models that contained any relevant variables within the climate class. Lastly, to assess seasonal importance, we used model suites that contained all summer or all winter variables within models (i.e., no mixed-season models). We then summed the weights of each season separately and divided this sum by the number of models within each season.

Widespread evidence suggests contemporary distributional shifts are predominantly driven by various aspects of climate change (Freeman et al., 2018; Tingley et al., 2012) or land-use change (Peters et al., 2019). Therefore, although we acknowledge biological and habitat complexities in contributing to range shifts, we assumed climate ultimately (albeit not unilaterally) underlies range shifts in our analysis of this species whose habitat extent and distribution have not changed appreciably over ecological time in our study domain. Because of the remoteness of these watersheds, lack of human development, and lack of change in other ecological disturbances (other than grazing, which we empirically accounted for), this assumption appears reasonable. Therefore, models for the two retraction responses did not contain "other" nonclimatic variables (e.g., patch size, slope, aspect, etc.) that are fixed through time. The removal of "other" variables was done prior to conducting retraction AIC (and weight) comparisons.

3 | RESULTS

We surveyed 3,360 50-meter patch transects across 760 talus patches and across 64 watersheds, spanning the Continental Divide region of the Northern Rocky Mountains. We documented 1,423 individual pikas during June–September of 2018 and 2019. Domain-wide, 479 patches (63.0%) were currently pika-occupied, 257 patches (33.8%) were extirpated, and 24 patches (3.2%) had no evidence of past pika occupancy. Current occupancy varied minimally among mountain ranges, ranging between 61.4 and 64.9%. Similar to other pika studies (e.g. Moyer-Horner et al., 2016), we found a small positive effect of sampling date on abundance (Estimate: 0.002, 95% CI: 0.001 to 0.004). Abundance was also positively, albeit weakly, associated with elevation (linear $R^2 = 0.064$, quadratic $R^2 = 0.068$, Figures S1 and S2).

Across the ecoregion, the mean elevation of all pika-occupied patches surveyed was 2,500 ± 10.2 m (mean ± 1 SE), formerly occupied patches averaged 2243 ± 18.0 m, and patches with no pika evidence averaged 1822 ± 69.3 m. Overall, 44 of the 64 watersheds experienced retraction at their lower limits (Table SI2). The mean minimum elevation of pika occupancy across all watersheds shifted from 2100 m (±31.4) to 2297 m (±25.3). In the 44 watersheds where retraction occurred, retraction at the lower edges averaged 281 ± 27.0 m upward (Figure 2), whereas retraction across all 64 watersheds averaged 197 ± 24.8 m. Pika populations in all eight watersheds on the western side of the Beaverhead Mountains experienced upslope retractions between 281–557 m at their lower elevational limit.

We conducted resurveys of the elevational-range-limit patches in the summer of 2020 in two watersheds that exhibited retraction within each mountain range ($n = 8$ watersheds). To do so, we surveyed the highest two patches that were extirpated and the lowest

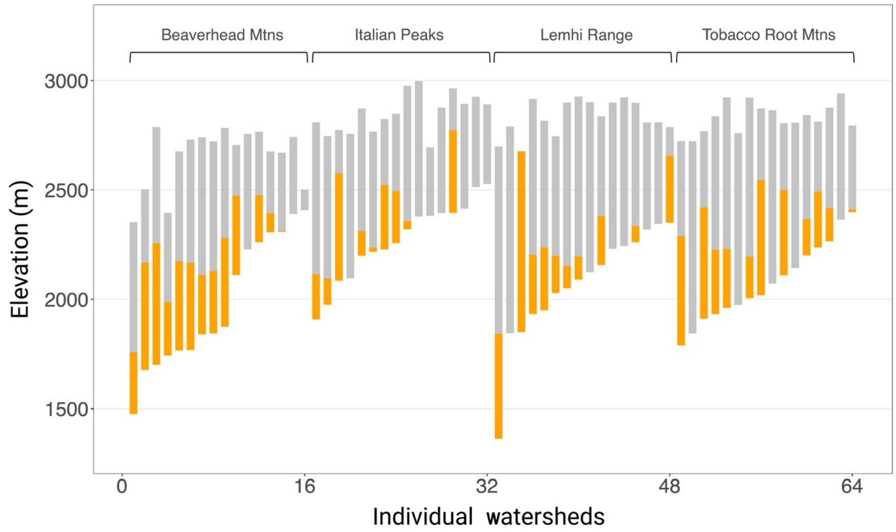

FIGURE 2 The magnitude of elevational retractions, by watershed and mountain range, of the range of American pikas (*O. princeps*) across the Northern Rocky Mountains. Upslope retractions were documented at the lower-elevational limits based on current occupancy versus historical evidence in patches. Gray bars indicate the elevational bands where pikas currently occur within each watershed, whereas orange bars indicate the elevational bands of historical occupancy based on detection of only old fecal pellets or old haypiles. This figure does not include unoccupied patches observed at the upper elevational limits within 10 watersheds; in these, downslope contraction averaged 23.2 ± 77.7 m. One watershed was devoid of pikas, except one individual at the highest-elevation patch. Retraction averaged 252 m across all Beaverhead watersheds, 119 m in the Italian Peaks, 178 m in the Lemhis, 239 m in the Tobacco Roots, and 197 m, domain-wide. Excluding watersheds in which pika distribution did not retract, retraction averaged 310 m in the Beaverhead watersheds, 211 m in the Italian Peaks, 285 m in the Lemhis, 319 m in the Tobacco Roots, and 281 m, domain-wide

two pika-occupied (in 2018) patches in each watershed (n = 32 patches total). We found that range limits were stable over the 2-year span, and no upslope or downslope shifts had occurred in any drainage. Overall, pikas have retracted upslope at the lower-elevation margins with few opportunities for upslope expansion because pikas already occupy the highest-elevation patches across most of this domain.

3.1 | Occupancy

On average, pika-extirpated sites had 11 more days ≥26°C (exceeding the species' thermal maximum) than did occupied sites and were 1.44°C warmer (T_{mean}) throughout the summer. Out of 66 paired regression models, models containing 10-year-mean conditions outperformed the 10-year-variance models in 64 instances (97%). Therefore, all subsequent occupancy analyses used 10-year-mean conditions (Table 1; Table S2). Standardized odds-ratio effect sizes for univariate climate predictors for occupancy are shown in Figure 3. The top-ranked model for site occupancy incorporated additive effects of acute heat stress (number of days ≥26°C during summer), AET, and patch size (Table 1; Figure S3). In this model, acute heat stress was negatively associated with occupancy (−1.112, 95% CI: −1.347 to −0.891), whereas AET (0.1595, 95% CI: 0.050 to 0.369) and patch size (0.811, 95% CI: 0.5427 to 1.110) were positively associated with occupancy. Six of the seven top-ranked models (plausible: ΔAIC < 2; Burnham & Anderson, 2002) included the terms for acute heat stress and patch size, whereas three models included AET (Table 1). Notably, patch size in its univariate model performed poorly (ΔAIC = 138.77 from the top model), and the variable only rose in the AIC rankings when it accompanied climate metrics, predominantly summer-based temperature predictors (Appendix A: Table S2; Figure S4). Based on variable weight per model, acute heat stress outperformed all other climatic predictors, followed by AET, and then patch size (Table 2; Table S6; Figure S5).

3.2 | Relative abundance

Relative abundance increased, on average, by 0.57 individuals (95% CI: 0.38–0.77) for every 1000 m increase in elevation. Across 54 model pairs, models with 1-year-lagged predictors outperformed the 2-year-lagged models in 51 instances (94%). Therefore, the abundance analyses only included models with 1-year-lagged conditions (Table S3). Standardized effects sizes for univariate climate predictors are shown in Figure 3. The top-ranked model for relative abundance included chronic cold stress in winter (i.e., mean winter temperature; Est. −0.119, CI: −0.175 to −0.064) and acute heat stress in summer (Est. −0.102, CI: −0.174 to −0.024) additively, both negatively associated with abundance (w_i = 0.37; Table 1). This model indicated that warmer mean winter temperatures and the number of days at or above 26°C in summer had negative effects on relative abundance of populations. However, this model showed a

TABLE 1 Top-ranked models with substantial support (ΔAIC < 2; Burnham & Anderson, 2002) for analyses of pika abundance, occupancy, magnitude of upslope retraction, and the residuals of retraction

Top-performing models by response	K	AIC	ΔAIC	Model likelihood	AIC w_i	Cumulative weight	Log likelihood	Residual log likelihood	R^2_c	R^2_m
(A) Occupancy										
Acute heat stress + home ranges + actual evapotranspiration (AET)	5	774.23	0	1	0.160	0.160	−382.117	–	–	–
Acute heat stress + home ranges	4	774.46	0.23	0.143	0.143	0.303	−383.230	–	–	–
Acute heat stress + home ranges + acute cold stress	5	774.63	0.39	0.132	0.132	0.435	−382.314	–	–	–
Heat runs + home ranges × AET	6	775.19	0.96	0.099	0.099	0.534	−381.595	–	–	–
Acute heat stress + home ranges × AET	6	775.36	1.13	0.091	0.091	0.625	−381.682	–	–	–
Acute heat stress × home ranges	5	775.58	1.34	0.082	0.082	0.707	−382.788	–	–	–
Acute heat stress + home ranges + soil moisture	5	775.64	1.40	0.079	0.079	0.787	−382.818	–	–	–
Acute heat stress + home ranges + grazing status	5	776.05	1.82	0.065	0.064	0.851	−383.027	–	–	–
Null	2	955.44	181.20	<0.001	0	1	−475.718	–		
(B) Abundance										
Chronic cold stress + acute heat stress	5	681.54	0	1	0.378	0.378	–	−335.769	0.106	0.096
Acute cold stress + acute heat stress	5	682.59	1.05	0.591	0.224	0.602	–	−336.294	0.119	0.099
Null	3	714.46	32.92	<0.001	0	1	–	−354.229	0	0
(C) Retraction (bottom patch, mean conditions)										
Chronic heat stress + chronic cold stress	5	805.44	0	1	0.751	0.751	–	−397.722	0.433	0.433
Null	3	855.19	48.43	<0.001	0	1	–	−424.601	0	0
(D) Retraction residuals										
Acute heat stress × summer precipitation	6	806.21	0	1	0.310	0.310	–	−397.107	0.018	0.018
Heat run × summer precipitation	6	806.62	0.41	0.815	0.252	0.562	–	−397.312	0.011	0.011
Chronic heat stress × summer precipitation	6	806.88	0.67	0.715	0.222	0.784	–	−397.442	0.010	0.010
Null	3	825.30	19.08	<0.001	0	1	–	−409.648	0	0

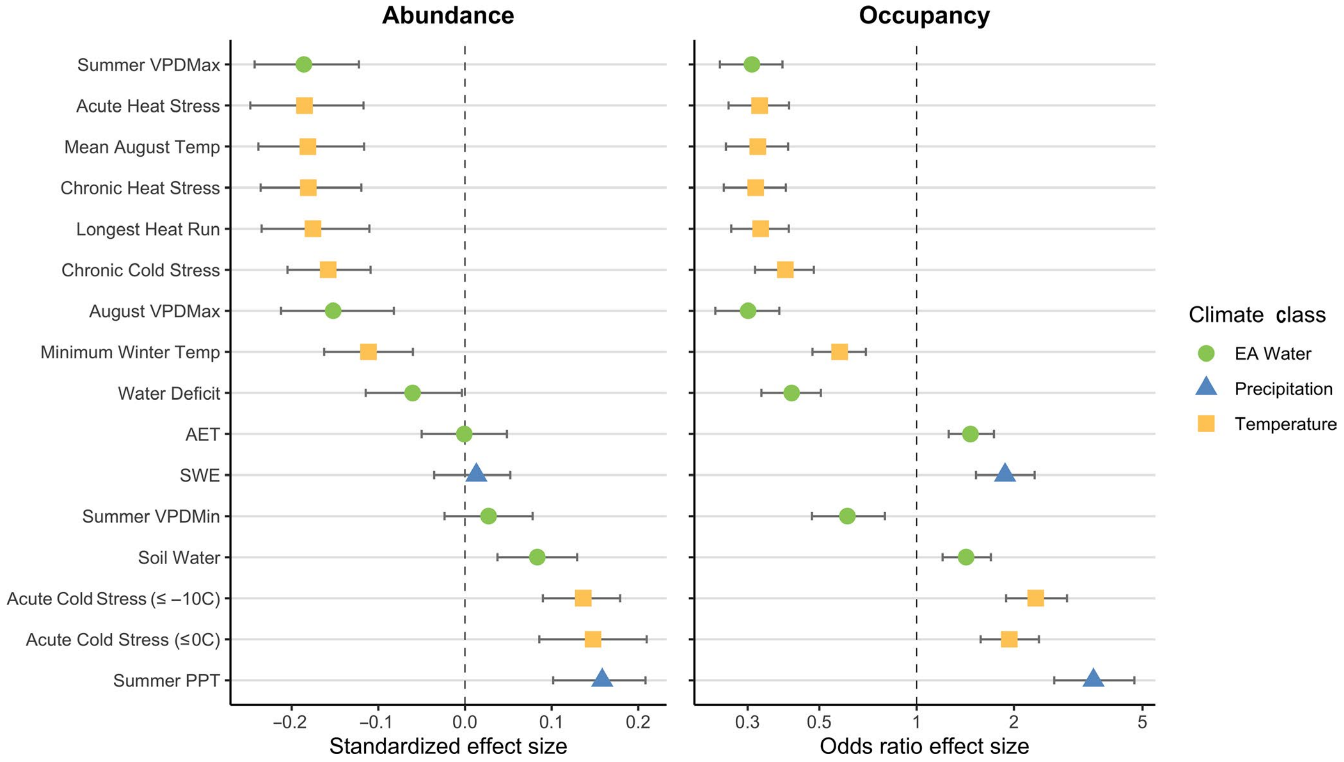

FIGURE 3 Standardized effect sizes for all univariate climate-predictor models for the abundance and occupancy analyses. Gray bars represent 95% confidence intervals. Directionality of variable effects (i.e., right or left of vertical axis, in each plot) remained the same between the two analyses for all climatic variables except actual evapotranspiration, snow-water-equivalent, and summer vapor pressure deficit (VPD_{min})

relatively weak fit to the data (conditional $R^2 = 0.106$). The second-best model was equally plausible (ΔAIC < 2) and included additive terms for acute cold stress (number of days ≤ −10°C) and acute heat stress (Table 1). Overall, chronic cold stress outcompeted all other variables, garnering 15.2% of the average variable weight per model (Table 2; Table S6).

3.3 | Range retraction

The models containing conditions at the lowest-elevation patch outperformed the watershed-mean models in 45 of the 54 model pairs (83%); therefore, analyses included only lowest-elevation-patch conditions, which were used as a proxy for the severity (or unsuitability) of climate exposure within a watershed. Next, models using 10-year climatic means outperformed models using 10-year-variance terms in 22 of the remaining 27 model pairs (81%), and thus, our final model suite consisted of 28 models, including the null, that used 10-year-mean climatic conditions at the lowest patch in each watershed (Table S4).

Warmer summer and winter mean temperatures (hypothesized to correspond to chronic heat and cold stress) were additively associated with retraction distances. Particularly, retraction magnitude was greater in watersheds where the lowest-elevation patches were warmer in summer and winter; warmer winters may correspond with decreased snowpack that otherwise would buffer pikas from cold temperatures in winter (see Johnston et al., 2019), whereas warmer summer temperatures at low elevations may now be too high for population persistence. This top model had strong support ($w_i = 0.75$), and the second-ranked model was not equally plausible (ΔAIC = 2.74). The fixed terms in the top model explained 43.3% of the variation, whereas the random effect of mountain range explained no additional variation. Upon averaging variable weights across models, chronic cold stress emerged as the best predictor in the model suite ($w_{i\text{-}avg} = 0.373$), followed by chronic heat stress ($w_{i\text{-}avg} = 0.158$; Table 2).

The minimum elevation of historical occupancy by watershed explained 38.1% of the variation in retraction residuals (Figure 4; Figure S6). Watersheds with low minimum elevations of historical evidence shifted further upslope than did watersheds that had higher minimum elevations of historical occupancy. Using the same 28-model suite as the retraction analysis above (mean conditions of the lowest-elevation patch), the best predictor of the residuals was an interaction between acute heat stress and summer precipitation (Table 1). The two next-best-ranked models were equally plausible and had terms for summer temperature and interactions with precipitation. However, all models had low predictive power, likely suggesting the importance of unmeasured factors, such as patch connectivity and configuration on the landscape. Overall, differences in minimum elevations of past pika occupancy across watersheds more strongly predicted retraction residuals than did the climatic factors.

TABLE 2 Ranks of the average variable weight per model for the five most-predictive variables for abundance, occupancy, upslope retraction, and retraction residuals. A full table for all predictor variables can be found in the Supplementary Material (Appendix: Table 6)

Variable	Cumulative weight	Num. of models	Variable weight per model, $w_{i\text{-}avg}$	Coefficient signs
Occupancy				
Acute heat stress	0.752	11	0.068	−
Actual evapotranspiration	0.355	6	0.059	+
Home ranges	1.000	21	0.048	+
Heat runs	0.201	6	0.033	−
Acute cold stress (−10°C)	0.132	7	0.019	+
Abundance				
Chronic cold stress	0.457	3	0.152	−
Acute heat stress	0.226	4	0.057	−
Summer vapor pressure deficit (VPD_{Min})	0.142	3	0.047	+
Summer VPD_{Max}	0.027	1	0.027	−
Chronic heat stress	0.246	19	0.013	−
Retraction				
Chronic cold stress	0.747	2	0.373	+
Chronic heat stress	0.950	6	0.158	+
Summer precipitation	0.203	7	0.029	6+, 1−
Soil water	0.042	3	0.014	1+, 2
Snow-water-equivalent	0.006	3	0.002	−
Retraction residuals				
Summer precipitation	0.818	7	0.117	+
Heat runs	0.264	3	0.088	−
Acute heat stress	0.324	4	0.081	−
Chronic heat stress	0.351	6	0.058	5+, 1−
Chronic cold stress	0.101	2	0.051	+

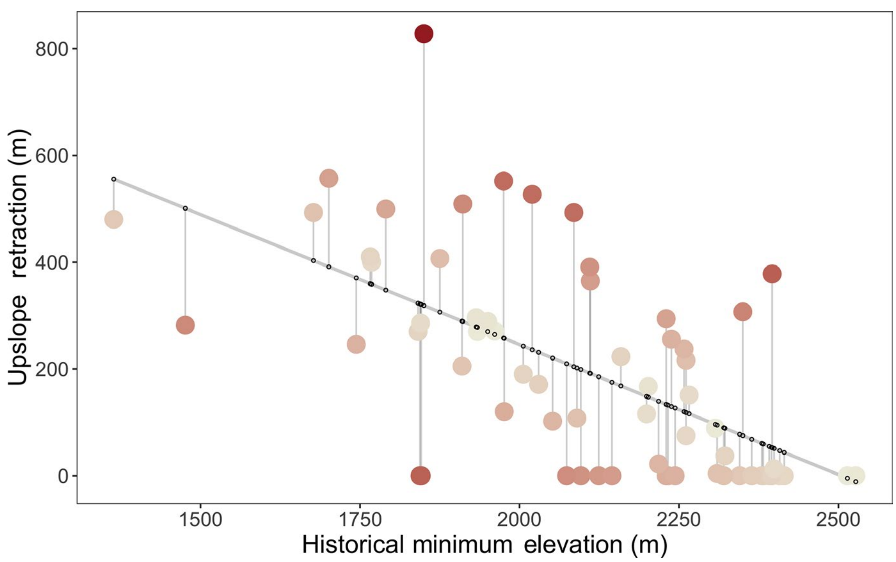

FIGURE 4 Plotted residuals of elevational-range retraction by watershed ($R^2 = 0.381$). We used the residuals of the amount of elevational retraction (in meters) from the minimum elevation of historical occupancy regressed against the historical minimum elevation of occurrence as a novel characterization of relative retraction that has occurred within a transect (in our case, watershed) across this region. The residuals explain differences between expected and observed magnitudes of range retraction (i.e., the relative magnitude of range retraction), given the historical minimum elevation of occurrence. Saturation color of each point increases as residuals become further from the predicted regression line. The residual extending farthest above the line is the watershed from which pikas were devoid except one individual at the top patch

3.4 | Importance of climate classes and seasonal predictors

The strength of performance and rank of climate variable classes varied markedly among the response variables (Figure 5). For the occupancy models, ecologically available water, temperature, and nonclimatic variables ("other") were near-equally strong in their overall average variable weight per model, $w_{cc\text{-}avg}$. For abundance, temperature metrics were the best supported and averaged 2.26% of the variable weight per model. Temperature was also the best supported class in the retraction model suite, averaging 5.26% of the climate-class weight per model. Lastly, precipitation metrics were dominant in explaining the retraction residuals, garnering 8.43% of the variable weight per model (Table S7).

In analyses using the reduced model suites where mixed-season models were removed to compare the explanatory capability of seasonal variables, occupancy was driven entirely by summer conditions (summer $w_{s\text{-}avg}$ = 0.062% per model, winter $w_{s\text{-}avg}$ = 0.000% per model; Table 3). For abundance, winter variables outperformed summer variables and had 3.24 times more support when averaged across all models (winter $w_{s\text{-}avg}$ = 0.084/model, summer $w_{s\text{-}avg}$ = 0.026/model). For retraction, summer variables again outperformed winter variables and had 7.25 times more support when averaged across all models (summer $w_{s\text{-}avg}$ = 0.053/model, winter $w_{s\text{-}avg}$ = 0.007/model). Lastly, for the retraction residuals, summer variables outperformed winter variables, with 28.34 times more support when averaged across all models (summer $w_{s\text{-}avg}$ = 0.055/model, winter $w_{s\text{-}avg}$ = 0.002/model).

4 | DISCUSSION

Comparisons of the mechanisms by which climate change is driving species' responses, which often diverge across space, time, and populations, are generally lacking (Cahill et al., 2013; Ockendon et al., 2014). There is growing recognition that understanding the species-specific mechanisms of change affecting demography and other life-history traits provides greater strength of inference than

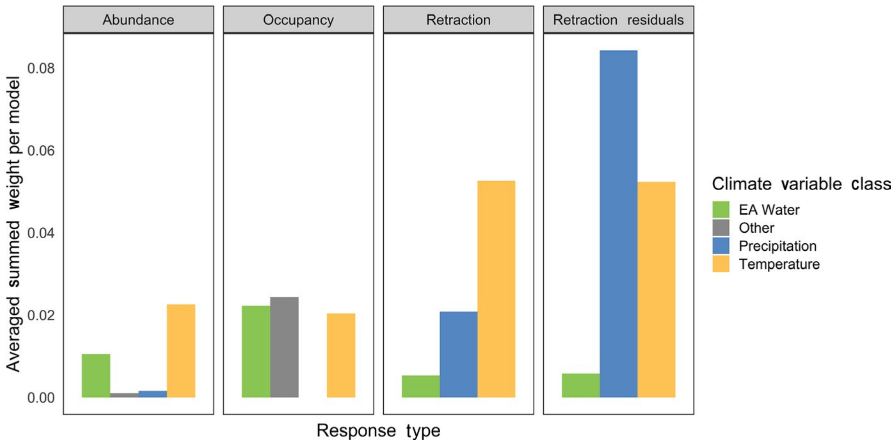

FIGURE 5 Average variable weight per model, averaged across all corresponding predictors in each of four climate classes ($w_{cc\text{-}avg}$), for each of four responses: abundance, occupancy, retraction, and retraction residuals. The importance of the climate classes varies greatly among response types, suggesting that results from one response type should not be extrapolated to other response types. EA water = measurements of ecologically available water (i.e., actual evapotranspiration, water deficit, soil moisture, and vapor pressure deficit). Temperature-related variables are defined in Table S1. Other = nonclimatic metrics (for Abundance: grazing status near the patch, insolation, lichen cover, moss cover, slope, grass cover, and forb cover; for Occupancy: the same metrics as well as patch size)

TABLE 3 Collective mean weight per model of seasonally based predictors for abundance, occupancy, upslope retraction, and retraction residuals. The summer season is defined as June 1–August 31, whereas winter spans November 1–March 31

Response variable	Season	Cumulative weight	Collective mean weight per model, $w_{s\text{-}avg}$
Abundance	Summer	0.4137	0.0259
	Winter	0.5863	0.0838
Occupancy	Summer	1.0000	0.0625
	Winter	0.0000	0.0000
Retraction	Summer	0.9631	0.0535
	Winter	0.0369	0.0074
Retraction residuals	Summer	0.9902	0.0550
	Winter	0.0097	0.0019

using strictly correlative analyses, as these models can more effectively be applied elsewhere in a species' range, extrapolated into no-analog environments, and help inform climate-adaptation planning (Beever et al., 2011). These benefits are particularly useful for species in data-poor and remote regions, such as mountainous areas.

In temperate regions, mountains support cold-adapted species that are highly specialized for surviving severe conditions in snow-dominated landscapes (Theodoridis et al., 2018). However, montane species are increasingly living near their physiological limits due to thermal specialization over evolutionary time, and in turn, may lack the adaptive capacity to persist *in situ* under further warming or more frequent climatic extremes (Hoffmann & Sgro, 2011). In some cases, gradual declines in patch-level abundance may forecast imminent extinctions, particularly near climatic niche margins (Newman & Pilson, 1997; Spooner et al., 2018, but see Abrams, 2002), whereas more-abrupt declines might suggest greater extinction debts. To better quantify the rate and magnitude of declines, estimates of both abundance and occupancy are needed, as are the factors governing each.

Numerous life-history characteristics and previous investigations suggest that American pikas are particularly sensitive to climatic variability and change. Consequently, the species has gained attention for its responses to different aspects of climate across its geographic range, in terms of occupancy and relative abundance (e.g. Beever et al., 2013; Jeffress et al., 2013; Johnston et al., 2019; Schwalm et al., 2016; Smith et al., 2019). Here, we provide strong evidence of widespread, climate-mediated range retraction at the geographic-range core of pikas in the Northern Rocky Mountains ecoregion. We found lower pika occupancy in these mountain ranges (averaging 63.0%) compared with the estimates from elsewhere in this region, such as Moyer-Horner et al., 2016 (Glacier National Park, MT: 79.7% of patches occupied), Schwalm et al., 2016 ([Figures 3 and 4] Yellowstone and Grand Teton National Parks, MT and WY: ≥98%), and Thompson, 2017 (three Montana and Idaho wilderness areas: 76.7%). The most likely explanation for this divergence in results is that we systematically surveyed the entire elevational span of talus patches within watersheds, whereas these other studies used probabilistic (spatially balanced) or trail-based site selection.

Although our study was the first to evaluate the effects of decadal-scale climatic variability on range dynamics for this species, we found substantially stronger support for the predictive ability of mean climatic conditions. This may be explained by the relatively short time span over which our variability coefficient was quantified, but this result is nevertheless surprising given that climatic variability has been documented to act more strongly on population dynamics than means for both short- and long-lived species (e.g. Campbell et al., 2012; Drake, 2005). We hypothesize that because our study region is essentially the geographic-range center of this species, prevailing climatic conditions may be relatively stable (albeit still trending warmer) compared with those of the range periphery. One mediating factor could be the buffering effect of the region's generally more stable and deeper snowpack, as snowpack can buffer pikas and other subnivean species from extreme fluctuations in winter conditions. However, this region has recently experienced significant reductions in snowpack due to climate warming (Mote et al., 2018). At midlatitudes in the western United States, Europe, and the Tibetan Plateau, climate change is predicted to continue causing significant decreases in snow-cover duration throughout the 21st century, and consequently, increases in the number of days where the ground is frozen without snow leaving subnivean species like pikas exposed to functionally colder winters (Zhu et al., 2019). Overall, the importance of climatic variability versus means, and the potential buffering effect of refugial conditions, such as pockets of stable snowpack, remain a research frontier that deserves further attention for understanding the drivers of species' range shifts (Ackerly et al., 2020).

In addition to our evaluation of climatic variability, we assessed the importance of temperature exceedances in affecting pika range dynamics. We found strong support for the role of acute heat stress (number of days ≥26°C) in both the occupancy and abundance analyses. Acute heat stress was calculated based on the observed thermal maximum of this species. American pikas have been shown to die quickly under high temperatures (2–6 h above 25.5–29.4°C) when experimentally prevented from behaviorally thermoregulating by retreating into the talus interstices (MacArthur & Wang, 1973; Smith, 1974). Although acute heat stress has been tested in previous studies (Beever et al., 2010; Jeffress et al., 2013; Wilkening et al., 2011), this is the first documentation of it being one of the most important determinants of pika range dynamics. This suggests that short-term, physiologically stressful conditions can lead to reductions in occupancy and explain patterns of abundance to some degree. Fitness consequences of temperature exceedances are well documented across taxa, for example, in mediating photosynthetic processes in tree species (Varhammar et al., 2015), or in influencing the growth and development rates of amphibians (Thurman & Garcia, 2017). Adjustments to temperature extremes can also affect species' foraging behavior, physiology and immune function, growth, and fecundity (Falcon et al., 2018; Kammerer & Heppell, 2013; Lafferty, 2009; Paniw et al., 2019). Increases in diel maximum temperatures have been shown to restrict pikas' foraging times outside the talus and can alter forage preferences (Hall & Chalfoun, 2018), which may in turn decrease the size of haypiles that are needed for winter sustenance. Thus, it is not surprising that frequency of temperature exceedances beyond pikas' physiological limits would be linked to their decline. Collectively, these results also highlight the need for further investigation into the behavioral flexibility in thermoregulation for species like *O. princeps*, across bioclimatic gradients. Such flexibility will be crucial for persistence in increasingly unfavorable environments.

The importance of acute heat stress further supports our findings that, in general, summer conditions better explained our response metrics than did winter conditions. For all responses but abundance, summer metrics collectively outperformed winter ones. This suggests that pikas, which are considered cold-adapted based on their high metabolic rates and thick, low-emissivity fur, may be more physiologically stressed during summer months than in winter months, amidst ongoing changes in conditions across our study domain. However, winter conditions, specifically chronic cold stress, performed best in the abundance analysis. Still, low R^2 values for abundance and retraction-residual analyses may reflect the following: (1) the influence of important (but unmeasured) non-climatic factors, (2) that coarse-grained climate data poorly represent organism-relevant conditions at finer scales, and (3) unidentified nonlinearities in biological responses to climate (Butikofer et al., 2020). Nevertheless, our results suggest that warmer winter and summer temperatures, whether occurring as press or pulse events, are both having detrimental effects on pika occupancy and abundances. These results illustrate the complexities in modeling the intricate relationships between species and their environments that can change seasonally and inter-annually. We encourage the use of multiple response types when assessing species vulnerability to future climate change to help uncover these complexities as we have done here.

One nonclimatic predictor appeared in all eight of the best-supported occupancy models: talus-patch size (i.e., the number of pika-suitable home ranges). This factor overwhelmingly accounted for "other" variables, which collectively outperformed climate metrics in models for occupancy, although metrics of ecologically available water and temperature had comparable weights (Figure 5). Island biogeography theory (IBT) suggests that populations are more likely to colonize and persist in larger patches than smaller ones (Macarthur & Wilson, 1967). Consistent with IBT, we found patch size was positively correlated with occupancy, and thus, our findings appear to support this notion similar to other studies on patchily distributed species, such as freshwater stream fishes (Dunham et al., 2002). However, we acknowledge that using a different threshold to define unique patches (i.e., >40 m) may change the modeled importance of patch size. Recall, however, that patch size only rose in AIC ranking after accounting for climatic variables. Mid-sized and larger patches were still unoccupied when located in hotter and drier areas (Figure S3); conversely, small patches were nearly always occupied when climatic conditions were cooler and wetter. This finding illustrates how IBT may oversimplify landscape-level patterns and trends when climatic variables are not incorporated into models.

Another important, yet often overlooked, phenomenon in ecology is time-lag effects. We examined the relative performance of 1-year- versus 2-year-lagged conditions in predicting relative abundance and found that 1-year-lagged conditions were far more predictive. This is expected for species like pikas that have small body masses and short generational times (<2.5 years) relative to many other mountain-dwelling mammals. Furthermore, pikas have a relatively low annual fecundity (one to two litters per summer under optimal conditions but low survival, Millar, 1973), which allows for greater synchrony and comparatively shorter lag times between demographic responses and environmental conditions (Smith & Weston, 1990). Lag effects can be strongly dictated by vegetation structure and composition, hydrology, fat storage, and other biotic and abiotic factors, for pikas (e.g. Millar, 1973) and numerous other species (Davies et al., 2013; Wu et al., 2015).

Metrics of ecologically available water (i.e., water balance) did not significantly affect abundance but individually performed well in occupancy analyses. AET and soil moisture both appeared in the top-ranked occupancy models. Both variables are expected to indirectly influence forage conditions by mediating the availability of aboveground biomass and vegetation quality (Stephenson, 1998). Forage quality and composition have been documented as important for pika persistence and abundance elsewhere, including across the Southern and Central Rocky Mountains (Erb et al., 2014; Yandow et al., 2015), hydrographic Great Basin (Wilkening et al., 2019), as well as in the Pacific Northwest (Varner & Dearing, 2014). Despite the predictive abilities of these two variables, our field measurements of vegetation cover and type performed surprisingly poorly, possibly due to high, near-patch forage availability in this ecoregion.

Observed patterns in abundance and changes in occupancy were mirrored in results of range retraction. Here, we corroborate other studies that indicate temperate montane species are responding strongly to changes in temperature and precipitation by shifting their distributions upslope (Battisti et al., 2005; Tingley et al., 2009, 2012; Wilson et al., 2005). As mean seasonal temperatures continue to increase, montane species are expected to continue expanding and shifting distributions upward, usually reducing their spatial domain and, consequently, carrying capacities. Mountaintop extirpations have been widely documented, as species often experience what is known as the "escalator-to-extinction" effect (Freeman et al., 2018). Simultaneously, mountaintop species may have limited capacity for dispersal, as they often occupy patchily distributed and isolated habitats and cannot disperse between mountain islands that are isolated by warmer lowlands (Rehnus et al., 2018). With *O. princeps*, however, this biogeographic truism must also be juxtaposed with the findings that dispersal distances are generally further in cooler and wetter areas but shorter in hotter and drier areas (Castillo et al., 2014, 2016; Schwalm et al., 2016).

Season-long measures of both heat and cold stress were positively associated with retraction (Table 2), suggesting that chronically warmer winter and summer temperatures induced greater magnitudes of retraction and act synergistically to shape range edges of pikas across this region. We also sought to improve methods for evaluating and comparing range retraction rates within and across species. Although resurvey efforts are one of the most robust methods for assessing range shifts (e.g. Freeman et al., 2018; Iknayan & Beissinger, 2018; Moritz et al., 2008), they frequently are not replicated across comparable units such as watersheds or mountain ranges, for numerous reasons (but see the following examples from California, USA: Rowe et al., 2015; Tingley et al., 2012). To address this concern of limited replication (and thus limited extrapolative ability), we examined a novel response metric that accounted for differences in minimum historical elevation to provide a relative evaluation of retraction (Figure 4). This approach allowed us to identify the factors that caused some watersheds to retract more or less than expected, given the minimum elevation of historical occupancy. As predicted, watersheds that extended lower in elevation retracted further than higher watersheds. We were not able to determine the exact dates at which each extirpated patch was last occupied, but evidence such as the existence of old haypiles and finding pellets on rock surfaces (rather than buried in interstitial soil) suggests that a greater proportion of these patches were last occupied by pikas from years to decades ago, and a much-smaller proportion of patches might have been last occupied over a century ago (table 3 of Beever et al., 2016). Our resurveys from 2020 found that lower-range edges were stable across a 2-year period, suggesting our results appear robust to interannual variability. Consequently, this transect-replication method could be more widely implemented for other species to better understand range edges and elevational shifts through time. Furthermore, our results suggest that annual (re) surveys may not be necessary to effectively track retractions for this species and others with similar life histories.

5 | CONCLUSIONS

Many species are likely to continue shifting their distributions to track cooler and wetter climates in the face of contemporary climate change. However, a more mechanistic understanding of how, why, and to what extent climate change affects range limits is still strongly needed (Sexton et al., 2009). Understanding how environmental stressors vary across multiple range margins is fundamental for a more holistic understanding of climatic influences on species' range dynamics. Here, we provide widespread evidence of recent range retractions of American pikas at their range core in North America, primarily driven by higher temperatures in both summer and winter. These results corroborate recent work indicating local environmental conditions (e.g., climate edges) may override the importance of geographic range position in determining local extinction risk (Boakes et al., 2018; Oldfather et al., 2020). Nevertheless, geographic range edges and climate edges may be coupled in some parts of species ranges but not others, creating complexity for predicting species' distributional responses to climate change.

The extent of retraction to date, and the correlations of all four responses with higher temperatures, suggest that retractions at warmer and lower elevations are likely to continue. Thus, populations in a region previously assumed to constitute a climatic refugium may not be as resilient to climate change as previously expected. Montane settings are experiencing some of the most rapid changes globally (Pepin & Lundquist, 2008). Therefore, future analyses across replicated units (e.g., watersheds, mountain ranges, ecoregions) will be fundamental for identifying strategies to support the long-term adaptive capacity of species and informing the selection of effective climate adaptation actions, globally.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Supplementary Information – Billman *et al.*

Description of environmental variables, full model suites, and supplementary figures.

Table S1. Full list of the hypothesized mechanism represented by each variable in models. Citations reference previous studies that used similar predictors or suggested that the factor influences this species' distributions.

Variable	Unit	Hypothesized Mechanism	Definition
Chronic Heat Stress	°C	Long-term, cumulative physiological heat stress from all times of the day, across the warmest period in summer. Pikas have low ability to dissipate heat, due to low-emissivity fur; also, upper lethal temperature is only ~3 C° above average resting body temperature	Mean daily temperatures for June 01 –August 01 (Beever et al. 2011, 2016, Stewart et al. 2015)
Acute Heat Stress	Days	As shown experimentally, temperatures at and above this threshold caused hyperthermia in caged pikas in <6 hrs (MacArthur and Wang 1974, Smith 1974). In the absence of cages, may also prevent above-talus foraging (*sensu* Mathewson et al. 2017).	Total number of days with temperature ≥26°C (Beever et al. 2011, 2016, Stewart et al. 2015)
Heat Runs	Days	Accumulation of sublethal, physiological stress from diel maximum temperatures, with no long-duration respite or recharge.	Largest number of consecutive days where temperatures reached ≥ 20°C (Thompson 2017)
Chronic Cold Stress	°C	Long-term, most-cumulative physiological stress from temperatures at all hours during the coldest season. If below the thermoneutral zone (e.g., cold snaps without sufficient snow cover), can cause increased energy demand and loss of brown fat (*sensu* Wunder 1992).	Mean daily temperature for November 01 – February 28 (Beever et al. 2011, Johnston et al. 2019)
Acute Cold Stress	Days	Exceeding the lower-temperature limit of the thermoneutral zone (e.g., cold snaps without sufficient snow cover); can cause increased energy demand and loss of brown fat (*sensu* Wunder 1992).Temperatures <0°C indicate conditions conducive to maintaining an insulative snowpack layer.	Number of days with temperature ≤-10°C or ≤0°C for September–August (Beever et al. 2011, Johnston et al. 2019) (Both <-10°C and ≤0°C were tested separately)
Winter T_{min}	°C	Long-term, cumulative physiological stress from coldest diel conditions. Alternatively, given that pikas have many apparent adaptations to live in cold climates, may indicate duration of insulative snow cover, which may leave individuals susceptible to cold snaps.	Mean of daily minimum temperature from Nov 01 - March 31 (Johnston et al. 2019, Beever et al. 2011)

Variable	Unit	Hypothesized Mechanism	Definition
Summer Precipitation	mm	Indicative of biomass and nutritional value of available herbaceous forage for consumption. At drier sites, may relieve dehydration stress via altered evaporative demand and formation of micro-scale water sources (e.g., in depressions in uppermost rock surfaces) accessible to pikas	Sum of daily precipitation for June 01 –September 30 (Beever et al. 2013)
SWE	mm	Insulative snowpacks provide buffering from fluctuating and extreme-cold temperatures in winter. Additionally, greater snowpack may finish melting later in summer and thus, provide water to pikas and plants later into the high-water-demand period of summer	Snow water equivalent mean from November 01-March 31 (Beever 2013)
Actual Evapotranspiration (AET)	mm	Across the bioclimatic-niche space of our research domain, higher AET is correlated with greater biomass of forage available for consumption.	Total daily actual evapotranspiration during late summer (i.e. from July 01 – August 31) (Stewart et al. 2015)
Moisture Deficit	mm	Quantitative index of (direct, physiological) dehydration stress. Secondarily, it also may indirectly affect animals via forage quality.	Total daily moisture deficit during late summer (July 01 – August 31) (Stewart et al. 2015)
Soil Water	mm	Correlated with amount of biomass available for consumption, and, secondarily, affects wildfire risk (*sensu* Hostetler et al. 2018), which can constitute short- to long-term disturbance for pikas, depending on ecological context.	Mean daily soil water storage during late summer (July 01 – August 31)
Vapor Pressure Deficit Max	kPa	Quantitative index of (direct, physiological) peak dehydration stress. Secondarily, it also may indirectly affect pikas via forage quality.	Mean daily maximum VPD for June 01 –September 30 (Beever et al. 2016, Millar et al. 2018, Johnston et al. 2019)
Vapor Pressure Deficit Min	kPa	Quantitative index of how physiologically 'unstressful' (with respect to dehydration stress) that VPD becomes. Likely indexes either chronically dehydrating conditions, or the ability to 'recharge'.	Mean daily minimum VPD for June 01 – September 30 (Beever et al. 2016, Millar et al. 2018, Johnston et al. 2019)
Insolation	W/m^2	If insolation is too high, it may constitute sublethal, physiological stress. Aspect and slope jointly influence insolation, which alters local conditions and vegetation. Greater insolation typically correlates with drier conditions.	Mean amount of solar radiation hitting the patch over a year (Millar et al. 2016)

Variable	Unit	Hypothesized Mechanism	Definition
Patch Size	m^2	Larger patches are likely to facilitate pika persistence than smaller patches, per Island Biogeography Theory. May act through demographic stochasticity, Allee effects, bet-hedging against a predator, or any ecological disturbance that does not affect the entire patch area (e.g., wildfires may affect patch interior less severely for large patches than for those with high edge:area ratio).	Number of total home ranges (20-m-diameter circles) within the patch (Beever et al. 2008). Synonymous with "home ranges" and "HRs" in model suites below.
Grasses	%	Higher grass cover indicates drier climates (Ray et al. 2016), and is a lower-quality forage item for cecal digestors like pikas (may be a function of lower digestibility, or C:N ratios [wherein high N is good]). Additionally, pikas require high energetic demand due to their high basal metabolic rate, and their complete lack of seasonal migration, hibernation, and torpor period.	Average % of graminoid species within 12-m radius of pika evidence, summed over all pika evidences in patch (Thompson 2017, Wilkening et al. 2011)
Forbs	%	Higher forb cover indicates cooler, more-moist climates (and is a higher-quality forage item for cecal digestors like pikas (may be a function of higher digestibility, C:N ratios [high N is good])	Average % of forb species within 15-m radius of pika evidence, summed over all pika evidences in patch (Thompson 2017, Wilkening et al. 2011)
Grass:Forb ratio		Relative nutritional value of available forage, and secondarily indicates site (meso-scale) climate.	Ratio of graminoid cover to forb cover (Thompson 2017, Ray et al. 2016, Moyer-Horner et al. 2016)
Slope	%	Affects heat load experienced by pikas, and slopes >60% have increased frequency of avalanches and rockfall, which constitute grave risks for pikas	Slope, estimated using a clinometer and averaged across all evidences within a patch (Thompson 2017)
Moss	%	Greater moss cover indicates higher local moisture levels, which eases water-balance stress for pikas. Also, can constitute up to 60% of an individual's nutritional intake (Varner & Dearing 2014)	Mean moss cover, by surface area, on talus over the entire patch. We used ocular estimation *in situ*. Moyer-Horner et al. (2016) found it important for current abundance.
Lichen	%	A nearby food source that requires no exposure by pikas to cold or predators to allow lichen consumption, during snow-covered seasons (*O. princeps* has been observed consuming them). Also, may indicate rock stability through time (more lichen = more stable = less risk of getting crushed)	Mean lichen cover, by surface area, on talus over the entire patch. We used ocular estimation from an aerial perspective, *in situ*.
Grazing Status	Y/N	Because pikas forage intensively at and near the talus edge, extensive removal of herbaceous biomass may constitute dietary competition with pikas, and may also create fear-based avoidance foraging patterns (interference competition; *sensu* Brown et al. 1999)	Prominent removal of biomass within 50 m of patch edge, or presence of cattle defecations within 50 m of patch edge (Beever et al. 2003, Millar 2010)

Table S2. Full model suite for the logistic-regression analysis for occupancy, only including 10-year-mean conditions, with mountain range as the random effect. Variable terms are found in the model names and are as follows: HRs = number of home ranges within the patch /habitat availability, AET = actual evapotranspiration, and SWE = snow water equivalent; remaining predictors are defined in Table S1. "+" indicates additive effects of >1 predictor, whereas "x" indicates interactions.

Model	**K**	**AIC**	**ΔAIC**	**Model Likelihood**	**AIC w_i**	**Log Likelihood**	**Cumulative w_i**
Acute Heat Stress + AET + HRs	5	774.23	0.00	1.00	0.16	-382.12	0.160
Acute Heat Stress + HRs	4	774.46	0.23	0.89	0.14	-383.23	0.303
Acute Heat Stress + Acute Cold Stress (<-10°C) + HRs	5	774.63	0.39	0.82	0.13	-382.31	0.435
Heat Runs + AET x HRs	6	775.19	0.96	0.62	0.10	-381.60	0.534
AET + Acute Heat Stress x HRs	6	775.36	1.13	0.57	0.09	-381.68	0.625
Acute Heat Stress x HRs	5	775.58	1.34	0.51	0.08	-382.79	0.707
Acute Heat Stress + Soil Moisture + HRs	5	775.64	1.40	0.50	0.08	-382.82	0.787
Acute Heat Stress + Grazed? + HRs	5	776.05	1.82	0.40	0.06	-383.03	0.851
Heat Runs + HRs	4	776.87	2.64	0.27	0.04	-384.43	0.894
Heat Runs x HRs	5	776.88	2.64	0.27	0.04	-383.44	0.937
Chronic Heat Stress + VPD_{min} + HRs	5	778.16	3.93	0.14	0.02	-384.08	0.960
Heat Runs + Grazed + HRs	5	778.87	4.63	0.10	0.02	-384.43	0.975
Chronic Heat Stress + Moisture Deficit + HRs	5	779.84	5.60	0.06	0.01	-384.92	0.985
Chronic Heat Stress x HRs	5	780.90	6.67	0.04	0.01	-385.45	0.991
Chronic Heat Stress + AET x HRs	6	781.72	7.48	0.02	0.00	-384.86	0.995
Chronic Heat Stress + Grazed? + HRs	5	782.49	8.26	0.02	0.00	-386.25	0.997
Chronic Heat Stress + Soil Moisture + HRs	5	783.25	9.02	0.01	0.00	-386.63	0.999
Summer Precipitation + Insolation + HRs	6	784.22	9.98	0.01	0.00	-386.11	1
Heat Runs	3	812.01	37.77	0.00	0.00	-403.00	1
Acute Cold Stress (<-10°C) + Chronic Heat Stress	4	812.8	38.56	0.00	0.00	-402.40	1
SWE + Acute Heat Stress	4	813.55	39.31	0.00	0.00	-402.77	1
Heat Runs + Acute Cold Stress (<-10°C)	4	813.65	39.42	0.00	0.00	-402.83	1
Chronic Heat Stress + VPD_{min}	4	814.36	40.13	0.00	0.00	-403.18	1
Acute Heat Stress + Acute Cold Stress (<-10°C)	4	815.74	41.50	0.00	0.00	-403.87	1
Chronic Heat Stress + Summer VPD_{min} + Grasses:Forbs	5	815.76	41.52	0.00	0.00	-402.88	1
Chronic Heat Stress + Moisture Deficit	4	816.72	42.49	0.00	0.00	-404.36	1
Acute Heat Stress + Summer Precipitation	4	816.80	42.56	0.00	0.00	-404.40	1
Chronic Heat Stress + SWE	4	817.25	43.02	0.00	0.00	-404.63	1
Chronic Heat Stress + Winter Tmin	4	817.34	43.11	0.00	0.00	-404.67	1
Acute Heat Stress	3	817.40	43.17	0.00	0.00	-405.70	1
Chronic Heat Stress	3	818.10	43.86	0.00	0.00	-406.05	1

Model	K	AIC	ΔAIC	Model Likelihood	AIC w_i	Log Likelihood	Cumulative w_i
Chronic Heat Stress + Summer Precipitation	4	818.54	44.30	0.00	0.00	-405.27	1
Chronic Heat Stress + Grazed?	4	818.71	44.48	0.00	0.00	-405.36	1
Chronic Heat Stress + SWE + Grasses:Forbs	5	818.81	44.57	0.00	0.00	-404.40	1
August VPD_{max}	3	818.91	44.68	0.00	0.00	-406.46	1
Chronic Heat Stress + Grasses:Forbs	4	819.41	45.18	0.00	0.00	-405.71	1
Acute Heat Stress + Grazed?	5	819.96	45.72	0.00	0.00	-404.98	1
Chronic Heat Stress + Insolation	4	820.10	45.86	0.00	0.00	-406.05	1
$SummerVPD_{max}$	3	820.25	46.02	0.00	0.00	-407.13	1
Chronic Heat Stress + Soil Moisture + Grazed?	5	820.67	46.43	0.00	0.00	-405.33	1
Summer Precipitation + Insolation + Grasses:Forbs	6	821.91	47.68	0.00	0.00	-404.95	1
Mean August Temperature	3	824.78	50.54	0.00	0.00	-409.39	1
Summer Precipitation + Grasses:Forbs + HRs	5	834.61	60.38	0.00	0.00	-412.31	1
Acute Cold Stress (-10°C) + Acute Cold Stress (>0°C) + HRs	5	841.92	67.69	0.00	0.00	-415.96	1
SWE + Summer Precipitation	4	852.85	78.62	0.00	0.00	-422.43	1
Chronic Cold Stress	3	855.15	80.91	0.00	0.00	-424.57	1
SWE + Moisture Deficit	4	864.24	90.01	0.00	0.00	-428.12	1
Summer Precipitation	3	871.49	97.25	0.00	0.00	-432.74	1
Summer Precipitation + Grasses:Forbs	4	872.54	98.30	0.00	0.00	-432.27	1
Summer Precipitation + Grazed?	4	873.01	98.78	0.00	0.00	-432.51	1
Summer Precipitation + Insolation + Grasses:Forbs	5	874.32	100.09	0.00	0.00	-432.16	1
Moisture Deficit	3	875.27	101.03	0.00	0.00	-434.63	1
Acute Cold Stress (<-10°C)	3	878.51	104.28	0.00	0.00	-436.26	1
Acute Cold Stress (<-10°C) + Soil Moisture	4	879.32	105.08	0.00	0.00	-435.66	1
Acute Cold Stress (<0°C) + Acute Cold Stress (<-10°C)	4	879.69	105.46	0.00	0.00	-435.85	1
SWE x Winter Tmin	5	893.50	119.26	0.00	0.00	-441.75	1
Winter VPD_{max}	3	897.25	123.02	0.00	0.00	-445.63	1
SWE + AET	4	901.00	126.77	0.00	0.00	-446.50	1
Home Ranges	3	913.01	138.77	0.00	0.00	-453.50	1
Acute Heat Stress (<0°C)	3	913.12	138.89	0.00	0.00	-453.56	1
SWE	3	913.41	139.17	0.00	0.00	-453.70	1
SWE + Grasses:Forbs	4	915.00	140.76	0.00	0.00	-453.50	1
Winter T_{Min}	3	918.8	144.56	0.00	0.00	-456.40	1
AET	3	933.59	159.36	0.00	0.00	-463.80	1
Summer VPD_{min}	3	938.15	163.92	0.00	0.00	-466.08	1
Soil Moisture	3	939.55	165.31	0.00	0.00	-466.77	1
Grazed?	3	939.57	165.33	0.00	0.00	-466.78	1

Model	**K**	**AIC**	**ΔAIC**	**Model Likelihood**	**AIC w_i**	**Log Likelihood**	**Cumulative w_i**
Lichen Coverage	3	943.84	169.61	0.00	0.00	-468.92	1
Patch Slope	3	947.29	173.05	0.00	0.00	-470.64	1
Forbs	3	947.60	173.36	0.00	0.00	-470.80	1
Grasses + Forbs	3	954.78	180.55	0.00	0.00	-474.39	1
Null	2	955.44	181.20	0.00	0.00	-475.72	1
Grasses:Forbs Ratio	3	955.53	181.30	0.00	0.00	-474.77	1
Moss Coverage	3	956.82	182.59	0.00	0.00	-475.41	1
Grass	3	957.20	182.96	0.00	0.00	-475.60	1
Winter VPD_{min}	3	957.32	183.09	0.00	0.00	-475.66	1

Table S3. Full model suite for the multiple-linear-regression analysis for abundance, only including the one-year lagged conditions, with mountain range included as a random effect. AET = actual evapotranspiration, and SWE = snow water equivalent; remaining predictors are defined in Table S1. "+" indicates additive effects of >1 predictor, whereas "x" indicates interactions.

Model	K	AIC	ΔAIC	Model Likelihood	AIC w_i	Residual Log Likelihood	Cumulative w_i
Chronic Cold Stress + Acute Heat Stress	5	681.54	0.00	1.00	0.38	-335.77	0.378
Acute Heat Stress + Acute Cold Stress (<-10C)	5	682.59	1.05	0.59	0.22	-336.29	0.602
Chronic Heat Stress + Summer VPDmin	5	683.76	2.23	0.33	0.12	-336.88	0.726
Chronic Cold Stress	5	686.07	4.54	0.10	0.04	-338.04	0.765
Chronic Cold Stress + Heat Runs	5	686.07	4.54	0.10	0.04	-338.04	0.805
Chronic Heat Stress	4	686.31	4.77	0.09	0.03	-339.15	0.839
Summer VPD_{max}	4	686.85	5.31	0.07	0.03	-339.42	0.866
Acute Cold Stress (<-10C)	4	687.42	5.88	0.05	0.02	-339.71	0.886
Chronic Heat Stress + Summer VPDmin + Grasses:Forbs	6	687.70	6.16	0.05	0.02	-337.85	0.903
Heat Runs + Acute Cold Stress (<-10C)	5	687.76	6.23	0.04	0.02	-338.88	0.920
Chronic Heat Stress + Summer Precipitation	5	687.94	6.41	0.04	0.02	-338.97	0.935
Heat Runs + Summer Precipitation	5	688.99	7.45	0.02	0.01	-339.49	0.945
Mean August Temperature	4	689.42	7.88	0.02	0.01	-340.71	0.952
Chronic Heat Stress + Grasses:Forbs	5	689.79	8.25	0.02	0.01	-339.89	0.958
Summer Precipitation	4	689.82	8.28	0.02	0.01	-340.91	0.970
Acute Cold Stress (<-10C) + Soil Moisture	5	690.51	8.98	0.01	0.00	-340.26	0.974
Chronic Heat Stress + Soil Moisture	5	690.97	9.43	0.01	0.00	-340.49	0.978
Chronic Heat Stress + (Grasses + Forbs)	5	691.41	9.87	0.01	0.00	-340.71	0.980
Acute Heat Stress	4	691.57	10.03	0.01	0.00	-341.78	0.983
Heat Runs	4	692.04	10.50	0.01	0.00	-342.02	0.985
Chronic Heat Stress + Grazed	5	692.16	10.62	0.00	0.00	-341.08	0.987
Chronic Heat Stress + Moisture Deficit	5	692.16	10.62	0.00	0.00	-341.08	0.989
Chronic Heat Stress x Grasses:Forbs	6	692.71	11.17	0.00	0.00	-340.35	0.990
Acute Cold Stress (-10C)+ Acute Cold Stress (<0C)	5	692.96	11.42	0.00	0.00	-341.48	0.991
Chronic Heat Stress + Winter Tmin	5	693.07	11.53	0.00	0.00	-341.53	0.993
Chronic Heat Stress + SWE	5	693.31	11.77	0.00	0.00	-341.65	0.994
Summer Precipitation + Grasses:Forbs	5	693.99	12.45	0.00	0.00	-341.99	0.994
Chronic Heat Stress + Insolation	5	694.06	12.53	0.00	0.00	-342.03	0.996
Chronic Heat Stress + Soil Moisture + Grasses:Forbs	6	694.17	12.63	0.00	0.00	-341.08	0.997
Heat Runs + Soil Moisture	5	694.30	12.77	0.00	0.00	-342.15	0.997
Acute Cold Stress (<-10C) + Moisture Deficit	5	694.60	13.06	0.00	0.00	-342.30	0.998
Summer Precipitation x Grasses:Forbs	6	694.77	13.23	0.00	0.00	-341.38	0.998
Summer Precipitation + Grazed?	5	695.61	14.07	0.00	0.00	-342.80	0.999

Model	K	AIC	ΔAIC	Model Likelihood	AIC w_i	Residual Log Likelihood	Cumulative w_i
Chronic Heat Stress + Moisture Deficit + Grasses:Forbs	6	695.74	14.20	0.00	0.00	-341.87	0.999
Chronic Heat Stress + SWE + Grasses:Forbs	6	696.61	15.07	0.00	0.00	-342.30	0.999
Summer Precipitation + (Grasses + Forbs)	5	696.75	15.21	0.00	0.00	-343.38	0.999
Acute Cold Stress (<-10C) + Acute Cold Stress (<0C) + Grasses:Forbs	6	696.89	15.36	0.00	0.00	-342.45	0.999
SWE + Summer Precipitation	5	697.14	15.60	0.00	0.00	-343.57	1
Chronic Heat Stress x (Grasses + Forbs)	6	697.47	15.93	0.00	0.00	-342.73	1
Chronic Heat Stress + Insolation + Grasses:Forbs	6	697.53	15.99	0.00	0.00	-342.76	1
Acute Heat Stress + SWE	5	699.02	17.48	0.00	0.00	-344.51	1
Acute Cold Stress (<0C)	4	700.16	18.62	0.00	0.00	-346.08	1
Summer Precipitation + Insolation + Grasses:Forbs	6	701.26	19.73	0.00	0.00	-344.63	1
August VPD_{max}	4	701.36	19.82	0.00	0.00	-346.68	1
Winter Tmin	4	704.05	22.51	0.00	0.00	-348.03	1
Summer Precipitation x (Grasses + Forbs)	6	704.84	23.30	0.00	0.00	-346.42	1
Forbs	4	705.12	23.58	0.00	0.00	-348.56	1
Summer Precipitation x Insolation + Grasses:Forbs	7	706.41	24.87	0.00	0.00	-346.21	1
Soil Moisture	4	709.60	28.06	0.00	0.00	-350.80	1
Null	3	714.46	32.92	0.00	0.00	-354.23	1
Soil Water + Moisture Deficit	5	715.71	34.17	0.00	0.00	-352.85	1
SWE x Winter Tmin	6	717.21	35.67	0.00	0.00	-352.61	1
Grasses:Forbs Ratio	4	717.98	36.45	0.00	0.00	-354.99	1
Grasses + Forbs	4	718.38	36.84	0.00	0.00	-355.19	1
Grazed?	4	718.84	37.31	0.00	0.00	-355.42	1
Moss Coverage	4	718.88	37.34	0.00	0.00	-355.44	1
Grasses	4	720.80	39.26	0.00	0.00	-356.40	1
Summer VPD_{min}	4	720.82	39.28	0.00	0.00	-356.41	1
Patch Slope	4	720.86	39.32	0.00	0.00	-356.43	1
AET	4	721.99	40.45	0.00	0.00	-356.99	1
SWE	4	722.02	40.49	0.00	0.00	-357.01	1
Insolation	4	722.15	40.61	0.00	0.00	-357.07	1
High Temp at Survey Time	4	723.99	42.45	0.00	0.00	-357.99	1
SWE + Deficit	5	724.85	43.31	0.00	0.00	-357.43	1
SWE + Grasses:Forbs	5	725.66	44.13	0.00	0.00	-357.83	1
SWE + AET	5	729.53	47.99	0.00	0.00	-359.77	1

Table S4. Full model suite for the multiple linear regression analysis for retraction, including only 10-year mean conditions of the bottom patch in each watershed, with mountain range as the random effect.

Model	K	AIC	ΔAIC	AIC w_i	Cumulative w_i	Model Likelihood	Residual Log Likelihood
Chronic Heat Stress + Chronic Cold Stress	5	805.44	0.00	0.75	0.751	1.00	-397.72
Chronic Heat Stress x Summer Precipitation	6	808.29	2.85	0.18	0.932	0.24	-398.15
Acute Cold Stress (<-10°C) + Soil Moisture	5	811.82	6.37	0.03	0.963	0.04	-400.91
Chronic Heat Stress + Summer Precipitation	5	814.28	8.83	0.01	0.972	0.01	-402.14
Chronic Cold Stress	4	814.56	9.12	0.01	0.980	0.01	-403.28
Chronic Heat Stress + Soil Moisture	5	815.13	9.69	0.01	0.986	0.01	-402.56
Chronic Heat Stress + SWE	5	815.29	9.85	0.01	0.992	0.01	-402.65
Heat Runs x Summer Precipitation	6	815.85	10.41	0.00	0.996	0.01	-401.92
Acute Heat Stress + Summer Precipitation	6	817.58	12.13	0.00	0.998	0.00	-402.79
Acute Cold Stress (<-10°C)	4	817.94	12.49	0.00	0.999	0.00	-404.97
Chronic Heat Stress	4	821.78	16.34	0.00	0.999	0.00	-406.89
Heat Runs + Summer Precipitation	5	822.03	16.58	0.00	0.999	0.00	-406.01
Mean August Temperature	4	822.63	17.18	0.00	1	0.00	-407.31
Acute Heat Stress + SWE	5	823.07	17.62	0.00	1	0.00	-406.53
Winter Tmin	4	823.36	17.92	0.00	1	0.00	-407.68
Acute Cold Stress (<0°C)	4	823.57	18.13	0.00	1	0.00	-407.78
Acute Heat Stress + Summer Precipitation	5	824.13	18.69	0.00	1	0.00	-407.06
Summer VPD_{min}	4	828.56	23.12	0.00	1	0.00	-410.28
Heat Runs	4	829.28	23.83	0.00	1	0.00	-410.64
Acute Heat Stress	4	831.34	25.90	0.00	1	0.00	-411.67
August VPD_{max}	4	832.64	27.20	0.00	1	0.00	-412.32
Summer VPD_{max}	4	832.99	27.54	0.00	1	0.00	-412.49
SWE	4	836.46	31.02	0.00	1	0.00	-414.23
Moisture Deficit	4	839.93	34.49	0.00	1	0.00	-415.97
Soil Moisture	4	841.24	35.80	0.00	1	0.00	-416.62
AET	4	841.87	36.43	0.00	1	0.00	-416.94
Summer Precipitation	4	842.10	36.66	0.00	1	0.00	-417.05
Null	3	853.71	48.27	0.00	1	0.00	-423.85

Table S5. Full model suite for residuals of upslope retraction and the historic minimum elevation occupied analysis, using only 10-year mean conditions of the bottom patch in each watershed, with mountain range as the random effect. There is a strong signal of AIC preferring complexity in the models.

Model Names	**K**	**AIC**	**ΔAIC**	**AIC w_i**	**Cumulative w_i**	**Model Likelihood**	**Residual Log Likelihood**
Acute Heat Stress x Summer Precipitation	6	947.31	0.00	0.35	0.351	1.00	-467.66
Heat Runs x Summer Precipitation	6	947.67	0.36	0.29	0.645	0.84	-467.83
Chronic Heat Stress x Summer Precipitation	6	947.81	0.50	0.27	0.918	0.78	-467.91
Chronic Heat Stress + Chronic Cold Stress	5	951.47	4.16	0.04	0.962	0.13	-470.73
Acute Cold Stress + Soil Moisture	5	954.13	6.81	0.01	0.973	0.03	-472.06
Acute Heat Stress + SWE	5	955.67	8.36	0.01	0.979	0.02	-472.83
Acute Heat Stress + Summer Precipitation	5	955.95	8.64	0.00	0.983	0.01	-472.98
Heat Runs + Summer Precipitation	5	956.09	8.78	0.00	0.988	0.01	-473.04
Chronic Heat Stress + Summer Precipitation	5	956.14	8.83	0.00	0.992	0.01	-473.07
Chronic Heat Stress + SWE	5	956.58	9.27	0.00	0.995	0.01	-473.29
Chronic Heat Stress + Soil Moisture	5	956.91	9.59	0.00	0.998	0.01	-473.45
Acute Cold Stress (<0°C)	4	961.29	13.98	0.00	0.999	0.00	-476.65
Winter Tmin	4	961.54	14.23	0.00	0.999	0.00	-476.77
Chronic Cold Stress	4	962.52	15.21	0.00	0.999	0.00	-477.26
Acute Cold Stress (<-10°C)	4	962.88	15.57	0.00	0.999	0.00	-477.44
Moisture Deficit	4	963.27	15.95	0.00	0.999	0.00	-477.63
AET	4	963.65	16.34	0.00	0.999	0.00	-477.83
Summer VPD_{max}	4	964.29	16.98	0.00	1	0.00	-478.14
August VPD_{max}	4	964.38	17.07	0.00	1	0.00	-478.19
Summer VPD_{min}	4	964.46	17.14	0.00	1	0.00	-478.23
Acute Heat Stress	4	964.55	17.24	0.00	1	0.00	-478.28
Summer Precipitation	4	964.73	17.42	0.00	1	0.00	-478.36
Heat Runs	4	964.97	17.65	0.00	1	0.00	-478.48
Soil Moisture	4	965.17	17.86	0.00	1	0.00	-478.59
Chronic Heat Stress	4	965.28	17.96	0.00	1	0.00	-478.64
SWE	4	965.29	17.98	0.00	1	0.00	-478.65
Mean August Temperature	4	966.10	18.79	0.00	1	0.00	-479.05
Null	3	973.45	26.14	0.00	1	0.00	-483.72

Table S6. Variable weight, number of models in which each variable appeared, and average variable weight per model for all variables for each the abundance, occupancy, upslope retraction, and retraction residuals, listed in decreasing order of weight per model. The variable weight $w_{i\text{-}avg}$ per model was calculated by summing the model weights for models containing a particular variable by the number of models containing the variable. Variables are each defined in Table S1.

Variable	Variable Weight	Num. of Models In	Average Variable Weight per Model, $w_{i\text{-}avg}$
Occupancy			
# of days Above 26°C	0.752	11	0.068
Actual Evapotranspiration	0.355	6	0.059
Patch Size	1.000	21	0.048
Heat Runs (# consecutive days where temp>20°C)	0.201	6	0.033
Total # of days below -10°C	0.132	8	0.019
Soil Water	0.081	5	0.016
Grazing Status	0.083	7	0.012
VPD_{Min} in Summer	0.022	3	0.007
Moisture Deficit	0.010	4	0.002
Summer Mean Temp	0.046	19	0.002
Insolation	0.001	4	0.000
Summer Precipitation	0.001	10	0.000
Snow Water Equivalent	0.000	9	0.000
August Mean VPD_{Max}	0.000	1	0.000
VPD_{Max} in Summer	0.000	1	0.000
% Grasses: % Forbs	0.000	6	0.000
August Mean Temp	0.000	1	0.000
# of days Below 0°C	0.000	3	0.000
Winter Mean Temp	0.000	1	0.000
Winter $Temp_{min}$	0.000	2	0.000
% Lichen	0.000	1	0.000
Slope	0.000	1	0.000
% Forbes	0.000	1	0.000
% Grasses + % Forbs	0.000	1	0.000
% Moss	0.000	1	0.000
% Grass	0.000	1	0.000
Abundance			
Winter Mean Temp	0.457	3	0.152
# of days above 26°C	0.226	3	0.057
VPD_{Min} in Summer	0.142	3	0.047
VPD_{Max} in Summer	0.027	1	0.027
Summer Mean Temp	0.246	19	0.013
Heat Runs (# consecutive days where temp>20°C)	0.044	5	0.009
August Mean Temp	0.007	1	0.007
Summer Precipitation	0.033	12	0.003
Soil Water	0.014	6	0.002
# of days Below -10°C	0.006	3	0.002
% Grasses: % Forbs	0.000	16	0.001
Grazing Status	0.002	3	0.001
% Grasses + % Forbs	0.003	5	0.001
# of days Below 0°C	0.001	3	0.000
Moisture Deficit	0.003	6	0.000
Winter $Temp_{min}$	0.001	3	0.000
Insolation	0.001	5	0.000

Variable	Variable Weight	Num. of Models In	Average Variable Weight per Model, $w_{i\text{-}avg}$
Snow Water Equivalent	0.001	9	0.000
August Mean VPD_{Max}	0.000	1	0.000
% Forbs	0.000	1	0.000
% Moss	0.000	1	0.000
% Grass	0.000	1	0.000
Slope	0.000	1	0.000
Actual Evapotranspiration	0.000	2	0.000
Retraction			
Winter Mean Temp	0.759	2	0.380
Summer Mean Temp	0.953	6	0.159
Summer Precipitation	0.196	7	0.028
Soil Water	0.037	3	0.012
Snow Water Equivalent	0.006	3	0.002
# of days Below -10°C	0.001	1	0.001
Heat Runs (# consecutive days where temp>20°C)	0.004	3	0.001
# of days above 26°C	0.002	4	0.000
August Mean Temp	0.000	1	0.000
Winter $Temp_{min}$	0.000	1	0.000
# of days Below 0°C	0.000	1	0.000
VPD_{Min} in Summer	0.000	1	0.000
August Mean VPD_{Max}	0.000	1	0.000
VPD_{Max} in Summer	0.000	1	0.000
Moisture Deficit	0.000	1	0.000
Actual Evapotranspiration	0.000	1	0.000
Retraction Residuals			
Summer Precipitation	0.931	7	0.133
Heat Runs (# consecutive days where temp>20°C)	0.298	3	0.099
# of days above 26°C	0.361	4	0.090
Summer Mean Temp	0.328	6	0.055
Winter Mean Temp	0.047	2	0.023
# of days Below -10°C	0.012	1	0.012
Soil Water	0.015	3	0.005
Snow Water Equivalent	0.009	3	0.003
# of days Below 0°C	0.000	1	0.000
Winter $Temp_{min}$	0.000	1	0.000
Moisture Deficit	0.000	1	0.000
Actual Evapotranspiration	0.000	1	0.000
VPD_{Max} in Summer	0.000	1	0.000
August Mean VPD_{Max}	0.000	1	0.000
VPD_{Min} in Summer	0.000	1	0.000
August Mean Temp	0.000	1	0.000

Table S7. Ranks of average variable weight per model, by climate metric, for abundance, occupancy, upslope retraction, and retraction residuals. **EA Water** = measurements of ecologically-available water (actual evapotranspiration, water deficit, soil moisture, and vapor pressure deficit). **Other** = non-climatic metrics (for Abundance: grazing status near the patch, insolation, moss coverage, slope, grasses, and forbs; for Occupancy: same as abundance + patch size).

Response Type	Climate Class Metric	Average Variable Weight, $w_{cc\text{-}avg}$, per model	Total Summed Weight
Occupancy	Other	0.0244	0.9989
	EA Water	0.0223	0.4680
	Temperature	0.0204	0.9989
	Precipitation	0.0000	0.0000
Abundance	Temperature	0.0226	0.9701
	EA Water	0.0105	0.1682
	Precipitation	0.0015	0.0305
	Other	0.0010	0.0296
Retraction	Temperature	0.0526	1.0000
	Precipitation	0.0245	0.1960
	EA Water	0.0046	0.0370
Retraction Residuals	Precipitation	0.0940	0.9400
	Temperature	0.0526	0.9994
	EA Water	0.0017	0.0121

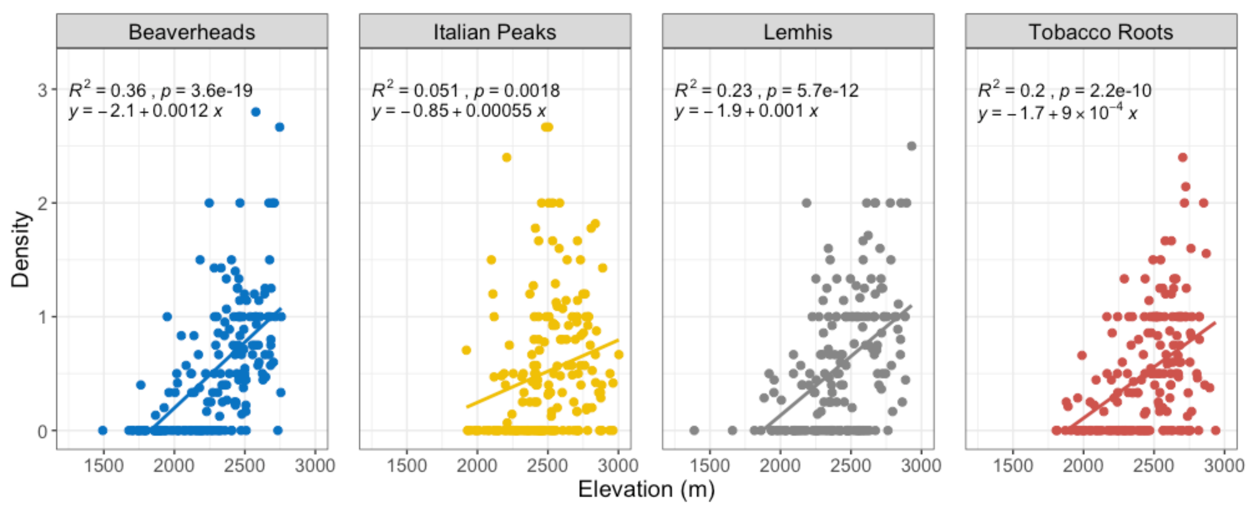

Figure S1. Scatterplot of abundance and elevation, by mountain range. Abundance appears to increase strongly with increasing elevations across all ranges in this ecoregion. However, the strength of this relationship varies, with the Italian Peaks showing the weakest relationship and the Beaverhead Mountains showing the strongest relationship.

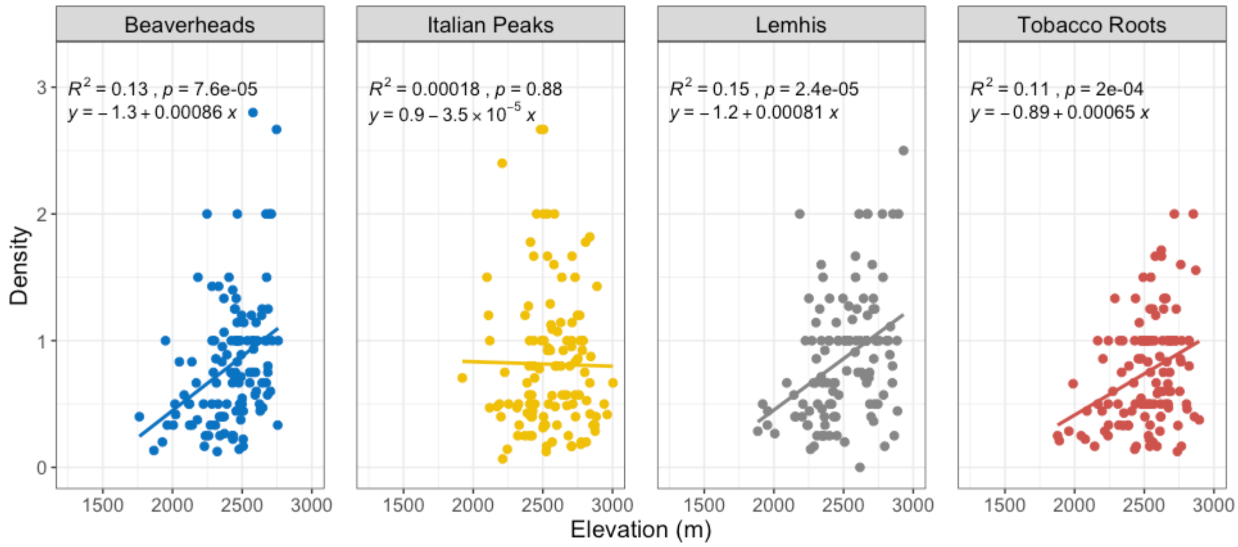

Figure S2. Scatterplot of abundance and elevation, by mountain range, after removing patches without any individuals. The strength of this relationship varies among mountain ranges, with the Italian Peaks showing effectively no relationship, and the Lemhi Range now showing the strongest positive relationship.

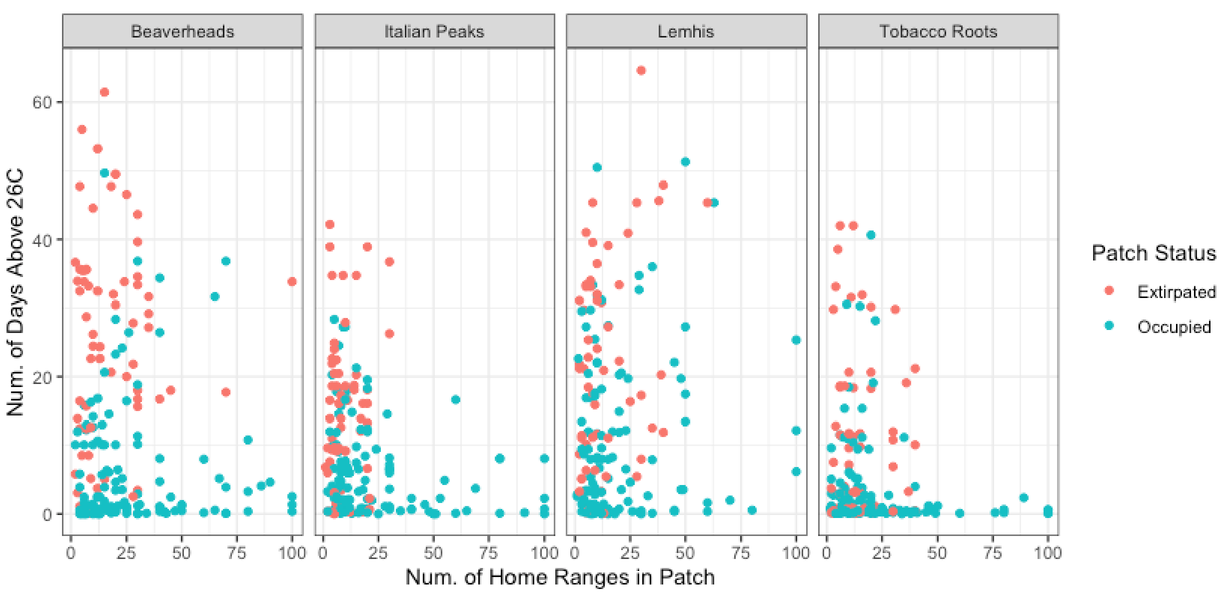

Figure S3. Scatterplot of the top model for occupancy including additive terms for habitat availability on the x-axis and acute heat stress on the y-axis, paneled by mountain range

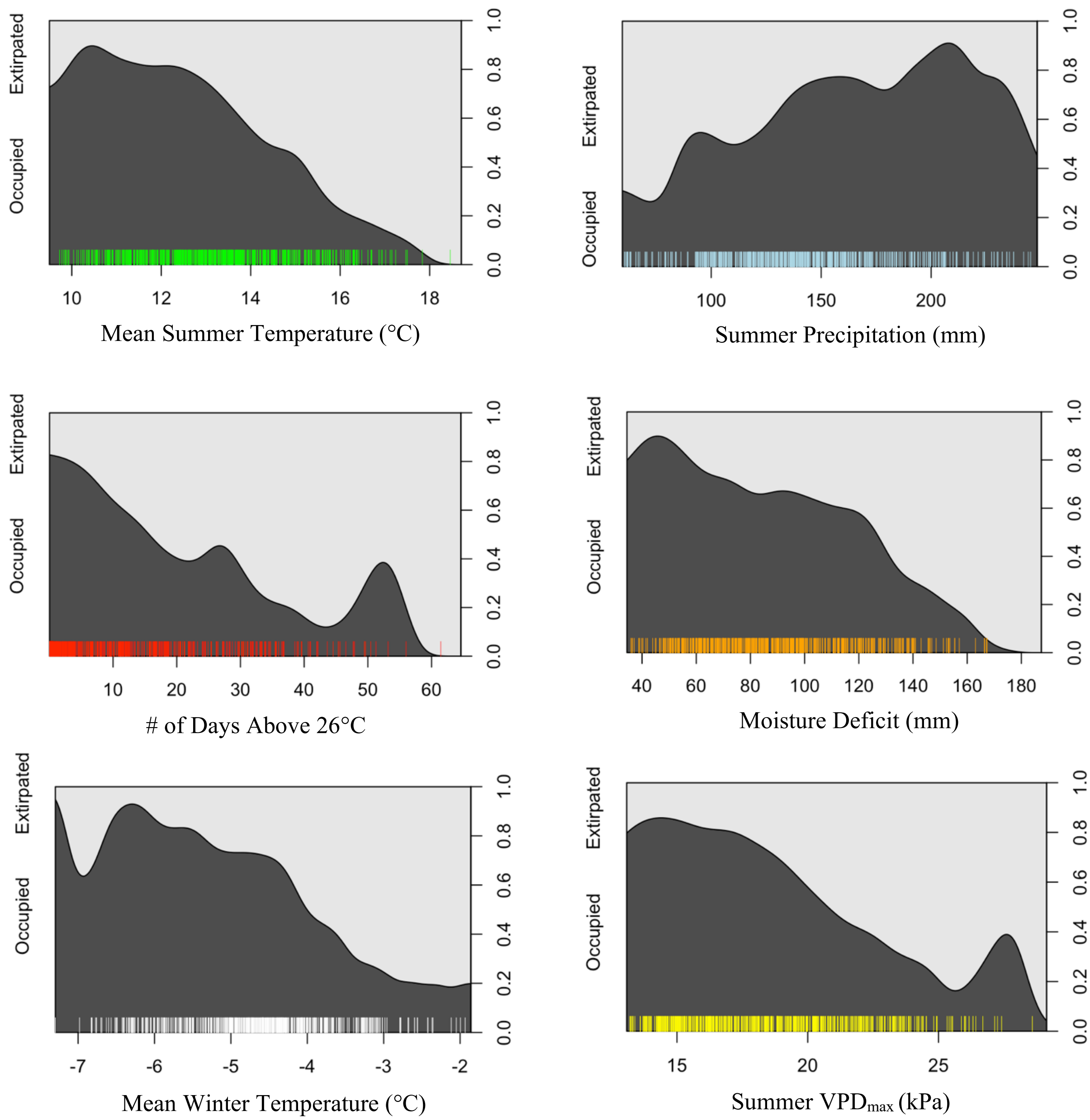

Figure S4. Conditional density plots of six prominent climate variables, each predicting the likelihood of any patch being pika-occupied, given the predictor variable's value on its original scale. Tick marks on the bottom represent values for individual patches. Height of the dark-grey areas represents occupancy likelihood, whereas the height of light-grey areas indicates likelihood of extirpation.

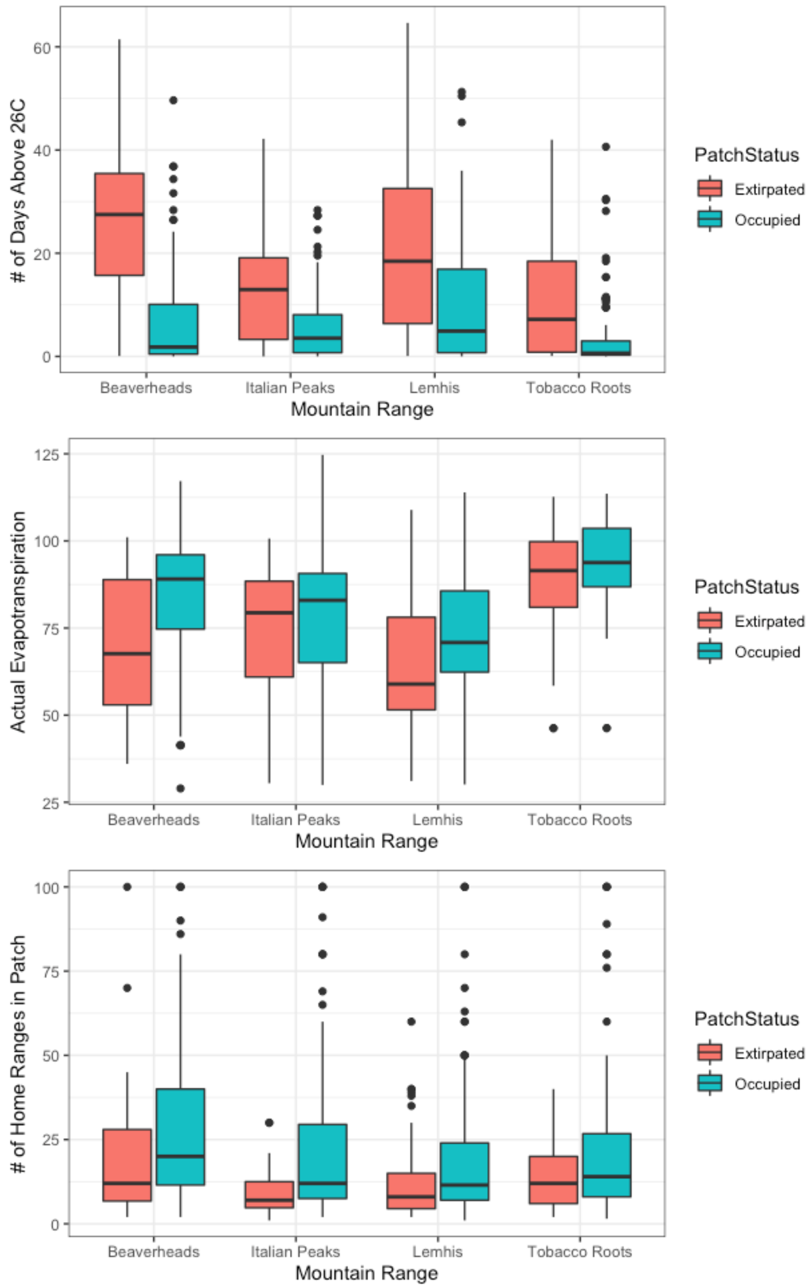

Figure S5. Boxplots of the three most-predictive variables for site occupancy in Table 2, split by mountain range. First, acute heat stress represents a direct mechanism by which climate is likely acting on the species' thermal physiological limits or limiting foraging time. Second, AET likely acts indirectly, as it is a proxy for vegetation quality and above-ground biomass. Third, habitat availability shows a strong signal that smaller patches have a higher probability of extirpation than larger patches across all four mountain ranges, hinting at an island-size effect.

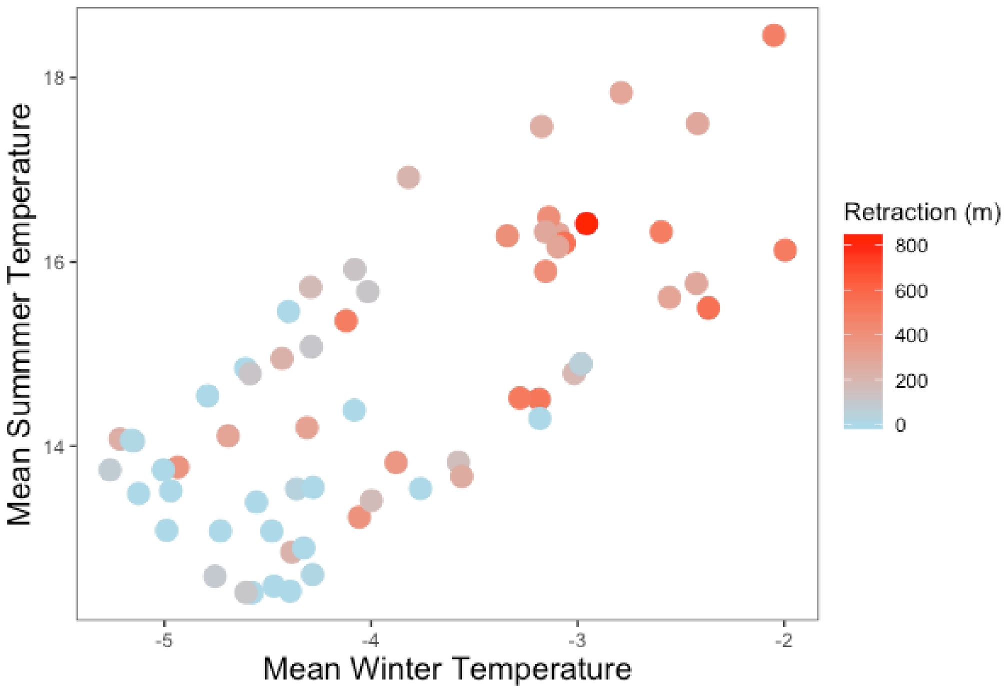

Figure S6. Scatterplots of the two variables, mean winter temperature and mean summer temperature, on their original scales and extracted for the bottom-patch conditions. Both terms appeared in the top model predicting the total amount of elevational retraction per watershed. Watersheds where the bottom patches had higher average temperatures in both summer and winter tended to retract further than watersheds that had cooler conditions. The additive model had an overall good fit to the data ($r^2 = 0.434$).

Table SI2: Raw data of retractions of American pikas (*Ochotona princeps*) across the 64 watersheds in the Northern Rocky Mountains, USA. Column A represents the Watershed ID, which is broken down into two letter abbreviations of mountains ranges (BH = Beaverhead Mtns, IP = Italian Peaks, LR = Lemhi Range, and TR = Tobacco Root Mtns), a number corresponding to the two watersheds' relative latitudinal position in the mountain range (e.g., 1 = southernmost watersheds in mtn range, and 8 = northernmost watersheds), and the "E" indicates east-facing watersheds and conversely, "W" indicates west-facing watersheds. Column B is the magnitude of retraction in each watershed, measured as the difference between the minimum elevation of historical evidence up to the minimum elevation of current evidence of occupancy. Column C is the total elevational extent of each watershed, measured as the elevational span between the lowest talus up to the highest talus in each watershed, all of which was surveyed. Column D is the lowest elevation of historical (or current) evidence in each watershed. Column E is the lowest elevation of current pika occupancy (surveyed 2017-2020). Where columns D and E are identical, there was no retraction. Lastly, Column F is the highest elevation of talus that was surveyed in each watershed. All measurements are in meters.

Watershed ID	Magnitude of observed retraction (m)	Total elevational span of talus habitat within watersheds (m)	Lowest elevation of current or historical evidence (m)	Lowest elevation of patch with current pika occupancy (m)	Highest-elevation talus surveyed within watersheds (m)
BH1E	364.9	595.9	2111.0	2475.9	2706.9
BH1W	400.0	963.8	1768.1	2168.0	2731.9
BH2E	0.0	351.4	2391.5	2391.5	2742.9
BH2W	407.0	908.9	1875.1	2282.0	2784.0
BH3E	0.0	94.5	2407.9	2407.9	2502.4
BH3W	286.0	878.1	1845.0	2130.9	2723.1
BH4E	89.0	369.1	2307.0	2396.0	2676.1
BH4W	410.1	910.1	1766.0	2176.0	2676.1
BH5E	216.2	506.0	2261.0	2477.1	2767.0
BH5W	557.0	1086.9	1701.1	2258.0	2788.0
BH6E	0.0	526.1	2229.9	2229.9	2756.0
BH6W	270.1	899.2	1841.0	2111.0	2740.2
BH7E	4.3	360.3	2309.8	2314.0	2670.0
BH7W	246.0	652.0	1744.1	1990.0	2396.0
BH8E	493.0	826.0	1677.0	2169.9	2503.0
BH8W	282.0	877.8	1476.1	1758.1	2354.0
IP1E	0.0	660.8	2096.1	2096.1	2756.9
IP1W	120.1	770.8	1976.0	2096.1	2746.9
IP2E	115.9	674.8	2199.1	2315.0	2874.0
IP2W	22.0	549.9	2218.0	2240.0	2767.9
IP3E	0.0	413.0	2514.0	2514.0	2927.0
IP3W	294.2	595.0	2229.9	2524.0	2824.9
IP4E	0.0	313.9	2382.0	2382.0	2696.0
IP4W	237.2	591.0	2258.0	2495.1	2849.0
IP5E	205.2	901.0	1909.9	2115.0	2810.9
IP5W	493.0	689.8	2085.1	2578.0	2774.9
IP6E	378.0	569.1	2396.0	2774.0	2965.1
IP6W	0.0	617.2	2379.9	2379.9	2997.1
IP7E	0.0	365.8	2527.1	2527.1	2892.9
IP7W	37.2	655.9	2322.0	2359.2	2977.9
IP8E	0.0	479.1	2414.9	2414.9	2894.1
IP8W	0.0	482.8	2395.1	2395.1	2877.9
LR1E	75.0	637.0	2261.0	2336.0	2898.0
LR1W	102.1	848.0	2051.9	2154.0	2899.9
LR2E	307.0	438.9	2350.0	2656.9	2788.9
LR2W	0.0	465.7	2345.1	2345.1	2810.9
LR3E	0.0	489.8	2320.1	2320.1	2810.0
LR3W	0.0	776.9	2124.2	2124.2	2901.1
LR4E	0.0	667.2	2232.7	2232.7	2899.9
LR4W	0.0	680.0	2243.9	2243.9	2923.9
LR5E	171.0	715.1	2030.0	2201.0	2745.0
LR5W	107.9	837.9	2090.0	2197.9	2927.9
LR6E	223.2	679.1	2158.9	2382.0	2838.0
LR6W	0.0	944.3	1845.9	1845.9	2790.1
LR7E	289.0	866.9	1950.1	2239.1	2817.0
LR7W	270.1	982.1	1934.0	2204.0	2916.0
LR8E	828.0	827.8	1850.1	2678.0	2678.0
LR8W	480.2	1335.0	1364.0	1844.0	2699.0
TR1E	390.9	696.8	2110.1	2500.9	2806.9
TR1W	296.0	905.0	1932.1	2228.1	2837.1
TR2E	167.1	641.0	2201.9	2368.9	2842.9
TR2W	0.0	577.9	2364.0	2364.0	2941.9
TR3E	190.2	916.2	2005.9	2196.1	2922.1
TR3W	527.1	854.0	2019.9	2546.9	2874.0
TR4E	0.0	663.2	2144.9	2144.9	2808.1
TR4W	271.0	961.9	1961.1	2232.1	2923.0
TR5E	12.8	396.8	2399.1	2411.9	2795.9
TR5W	0.0	791.3	2073.9	2073.9	2865.1
TR6E	552.0	785.8	1975.1	2525.0	2760.9
TR6W	151.2	611.1	2265.9	2417.1	2877.0
TR7E	499.7	934.5	1790.4	2290.0	2724.9
TR7W	0.0	880.9	1844.0	1844.0	2724.9
TR8E	255.8	575.8	2238.1	2493.9	2813.9
TR8W	509.1	858.0	1911.1	2420.1	2769.1
Averages:	**197.0**	**693.4**	**2100.1**	**2296.9**	**2793.5**

Method 1: Average retraction of all watersheds

Beaverheads	Italian Peaks	Lemhi Range	Tobacco Roots	Total Avg
251.6	118.9	178.4	238.9	197.0

Method 2: Average retraction of retracted watersheds only

Beaverheads	Italian Peaks	Lemhi Range	Tobacco Roots	Total Avg
309.7	211.4	285.4	318.6	281.3