ASSESSING ALTERNATIVE DRIVERS OF OCCUPANCY, ABUNDANCE, AND ELEVATIONAL RANGE RETRACTION AT THE RANGE CORE OF A CLIMATE-SENSITIVE MAMMAL

by

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ABSTRACT

Ecological niche theory and niche conservativism suggest that rising temperatures globally will continue pressuring species to track cooler environments. Examining changes in occupancy and abundance together across bioclimatic gradients can inform forecasts of expected range shifts. Although occupancy and abundance reflect similar aspects of species-environment relationships, they are governed by different underlying processes. Abundance is thought to be more reflective of shorter-term conditions affecting vital rates, whereas site occupancy often reflects habitat suitability. By directly comparing results of both response types, as well as elevational range retraction, we offer a robust method for assessing complex species-climate relationships. In this study, we test how populations of the American pika (*Ochotona princeps*), a small montane lagomorph, respond to varying climatic conditions. To do so, we tested and compared the drivers of site occupancy, abundance, and upslope retraction, across 760 talus patches, nested within 64 watersheds across the Northern Rocky Mountains, USA. Using mixed-effects modeling, paired with an information-theoretic approach, we tested model suites that reflected hypothesized species-climate relationships to identify the top models of each of our response classes. Approximately one third (33.9%) of patches were found extirpated. The most important environmental predictors differed among occupancy, abundance, and amount of upslope retraction. For site occupancy, the top model included metrics of summer acute heat stress, actual evapotranspiration, and habitat availability. For abundance, acute heat stress and the preceding winter's mean temperature (i.e. chronic cold stress) was the top-ranked model, suggesting rapid responses of populations to recent climatic conditions. Furthermore, we found that a model including both chronic heat and chronic cold stress best predicted the total amount of vertical retraction across watersheds, whereas acute heat stress and summer precipitation best explained the residuals. Our results emphasize the complexity associated with evaluating species responses to environmental change and that results from occupancy analyses should be used with caution when extrapolating to predicting abundances across varied landscapes. Our method for assessing the drivers of elevational retraction across a suite of watersheds has widespread applications for evaluating species response to changing climatic conditions elsewhere.

ENVIRONMENTAL DRIVERS OF OCCUPANCY, ABUNDANCE, AND RANGE RETRACTIONS IN A MONTANE SPECIES

Introduction

Globally, contemporary climate change has resulted in increases in seasonal, and annual temperatures, decreases in snowpack, a lengthening of the growing season, as well as increases in the intensity and frequency of temperature and precipitation-related extremes, among numerous other changes (Mote et al. 2018; IPCC, 2013). A growing body of literature has documented species responses to short-term extreme weather events (e.g., Prugh et al., 2018), as well as to long-term climate shifts (Wilson et al., 2005; Sekercioglu et al., 2008; Iknayan & Beissinger, 2018). Climate change-driven responses can manifest in many forms, including shifts in phenology (Bartomeus et al., 2011), morphology (Hoy et al., 2018), physiology (Van de Ven et al., 2019), genetics (Rubidge et al., 2012), behaviors (Beever et al., 2017), and distributions (I.-C. Chen et al., 2011). However, the way in which species respond appears highly variable, differing considerably across species, space, time, biophysical gradients, and even life stages (Fritz et al., 2009; Moritz et al., 2008; Freeman et al., 2018; Hallett et al., 2004; Rapacciuolo et al., 2014; Tingley et al., 2012).

Ecological niche theory suggests that rising temperatures will pressure species to track cooler environments; therefore, low-elevation species will generally shift poleward, whereas mountain-dwelling species will move upwards in elevation (Guralnick, 2007). The distances needed to track these environmental conditions are much greater for low-elevation species, whereas moving to reach the same historic conditions in montane systems remains more feasible. Lowland species tend to gain available habitat as they expand upwards when trailing edges do not shift as quickly, whereas subalpine-alpine species substantially lose area as they reach mountain 'islands', leaving them particularly vulnerable to climate change (Freeman et al., 2018). For example, the Rocky Mountains of North America have a mean elevation of 1,844 m, yet land area decreases rapidly at elevations above 2,080 m (Elsen & Tingley, 2015).

Examining changes in abundance and occupancy along bioclimatic gradients informs forecasts of species' ongoing and future range shifts, for example, by identifying whether distributions are 'leaning' upslope (Breshears et al., 2008). Though occupancy and abundance reflect similar aspects of species-environment relationships, they are reflective of differing underlying processes. Site occupancy is believed to better represent overall habitat suitability, whereas abundance more reflects habitat quality (Thomas et al., 2010; Mortelliti et al., 2010, but see Van Horne, 1983). Moreover, abundance is likely more representative of shorter-term conditions (i.e. seasonal changes) affecting the vital rates of local populations, whereas site occupancy may be driven by the prevailing climate (i.e. longer-term climatic changes), in addition to rescue effects and metapopulation dynamics acting across broader spatiotemporal scales. Rapid and stochastic changes can immediately influence population abundance, demonstrating how abundance can be more sensitive to environmental change than site occupancy, the latter of which would require a population's abundance dropping to zero to change its state. This stresses the importance of identifying climatic influences on species' abundance and occupancy, as they may synergistically influence the pace and trend of species' range shifts. Directly comparing results of such paired analyses appears to be one of the most robust means for assessing species-climate interactions through space and time, yet appears only rarely in the literature (Dibner et al., 2017; Beever et al., 2013).

Just as species are responding to both short- and long-term changes in climate, they are simultaneously exposed to shifts in the predictability and directionality of these changes. Thus, there is a growing trend towards assessing the effects of climate variability and extremes on species, not just means and directional trends (Campbell et al., 2012; Berger et al., 2018; Stewart et al., 2019). This interest in how species adapt to the overall predictability of the environment extends back as early as the 20th century (Fisher, 1930). Contemporary climate change has markedly increased climate variability and frequency of extreme weather events, the magnitude of such are predicted to become greater. Increased variability can have carry-over effects on population vital rates, and lead to population declines or collapses if species do not have the adaptive capacity to cope or adjust. Campbell et al. (2012) demonstrated that variability, rather than climatic means, can have significantly stronger effects on survival rates and recruitment, and can affect different life stages in opposing ways, all within a single species. Climatic variability can also act indirectly on species by changing the total amount of food and habitat available in any given year. Thus, understanding such variability is vital for species-climate studies (Benton et al., 2002; Johnson et al., 2005; Forcada et al., 2005).

Extreme events such as heatwaves, severe droughts, high-rainfall events, and snow droughts can play a significant role in determining and altering species distributions at numerous scales as well (e.g. Prugh et al., 2018; Hale et al., 2016; Greenville et al., 2012), often by stressing individuals beyond their physiological limits (Riddell et al., 2019). However, changes in extremes can be subtler. For example, climate change has increased the maximum daily temperatures throughout the 21st century, in turn, potentially exceeding species-specific thermal maxima. If the current daily maximum temperatures exceed physiological limits, conditions can become too stressful for various demographic processes to occur. Therefore, the greater the number of days above the maximum (or below the minimum), the lower the probability of the species' persistence at a given location. Conditions may be considered extreme to species if these conditions were not experienced throughout their evolutionary history. Responses to these 'extremes' are often challenging to quantify in modeling, but their ecological relevance remains critical and is broadly under-investigated for vertebrates. Given the various processes and underlying mechanisms that are affecting range shifts, identifying the most influential environmental variables correlated with these responses remains a priority in ecology, as universal patterns and responses rarely exist across taxa.

Here, we test how populations of the American pika (*Ochotona princeps*), a small montane lagomorph, are responding to contemporary climate change by quantifying the determinants of site occupancy, abundance, and upslope retraction. We test the importance of seasonal means, extremes, thresholds, and inter-annual variability using numerous climate metrics, as well as habitat characteristics. These relationships remain frontiers of ongoing investigations and discovery in the field of global change biology, yet are rarely tested holistically for multiple responses. We used an *a priori* model suite with an information-theoretic approach to assess hypothesized mechanisms responsible for observed patterns and speculate whether climate is acting directly or indirectly to influence range shifts. Our models reflect a variety of stressors, addressing summer and winter conditions separately. These seasonal effects relate to specific mechanisms tied to life histories (e.g. chronic heat stress in summer causing mortality), as opposed to using annual measures where specific mechanisms driving response can be difficult to identify.

Overall, we sought to: 1) evaluate whether changes in site occupancy and abundance have occurred in recent decades at the center of the species' geographical range, the Northern Rocky Mountain ecoregion; 2) compare the dominant drivers for occupancy and abundance to test whether the same mechanisms influence both responses, and 3) identify which combination of climatic and/or non-climatic factors best predict the patterns of occupancy, abundance, and upslope retraction, across several mountain ranges that encompass gradients of climatic conditions. Moreover, we are unaware of any studies to date that: (a) quantify range retraction across dozens of replicated watersheds and across multiple mountain ranges for any animal species, (b) regress vertical retraction against a suite of climatic factors other than temperature metrics alone, and (c) explore the specific mechanisms that best predict the relative extent of retraction amongst watersheds across an ecoregion.

We expected that: 1) there would be minimal upslope retraction, if any, since this region is at the species' range core, 2) chronic heat stress would be the primary mechanism governing density, occupancy, and the amount of retraction, 3) the bottom talus patch conditions would be more important than the watershed-wide conditions in determining the amount of retraction, 4) one-year lagged conditions would outperform two-year lagged conditions for abundances in this short-lived species, 5) 10-year means would outperform 10-year variances in determining occupancy as might be expected with gradual population declines, and 6) that summer conditions will be more important than winter conditions for our measured response types because of relatively high and consistent snow packs in winter across this ecoregion, as well as this species' physiological and behavioral adaptations for winter survival under the snow.

Methods

Model Species

American pikas (*Ochotona princeps*) are small (125-200g) lagomorphs that are considered dietary generalists and habitat specialists, occupying rock habitats that passively aid in thermal buffering. Importantly, the structure and integrity of this habitat changes very little through time, thus eliminating habitat alteration as a confounding factor. This species is ideal for examining questions related to meta-population (Hanski 1998) and local extinction dynamics (McDonald & Brown, 1992) due to its high detectability in field surveys (~92-95.9% (Rodhouse et al., 2010; Beever, 2011), philopatry to individual territories where individuals exhibit central-place foraging (Smith & Weston, 1990), obligation to patchily distributed talus and broken rock habitats, and because its evidences (fecal pellets, urine stains, old haypiles) can last in talus interstices for years to centuries (Millar et al., 2014). The presence of old evidence allows us to estimate how far pikas have retracted upslope within watersheds in recent decades.

American pikas are cold-adapted and although they do not hibernate, they remain sensitive to a spectrum of climatic conditions and extremes (e.g. Johnston, 2019; Beever, 2011). For example, Johnston et al. (2019) found drastic declines in pika abundances the year after a brief snow drought, exemplifying how *O. princeps* is an excellent indicator species for quantifying responses to climate change and short-term weather conditions. Finally, this species exhibits a "live-fast, die young" life-history strategy which makes it particularly vulnerable to the effects of environmental change (Postuma et al., 2020).

Study Area

We surveyed throughout four mountain ranges in the Northern Rocky Mountains, (USA) of western North America (Figure 1) during 2017-2019. The minimum convex polygon of these ranges spans 2.3 million ha and occurs in roughly the center of this species' geographic range. Annual mean monthly minimum temperatures have increased ~1.7 C since 1895 across the entire region, whereas annual mean monthly maximum temperatures increased ~0.3 C (Halofsky, 2018). From 1951-2010, the number of growing degree days per year increased from 194 to 206, while frost days per year declined from 171 to 159; however, there has been no significant changes in annual precipitation in this period (Whitlock et al., 2017). Nevertheless, this ecoregion has been repeatedly predicted to be a critical stronghold for pikas in the future (e.g., Galbreath et al., 2009; Calkins et al., 2012).

Research Design: Space-for-Time Substitution

Our research design involved an indirect space-for-time substitution (*sensu* Fukami & Wardle, 2005). This design involves sampling locations along abiotic gradients to infer and/or predict responses of organisms to future environmental conditions, which in this study are metrics of climate and habitat quality (Appendix A, Table 1). We studied two levels of space-for-time substitutions (hereafter "SFTs"), consisting of 1) elevational gradients within ranges (wherein lower-elevation dynamics are predicted to be experienced at higher elevations, in the near future), and 2) climatic gradients across multiple mountain ranges. First, within the four mountain ranges, a continuum of elevationally mediated climate zones exists, characterized by semiarid sagebrush-steppe at low elevations, to conifer-dominated forests at intermediate elevations, up to barren tundra at highest elevations. Secondly, conditions in these mountain ranges vary from comparatively hot and dry, to increasingly cold and wet, as follows: Lemhi Range, Beaverhead Mountains, Italian Peaks, Tobacco Root Mountains (Fig. 1 and Appendix A: Fig. 1). In these ranges, watershed-based elevational transects were delineated to quantify range shifts using the elevational SFT design; examining where the populations are now, where they used to be based on evidence of historical occupancy, and infer where the species will shift in the future (Blois et al., 2013).

Although methods for quantifying occupancy and abundance have long been debated and fine-tuned in ecology, methods for detecting and measuring upslope range shifts are sparser and more variable (Sexton et al., 2009). Importantly, most transect studies examining these trends are limited in either spatial or temporal extent. Although fine-scale, single-transect studies are robust and informative for many questions, these survey and resurvey efforts typically only use single transects that likely under- or overestimate broader-scale patterns (e.g. Brusca et al., 2013; Freeman et al., 2018; Moritz et al., 2008; Whittaker & Tribe, 1996, but see McCain et al., 2018; Tingley et al., 2009; and Caddy-Retalic et al., 2017). For example, the amount of retraction for a given species may be biased by the length and elevational span of a transect, or by the elevations of sampling points. Therefore, we sought high replication of transects (N = 64) and varying transect lengths to provide rigorous results. Overall, this spatially extensive sampling allowed us to determine occupancy and abundance at the patch level, and the total amount of upslope retraction at the watershed level using the occupancy results.

Field Methods

Scouting and testing of field protocols began in the Tobacco Root Mountains in June of 2017. We then field-surveyed patches for unequivocal evidences of current and historic pika occupancy from June to September in 2018 and 2019. Patches were selected and digitized along elevational transects within watersheds before each field season using CalTopo (https://caltopo.com). Each talus patch was delineated as a polygon, and patches were separated by at least 40 m (although ≥100 m, in most cases). Watersheds were latitudinally paired, with one on the west side of the ridgeline and one on the east (Fig. 1).

We began field surveys at the lowest-elevation talus patch in each drainage, up to the highest patch, for a total of 12 patches per watershed. Opposing east and west side watersheds were always surveyed on or near the same date and within the same year. Paired watersheds were surveyed in random order from June-September to avoid confounding latitudinal position within the mountain range with Julian date. In total, sixteen watershed transects were surveyed in each mountain range and all were separated along the ridgelines by ≥1 km. Within 64 watersheds, we surveyed 760 patches spanning the two summers. Eight patches were found to be unsuitable for pika occupancy during field surveys (i.e. too shallow or too small of rocks) and not included in analyses.

To maximize detections and for consistency among other studies, we adapted patch survey methods from previous research on this species (Beever et al., 2011). In brief, these methods involve walking 50-m-long transects along elevational contours, spaced 15 m elevationally apart (with reduced spacing, until old, and then current, evidence was found), covering the entire talus patch to determine occupancy and relative abundance. A patch was considered occupied when ≥1 pika was detected by aural and/or visual observation, or from fresh hay piles (containing ≥10 pieces of green vegetation). A patch was considered extirpated when only old fecal pellets and/or old hay piles were found. Surveys occurred shortly after sunrise and before sunset each day, avoiding the warmest hours (12:00-16:00) unless there was consistent cloud coverage.

Climate Data:

For each site, we characterized the prevailing climate with metrics of temperature, precipitation, and vapor pressure deficit (VPD) using PRISM (Parameter-elevation Relationships on Independent Slopes Model; version AN81 gridded data at 1-arc-second resolution (~800m)), daily values (Daly et al., 2008). We also obtained gridded, water-balance model data from the National Park Service at 1-km resolution for actual evapotranspiration (AET), moisture deficit, and soil water storage (Tercek et al *placeholder*). Lastly, we obtained gridded snow water equivalent (SWE) data from the National Weather Service's National Operational Hydrologic Remote Sensing Center (NOHRSC) SNOw Data Assimilation System (SNODAS) at 1-km spatial resolution. To obtain SWE data, we extracted raw daily values as a time series using a reference file of locations by modifying the functions within R package *rwrfhydro* (McCreight et al 2015). The SWE values were then calculated as winter means (Nov 01 – Mar 31).

For each variable in the abundance analysis, we include one- and two-year lagged conditions to test the temporal scale at which populations are most strongly responding. For each variable in the occupancy and retraction analyses, we included 10-year mean and 10-year variance terms to test whether the species is responding more strongly to mean conditions or overall climatic unpredictability. The 10-year means and variances were calculated as the means and standard deviations of annual means (or totals) across the 10 years prior to surveys. All analyses on climate and water-balance data were done in R version 3.4.1 using packages *dplyr* (Wickham et al 2019), *gtools* (Warnes et al 2015), *heatwaveR* (Schlegel & Smit 2008), *lubridate* (Warnes et al 2015), *ncdf4* (Pierce 2019), *purrr* (Henry & Wickham 2019), *raster* (Hijmans 2018), *rgdal* (Bivand et al 2018), *rwrfhydro* (McCreight et al. 2015), and *tidyverse* (Wickham 2018),

Analytical Methods

We tested each of our following response classes using model suites that were developed *a priori,* where each model represented a specific mechanism(s) that is hypothesized to influence the species (Appendix: Table 1).

Occupancy Analyses: To evaluate the influence of climatic conditions and identify the best predictor(s) for site occupancy, we used generalized linear mixed-effects models (GLMMs) in R package *lme4* (Bates et al. 2015, R Core Team 2019) with a binomial distribution and logit link that included the prevailing climate of the site (10-year means and variances) and habitat characteristics as predictor variables (Appendix A: Table 2). Given our sampling design, we used mountain range as a random effect, with the climatic and habitat variables as fixed effects. For these occupancy models, we compared occupied patches to unoccupied patches, removing patches that had no pika evidence ($n = 23$), because we assumed that they have 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. We used only the best temporal scale for final analyses, which was determined by testing all models in a paired manner and then evaluating the pairs with Akaike information criterion. For example, we ran one model including mean summer temperature means and one model for mean summer variances, then determined which performed best. For both occupancy and abundance model suites, we created a suite of additive models, as well as models with interactive effects among variables. Variables were not combined within models if they were highly correlated ($r > 0.75$; (Johnston, 2019)). Additionally, all univariate models were included. All variables were scaled using z-score standardization, with a mean of 0 and standard error of 1. We paired our I-T approach with the information criterion of AIC (Burnham & Anderson, 2002) and model fit was also tested (R^2) for both marginal and conditional coefficients of determination.

Relative Abundance Analyses: To evaluate the influence of climate and identify the best predictor(s) for relative abundance, defined as the number of individually distinguishable pikas detected per 50 m surveyed (*sensu* Beever et al. 2013), we used linear mixed-effect models in R package lme4 (Bates et al. 2015, R Core Team 2019) that included the prevailing climate of the site with one and two-year lags, as well as habitat characteristics as predictor variables (Appendix: Table 3). For this analysis, we only included the subset of patches that included patches with one or more pikas (N = 479). Thus, to clearly distinguish the factors governing occupancy from those governing abundance, we did not include unoccupied patches. We tested *a priori* whether the previous year's conditions or a lagged year's conditions better predicted abundance. This was fundamental to test the temporal scale at which this species is most responsive. We used the model suite (one vs two year lags) that performed better.

Amount of Retraction Analysis: We quantified the amount of upslope retraction as the elevational difference between the lowest elevation within the lowest patch containing evidence of historic occupancy up to the lowest elevation of the lowest currently pika-occupied patch. These elevation measurements were all conducted in CalTopo, as opposed to on our GPS units, to ensure the most accurate elevations at both patch locations. If the bottom patch in a watershed had two or more pikas, retraction was considered zero meters. However, if only one pika occupied the lower elevational boundary patch, the population was classified as functionally extinct (following Beever et al. 2011), due to an inability to repopulate the patch and not considered occupied in the above CalTopo measurement. These estimates for upslope retraction are conservative, as retraction could be greater if old evidences have degraded to the point where they are no longer detectable at the bottom-most patches.

Climatic Influences on Magnitude of Retraction: We tested our model suite using linear mixed-effects models in the R package *lme4* (Bates et al. 2015), with amount of retraction in meters as the response variable and mountain range as a random effect (Appendix A: Table 4). Similar to the occupancy analysis, we assessed the importance of climatic means versus variances in determining retraction using 10-year conditions. Additionally, we sought to identify the spatial scale at which these variables should be examined. To address these two questions, we developed two novel approaches for calculating predictor variables that we believed would best explain the amount of retraction. In the first approach, we compared conditions of the lowest-elevation talus patch in the watershed (i.e., a proxy of climatic harshness at the historic trailing edge), versus the average conditions across all 12 patches within the watershed (i.e., proxy of how harsh conditions are watershed-wide). The proxy that performed better would be retained for the final model suite. Next, our second approach involved testing again whether the climatic means or variances were more important in the model suite. As above, only the better predictor type would be kept in the final model suite. The final suite contained 28 models. We then ranked models using the Akaike information criterion to determine what best predicted the amount of retraction by watershed. We fit each model using R^2 to estimate the amount of variation explained by the top model(s). We included all 64 watersheds in this analysis, including watersheds that did not retract at all (i.e. lowest-elevation patch is still occupied with more than one individual).

Residuals of Retraction Analysis: To standardize the comparison of the degree of range retraction across all 64 watersheds, we calculated 'retraction residuals' from a linear mixed-effect model, containing the distance retracted as the dependent variable and historic minimum elevation as the independent variable, with the random effect of mountain range (Appendix: Table 5). The residuals were then used as the dependent variable in a new analysis of retraction that used the same model suite as the above retraction analysis. This model suite included mixed-effect models and the *lme4* package in R (Bates et al. 2015). This residual analysis can be interpreted as ascertaining which predictor variables cause certain watersheds to experience more or less retraction than expected based on their minimum elevations. When evaluating range retraction across watersheds, we expected the relationship between historic minimum elevation of occurrence and the total distance of retraction to be relatively linear and negative; that is, with increases in historic minimum elevation of occurrence, the amount of range retraction was hypothesized to decrease proportionately due to less total area available for retraction. Furthermore, watersheds that span to lower elevations would be expected to retract further than those with higher minimum elevations, as the lower patches within low watersheds are likely to have greater extinction debt if we assume atmospheric lapse rates are relatively equal throughout the region. In other words, low elevation patches would be further outside the climate niche space for this cold-adapted species as patches extend lower into the semiarid sagebrush valleys, and therefore, retraction in those lower extending watersheds would be greater in theory. However, the degree of range retraction is likely to be variable, with some watersheds exhibiting greater or lesser retraction than would be expected by this linear relationship. In this case, the residuals can be used to explain differences between expected and observed distances retracted (i.e., the degree of retraction), dependent on the historic minimum elevation of occurrence. Thus, more positive residuals would indicate greater retraction than expected and, conversely, negative residuals would indicate less retraction than expected for a given elevation. Residual values were thus used in a novel way, as response variables, with the goal to better understand which aspects of climate influence some watersheds to retract more or less than anticipated given historical minimum elevations of occupancy.

Water-Availability-, Temperature-, and Precipitation-Based Variable Importance: Following methods from Kittle et. al (2008), we determined the relative importance of predictor variables by summing the weights of all the models that contained each variable. This cumulative Akaike weight per variable was then divided by the number of models that contained the variable to create a measure of average variable weight per model, w_j (Appendix A: Table 6). This method has been applied elsewhere (e.g. (Johnston et al. 2019, Beever et al. 2010) and allows for the comparison of variable importance when variables are unequally represented across models.

Using this method, we then grouped variables into what we call ‘climate classes’, which included temperature, precipitation, ecologically-available water, and other (non-climatic variables). We summed the average variable weights per model for each climate variable (w_i) by climate classes (e.g. precipitation included both summer precipitation + snow water equivalent) and divided this cumulative weight by the number of variables in the climate class (Appendix A: Table 7). We calculated the importance of these climate classes for each of our four response types, removing all models with “other” variables from the two retraction analyses.

Summer Versus Winter Variable Importance: Following the above method for climate classes, we summed the average weights by per model by variable into two seasons, summer and winter. Therefore, we used reduced model suites in which we removed all models that contained summer and winter terms together. This cumulative weight by season was then divided by the number of variables that went into this summed weight by season. We calculated the importance of each seasons for each of our four response types separately, removing models that contained variables that were not seasonal such as slope, aspect, and habitat size/availability.

Results

We surveyed 3,360 50-meter transects, across 760 talus patches, and across 64 watersheds spanning 2.3 million ha and the Continental Divide of the Northern Rocky Mountains of North America. We documented 1,423 individual pikas during June-September of 2018 and 2019. Domain-wide, 479 patches (63.0%) were currently occupied, 258 patches (33.9%) were unoccupied and had evidence of historical pika occupancy (i.e. extirpated), and 23 patches (3.0%) had no evidence at all. Occupancy among mountain ranges varied minimally from 61.4-64.9%. Similar to other studies on the species (e.g. Moyer-Horner et al., 2016), we found a small positive effect of sampling date on abundance (Estimate: 0.0024, 95% CI: 0.0006 to 0.0041). Furthermore, abundance was also positively, albeit weakly, associated with elevation (linear $r^2 = 0.064$, quadratic $r^2 = 0.068$, Appendix A: Figs. 3 and 4). Across the ecoregion, the mean elevation of all occupied patches surveyed was 2511 m, unoccupied patches was 2248 m, and the mean for patches with no evidence was 1822 m.

Occupancy Modelling

Overall, we found lower than expected occupancy levels in these mountain ranges (mean: 63%) as compared to other studies in the Northern Rocky Mountain ecoregion, such as Moyer-Horner et al. 2016 in Glacier National Park, MT (79.7% of patches pika-occupied), Thompson et al. 2017 across three Montana and Idaho wilderness areas (76.7%), and Beever et al. (unpublished data) in Grand Teton National Park, WY (100%).

Out of 66 climate-and habitat-related paired regression models (means + variances), 10-year mean conditions outcompeted the 10-year variance models in 64 instances (97.0%). Therefore, all subsequent occupancy analyses only used 10-year-mean conditions (Table 1 and Appendix A: Table 2). The top-ranked model for site occupancy incorporated additive effects of acute heat stress (number of days ≥ 26°C during summer), AET, and the number of home ranges in the patch (Table 1). In this model, acute heat stress was negatively associated with occupancy (Est. = -1.1122, 95% CI: -1.3468 to -0.8905), whereas AET (Est. = 0.1595, 95% CI: 0.0500 to 0.3691) and the habitat availability (Est: 0.8111, 95% CI: 0.5427 to 1.1098) were positively associated with occupancy. On average, extirpated sites had 11 more days ≥ 26°C than the occupied sites, and were 1.43°C warmer throughout the summer, by PRISM estimates. Six of the following top-seven-ranked models included the terms for acute heat stress and habitat availability, plus one additional variable, whereas one model included heat runs rather than acute heat stress (Table 1). All seven models were all equally plausible (ΔAIC < 2). Notably, habitat availability in its univariate model performed poorly (ΔAIC = 138.77 from the top model) and the variable only rose in the AIC ranks when added to climate metrics, predominantly summer-based temperature predictors (Appendix A: Table 2). Overall, acute heat stress outcompeted all other mechanisms when averaging variable weights (Table 2), with 6.84% of the average variable weight, followed by AET and then habitat availability.

Relative Abundance Modelling

Across 59 climate-and habitat-related model pairs (one and two-year lags) of regression models, models with one-year-lagged predictors outcompeted the two-year-lagged models in 51 paired instances (86.4%). Therefore, the following analyses only assessed the models for the one-year-lagged conditions (Appendix A: Table 3). The top-ranked model for relative abundance included both chronic cold stress in winter (Est. -0.1189, CI: -0.1746 to -0.0638) and acute heat stress in summer (Est. -0.102, CI: -0.1739 to -0.0244), which were both negatively associated with abundance (w_i = 0.37, Table 1). However, this model showed a relatively weak fit to the data (conditional R^2 = 0.106). The second top model was equally plausible (ΔAIC < 2) and included additive terms for acute cold stress (# of days ≤ -10°C) and acute heat stress. Overall, chronic cold stress outcompeted all other mechanisms with 15.2% of the adjusted model-averaged weight per model (Table 2).

Shifts in Elevational Distribution

Across the 64 watersheds, minimum elevation of pika occupancy retracted upslope in 46 watersheds, and averaged 277 meters upslope at the trailing edge across these drainages (Figure 2). Patches where we could not find old evidence (n=23) were removed from the retraction analysis and not included in the vertical-retraction estimates. Doing so, however, makes our estimates conservative since these patches were pika suitable in terms of diameter, interstitial spaces, and forage availability. Therefore, retraction may be greater for watersheds where we could not find old evidences at bottom patches that may have degraded over time. Of note, all eight western watersheds in the Beaverhead Mountains retracted upslope 281-557 m, three of which had no evidence at the bottom patch. Additionally, the northernmost, eastside watershed in the Lemhi Range was completely extirpated, with only one pika at the highest patch which we consider functionally extinct.

Overall, the mean minimum elevation for *O. princeps* across all surveyed watersheds has moved from 2100 m up to 2299 m in this ecoregion. Based on the standard adiabatic lapse rate of 0.65°C per 100 m of altitude gain, the difference of the historical minimum elevation occupied and the current minimum elevation occupied is approximately 1.29°C. However, the documented shift in pikas is less than the expected distance based on the mean rates of warming alone in this region from 1950-2015 (0.35°C/decade) (Whitlock et al., 2017), which would have predicted pikas had shifted 350 m if they were tracking temperature isotherms only. This may suggest that extinction debts are greater for low elevation populations, particularly those below 2,450 m. To summarize, this species has retracted upslope at the lower elevational trailing margins without any opportunity for expansion at the peaks, as they already occupy the highest elevations across this region.

Vertical Retraction and Climate Relationships

Using a reduced model suite from the previous occupancy analysis (Appendix A: Table 4), we tested the importance of spatial scale and temporal scales on retraction. The bottom patch models outperformed the watershed mean models in 45 of the 54 model pairs (83.3%); therefore, the following analyses consider only models using bottom-patch conditions which is interpreted as the 'severity' (or unfavourability) of climate conditions at the lowest elevations within watersheds. Next, models using 10-year climatic means outperformed models using 10-year variance terms in 22 of the remaining 27 model pairs (81.48%), and thus, our final model suite consisted of 28 models (including the null) that used only mean climatic conditions at the bottom patch of each watershed.

The top-ranked model predicting the amount of retraction by watershed included additive effects of summer mean temperature and winter mean temperature (i.e., chronic cold stress and chronic heat stress), where both terms positively influenced retraction. In other words, the warmer the summer and winter conditions were, the further the watershed retracted upslope. This model had strong support (Akaike weight = 0.75), and the second-top model was not equally plausible (ΔAIC = 2.85). The fixed terms in the top model explained 43.36% of the variation, whereas the random effect of mountain range explained no additional variation. Upon averaging variable weights, chronic cold stress emerged as the overall best predictor across the model suite (w_j = 0.380), followed by chronic heat stress (w_j = 0.159) (Table 2).

Relationship Between the Residuals of Retraction and Climate

Minimum elevation of historic occupancy explained 37.9% of the variation in retraction residuals (Fig. 3). Using the same 28-model suite as the retraction analysis above (bottom patch, mean conditions), the best predictor of the residuals was an interaction between acute heat stress and summer precipitation (Table 1). Two following models were equally plausible and had terms for summer temperature and interactions with precipitation. However, all models showed weak support in predictive power, potentially suggesting non-climatic complexities in predicting the residuals of retraction.

Water-Availability-, Temperature-, and Precipitation-Based Metrics

The strength and rank of climate variable classes varied sizably among the four response types (Fig. 4). For the occupancy models, non-climatic variables ('other'), ecologically available water, and temperature were equally strong (2.44%, 2.23%, and 2.04%, respectively) in their overall average variable weight per model. For abundance, temperature metrics were the best supported and had 2.26% of the variable weight per model. The retraction model suite was also dominated by temperature with 5.26% of the variable weight per model. Lastly, precipitation metrics were dominant for the retraction residual models, with 9.40% of the variable weight per model (Appendix A: Table 7).

Summer and Winter Variable Importance

In our reduced model set for discriminating seasonal differences (i.e. removing models that had terms that are not seasonal, e.g. insolation and habitat availability), occupancy was driven entirely by summer conditions (summer w_j = 0.062/model, winter w_j = 0.000/model) (Table 3). For abundance, winter variables outperformed summer variables and had 3.24 times more support when summed across all models (winter w_j = 0.084/model, summer w_j = 0.026/model). For retraction, summer variables again outperformed winter ones and had 5.91 times more support when summed across all models (summer w_j = 0.053/model, winter w_j = 0.009/model). Lastly, for the retraction residuals, summer variables outperformed winter variables with 25.97 times more support when summed across all models (summer w_j= 0.055/model, winter w_j = 0.002/model).

Discussion

Species and population responses to climate change vary considerably through space and time, even among closely related taxa (Prugh et al., 2018; Freeman et al., 2018; Rapacciuolo et al., 2014; Rowe et al., 2015; Moritz et al., 2008). However, the particular mechanisms by which climate change is acting on species often go untested (Cahill et al., 2013; Ockendon et al., 2014). There is growing interest and recognition among ecologists that understanding the spatial and temporal scales by which these mechanisms are affecting species provides greater strength of inference than using strictly correlative analyses, as more mechanistic-based approaches can also be applied elsewhere in a species' range, extrapolated into no-analog environments, and help identify possible climate-adaptation management actions.

In temperate regions, mountains often support cold-adapted species exhibiting traits that are highly specialized for surviving severe conditions in snow-dominated landscapes (Theodoridis et al., 2018). Adaptations to cold often include seasonally based morphological (e.g., molting) and/or physiological changes (e.g., neuroendocrine changes, hibernation, elevational migration to summer and winter ranges). Still, montane species are increasingly living near their warm physiological limits due to this thermal specialization over evolutionary time, and in turn, may lack the adaptive and genetic capacity to persist *in situ* under further warming (Hoffmann & Sgro, 2011). For those species with limited phenotypic plasticity, inadequate evolutionary adaptive capacity, and limited dispersal abilities, extirpations can occur on relatively quick time scales (Botero et al., 2015). In some cases, gradual declines in patch 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; therefore, both estimates are fundamental for managers in conservation planning. Abundance is also a more-sensitive and earlier-warning indicator, and for a given sample size, regressions of continuous variables will have greater statistical power than will logistic regressions.

The American pika has been recognized as an early indicator species of the effects of climate change due to its high physiological sensitivity, narrow thermoneutral zone, and generally low adaptive capacity to changes in daily climate extremes (e.g., maximum and minimum temperatures). Additionally, this species has gained attention in recent studies for its responses to different aspects of climate across the many ecoregions it occupies, in terms of both occupancy and abundance (Smith et al., 2019; Beever et al., 2011; Johnston et al., 2019). Because American pikas inhabit naturally patchy habitats, metapopulations are influenced by patch size, number of patches, and interpatch distance. Given that dispersal distances for *O. princeps* are markedly lower in areas with hotter, drier climates (Castillo et al., 2014; Castillo et al., 2016; Schwalm et al., 2016), this patchiness further limits the species distributional response potential under future climate change (Rehnus et al., 2018). Here, we provide strong evidence of widespread, climate-mediated range retractions of the species across the Northern Rocky Mountain ecoregion. Our primary prediction in this study was that summer conditions would be most influential on patterns of occupancy, abundance, and upslope retraction for this cold-adapted species. This was generally supported by the occupancy, retraction, and retraction residual analyses, but not for relative abundance. There were many nuances, however, when assessing the mechanisms in top-performing models among responses, as well as investigations into climate metric classes.

Mechanisms Influencing Occupancy

We found strong support for acute heat stress, AET, and habitat patch size collectively influencing site occupancy. Our analysis using model-averaged variable weights further corroborated that acute heat stress (# of days ≥ 26°C) was the leading occupancy predictor in this ecoregion, closely followed by the latter two variables (Table 2). The presence of patch size in top-performing models lends support to Island-

Biogeography Theory; large patches or islands often support larger populations and thus, have lower probabilities of extinction (MacArthur and Wilson, 1967). Additionally, larger populations typically have greater genetic variation and consequently, greater capacities to adapt *in situ*, whereas small populations of only a few individuals lack the necessary genetic variation for persistence (Caughley, 1994).

We suspect acute heat stress acts directly on populations in this region by exposing individuals to thermal maxima that exceed physiological tolerances. Fitness consequences of temperature exceedances are well documented in plant physiology, for example, in determining how photosynthetic processes respond to exceedances of optimum temperatures and humidity (Varhammar et al., 2015). These exceedance predictors are also used to understand transmission and survival rates of infectious diseases (Rohr et al., 2011; Woods et al., 2005). However, there are few studies that examine the importance of such exceedances, particularly climatic ones, on free-roaming terrestrial vertebrates. American pikas have been shown to die quickly under experimentally high temperatures (~two hours above 28°C) when restricted from behaviorally thermoregulating (i.e., retreating into the talus interstices) (MacArthur & Wang, 1973). Although we hypothesized long-term heat stress would best predict occupancy, acute heat stress performed better suggesting short-term stressful conditions can culminate and lead to extirpation. While our study was not the first to assess climatic exceedance predictors for *O. princeps (*e.g. Beever et al., 2010), we found much stronger support for the acute heat stress mechanism than previous studies.

The presence of AET and soil moisture in the top models, both vegetation-proxy variables, imply that climate may also act indirectly on *O. princeps* by reducing the total amount of aboveground biomass and vegetation quality, given that both variables were positively associated with occupancy. Despite the predictive abilities of these two variables, our field measurements of vegetation cover and type performed poorly, garnering 0% of the overall average variable weights (Appendix A: Table 6). Large-scale climate indices may therefore highlight mechanisms affecting distributions when local-scale vegetation measurements are unavailable or of poor quality. Forage quality and composition have been documented as important for pika persistence and abundance elsewhere 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). Our results differ from some of these previous studies in that *in situ* vegetation metrics consistently performed poorly; possible explanations include: 1) there simply may not be a shortage of forage availability in our ecoregion, 2) differences among vegetation sampling protocol among studies may be influential, although unlikely to this extent, or 3) other ecoregional differences in limiting factors. Nevertheless, these results highlight the importance of investigating how factors determining occupancy vary throughout a species' range, depending on scale, ecoregion, and sampling period.

Though our study was the first to formally evaluate the effects of decadal climate variability on occupancy in this species, we found substantially stronger support for seasonal mean predictors. We hypothesize we did not see a stronger influence of climate variability on occupancy, in part, due to the relative annual stability of these inland mountain ranges when compared to more-coastal regions that are exposed to oceanic anomalies, such as El Niño and La Niña. Unpredictable conditions in these coastal regions have been shown to have strong effects on the species over short time scales (Johnston et al., 2019). Additionally, the timespan over which our variability coefficient was quantified may partially explain the lack of support (i.e. too long or short of a timespan), as may the interpolated nature of the climate data. This result is still perplexing, as climatic variability has been documented to act more strongly on population dynamics than climatic means in various studies for both short and long-lived species (Campbell et al., 2012; Drake, 2005). However, this remains a research frontier that deserves further attention for understanding the drivers of species range limits.

Mechanisms Influencing Relative Abundance

Relative abundance was most strongly affected by chronic cold stress, acute cold stress, and acute heat stress in the top two models, suggesting that abundance is highly sensitive to recent seasonal temperatures. Although acute cold stress appeared in the second-best model, our analysis using average variable weights per model indicated that chronic cold stress had the highest relative importance in this region, followed by the acute heat stress and summer VPD_{min} (Table 2). While acute heat stress has been tested as a potential mechanism for abundance in previous studies (Beever et al., 2010; Millar et al., 2016; Wilkening et al., 2011), this is the first documentation of this mechanism being one of the most important determinants of relative abundances.

These results suggest climate is acting both directly and indirectly on *O. princeps* via exceeding the species thermal physiological limits in different seasons. These mechanisms may act on individuals by altering foraging behavior, physiology, and fecundity. For example, increases in diel maximum temperatures have been shown to restrict available foraging times outside the talus and can also alter forage preferences (Hall & Chalfoun, 2018), which may in turn decrease haypile size for winter sustenance. However, behavioral plasticity related to foraging, such as shifting foraging times, has been documented among a diversity of species globally and may be one possible *in-situ* adaptation to buffer individuals against weather and climate extremes (Beever et al., 2017). Likewise, high temperatures, even over short periods of time or separated by days of cooler temperatures, affect a plethora of taxa across biomes in numerous ways and often in a non-linear fashion or via indirect pathways (Ockendon et al. 2014; Cahill et al., 2013; Marbà et al., 2015; Cziesielski et al., 2019). For example, thermal stress can directly affect growth rates, activity patterns, body size, and total body fat in species (Kammerer & Heppell, 2013; Falcon et al., 2018; Paniw et al., 2019).

Heat and cold stress has been shown to, indirectly, alter parenting behaviors of birds that results in chicks being left alone and susceptible to fatal attacks by neighboring birds (Oswald et al., 2008). Another important indirect response can be suppressed immune system functioning, which allows infectious diseases to more readily enter and infect vectors and hosts (Lafferty, 2009). Further investigations into thermal stress in *O. princeps* are warranted and should explicitly test the mechanisms by which this thermal stress affects the species under controlled conditions. Additionally, further studies should test whether short-term, high temperature stressors act only on single generations, or if it has legacy effects on fertility, sex ratios, and lifespan (H. Chen et al., 2018), or possibly leave epigenetic signatures on future generations (Weyrich et al., 2016).

Our findings also suggest that one-year lagged climatic conditions are much stronger in predicting abundances than two-year lagged conditions (i.e., in 86% of the paired models). This finding matched our *a priori* suspicions, given the short generational times (2-2.5 yrs), small body mass, and high annual fecundity of this species, which under ideal conditions can allow two litters in a given summer, therefore allowing the species to quickly responding to current conditions (Smith & Weston, 1990). The importance of single-year lags has also been shown to be important for abundance in this species in another study (Johnston et al., 2019). Time-lag effects are an often-overlooked, albeit challenging-to-quantify, phenomenon in ecology. Lag effects can be strongly dictated by vegetation structure and composition, hydrology, fat storage in larger animals, and other biotic and abiotic conditions, which in turn can affect species' presence, abundance, and behavior across multiple time steps (Wu et al., 2015; Davies et al., 2013). In addition, reductions in species abundance may not immediately result in loss of occupancy, but a continuation of deteriorated conditions can amalgamate leading to delayed extirpation, long after conditions became unfavorable (i.e., local extinction debt). Managers are frequently tasked with identifying the species and populations at greatest risk of extinction; however, identifying such populations remains difficult when species-environment relationships are masked by time-lagged effects. Understanding and testing multiple temporal scales will be crucial in narrowing the overall uncertainty in models measuring the effects of weather and climate on species globally.

Overlap in Drivers of Occupancy and Abundance

Overall, we found occupancy was most strongly influenced by metrics of heat stress, indirect measures of vegetation quality, as well as habitat availability in the top model. This was further corroborated by analysis of average variable weights per model, wherein the same predictors were the best supported. Although acute heat stress also appeared as top predictor for abundance, the next-best-ranked variables were quite different (Fig. 4). Caution is necessary when directly comparing the drivers of occupancy and abundance because they operate on different spatial and temporal scales (Orrock et al., 2000; Dibner et al., 2017). Developing robust models in the face of global change requires substantial amounts of data, and extrapolations are often necessary to predict responses in data-deficient locations (Elith & Leathwick, 2009). Results from occupancy models, typically using only presence-absence data, have been used to draw conclusions about abundance patterns on landscapes (e.g. Tempel & Gutiérrez, 2013). However, caution in how this data is interpreted is necessary due to the different scales that each of these responses is measured at, and the fact that factors driving one response may have little to no effect on the other (Fig. 4). Studies have found that, indeed, the environmental drivers of these two responses often differ substantially in their coefficient effect size and direction (e.g. Dibner et al., 2017).

We found the standardized effect sizes for occupancy were much larger than those for abundance (Fig. 5), and the order of best predictors, using univariate models only, differed considerably between occupancy and abundance. Coefficient signs, overarchingly, were consistent between the two responses, with the exceptions of snow water equivalent, actual evapotranspiration, and summer VPD_{min}, again only using univariate models. Future studies should continue assessing discrepancies between climate variable effect sizes and directions for both occupancy and abundance together, as results can be informative to managers in identifying important habitat requirements that influence species directly and indirectly.

Range Retraction and Climatic Drivers

Relationships between species and environmental conditions at range edges have long been of interest to ecologists (Merriam, 1894). Under contemporary climate change, species are tracking their environmental niche in response to changing climatic conditions (Davis & Shaw, 2001; Tingley et al., 2009). However, few studies examine this spatial tracking at species' range cores, leaving many questions unaddressed. Montane species represent ideal study organisms for such questions, as both elevational and latitudinal range cores can typically easily be identified. Recent analyses have suggested that the relationship between mean temperature and species elevational limits is much weaker in temperate regions as compared to the tropics (Freeman & Class Freeman, 2014). Notably, our findings corroborate other studies that temperate montane species are still responding quite strongly to increases in temperatures (and precipitation) when shifting their distributions upwards (Tingley et al., 2009; Wilson et al., 2005; Battisti et al., 2006). As mean seasonal temperatures continue to increase, species are expected to continue expanding and shifting distributions upwards, usually reducing their overall spatial domain and consequently, carrying capacities (White et al., 2018). Mountain-top extirpations have been widely documented, as species in these highlands often experience what is known as the “escalator-to-extinction” effect (Marris, 2007; Pauli et al., 2012; Colwell et al., 2008; Freeman et al., 2018). Simultaneously, montane species in highest-elevation life zones can be limited in their dispersal capacities as they often occupy patchily-distributed habitats that may be far apart and cannot disperse between mountain islands that are isolated by warmer lowlands (Rehnus et al., 2018). Conversely, populations living near their warm edges (i.e. southern distribution and lower elevational limits) are particularly vulnerable to thermal stress, in part due to evolutionary constraints to dissipating heat. However, a multitude of stressors in addition to high temperatures can dictate warm-edge distributional limits and shifts (Sexton et al., 2009), and thus, using competing hypothesis frameworks is fundamental for investigating all potential drivers.

Mean elevation of occupancy has shifted upslope by 100 meters, whereas the mean minimum elevation of occupancy shifted up 199 meters, for pikas in this region. Based on our sampling strategy and the lack of historical surveys, however, we cannot make any inferences about upper elevational limits, as pikas currently occupy the highest elevation in 54 of the 64 watersheds. The ten watersheds with unoccupied patches at the highest elevations may experience winter conditions that are too severe for pikas to persist consistently. In addition, we observed less-developed talus slopes that are too shallow to buffer pikas from the wind at these sites. It is possible that these high-elevation sites were previously unoccupied and have experienced only recent colonization (and then extirpation), but that evidence is indiscernible. Each of these highest-elevation patches had abundant evidence of previous occupancy, suggesting they may represent sink populations until the climate becomes more favorable.

Using our novel approach for quantifying the relationship between the extent of retraction and climate across replicated units (i.e. watersheds), we found that chronic heat stress as well as chronic cold stress were positively associated with retraction (Table 2), suggesting warmer winter temperatures and warmer summer temperatures are important at shaping range edges in the Northern Rocky Mountains. However, the mechanism of chronic cold stress remains somewhat unclear given this region's relatively stable and insulative winter snowpacks which buffer pikas from extreme cold within the talus. Nevertheless, winter temperatures appear important in this region. This result contrasts the results of our occupancy and retraction residual analyses, where winter metrics consistently performed poorly when grouped by season. Similar to other studies (e.g. Rubidge et al. 2012), we found temperature alone was the strongest driver of upslope shifts via compound pathways spanning winter and summer. Our results suggest chronic heat and cold stress influence the extent of retraction rather than mean annual temperatures. Our results underscore the importance of examining alternative processes and stressors that may act directly or indirectly at range edges by altering competition, habitat structure, and biotic interactions, although none of which appeared important in our analysis or were not assessed (e.g. interspecific competition has not been documented in this species, as few species occupy talus slopes). These results motivate new efforts to connect species-relevant climatic drivers to elevational range shifts.

Resurveys conducted in southern California in and around Yosemite National Park (Rubidge et al., 2011) found that although single and multi-species climate-only models predicted distributions well in some periods for three *Tamias* species, their models struggled to predict distributions across eras in a few cases, exemplifying how mechanisms may shift through time. The authors hypothesized that interspecific competition may become a limiting factor when climate changes the distributions of closely-related species. Another study illustrating this concept examined the same focal species as our study, *O. princeps*. Beever et al. (2011) found that although August maximum temperatures were the strongest predictor for pika persistence in the Great Basin in the recent period surveys (1990s-2000s), maximum elevation of habitat nearby that individuals could disperse to was the strongest predictor in the historical period (20th century). These works and our own demonstrate the intricate nature of species-climate interactions that underlie upslope retractions, and illustrate that these current mechanisms identified may shift through time and space (Beever et al., 2011). Furthermore, it remains a research frontier determining whether contemporary climate change, with its continuing upslope movement of thermoclines, will alter the harshness of microclimatic suitability on mountain summits that are typically characterized by high winds and thus, soon create desiccating conditions. This may present challenges for species migrating to high peaks where conditions are no longer favorable and outside the atmospheric boundary layer that montane valleys and canyons create, leaving them susceptible to the most severe environmental conditions.

Relationship Between the Residuals of Retraction and Climate

Although resurvey efforts are one of the strongest examples of distributional shifts and abundance changes to date (e.g. Moritz et al., 2008; Freeman et al., 2018; Iknayan & Beissinger, 2018), they frequently are not replicated across comparable units such as watersheds, mountain ranges, or continents, for numerous reasons. Without replication, results of species responses can be under- or over-estimated when applied to the broader landscape. To assess this concern, we created a novel response variable that standardized our 64 watersheds and accounted for the difference in minimum elevation in each watershed, while standardizing the amount of vertical retraction (Fig. 3). We sought to identify the factors that cause some watersheds to retract more or less than expected given the minimum elevation in each watershed. Although we identified the additive effects of acute heat stress and summer precipitation in a single top model, the relationship was considerably weak (Table 1). Nevertheless, this method of standardizing comparable units that differ in elevational span should prove useful as a tool to model and estimate retraction rates across watersheds and mountain ranges when elevational spans differ among units.

Differences Among Climate Variable Classes

Different climatic predictors have been suggested to act independently across response types within single species (e.g. Van de Ven et al., 2019). For example, results from an occupancy analysis that suggest temperature is the strongest predictor should not be assumed to hold true to another response type, such as abundance or growth rates. Our analysis used the average variable weight by climate class found varying ranks of climatic predictors, with temperature dominating all responses classes except retraction residuals (Fig. 4). Studies have shown that important climate variables can exhibit opposing directions that may differ among responses. For instance, Dibner et al. (2017) found that although annual mean precipitation was positively associated with population abundance in greater short-horned lizards (*Phrynosoma hernandesi*), it was negatively associated with site occupancy. These results illustrate the complexities in modeling the intricate relationships between species and their environments, and encourage the use of multiple response types when assessing species vulnerability to future climate change as we have done here.

Seasonal Differences Among Mechanism Strength

As predicted for this ecoregion, we found that the summer conditions were more strongly supported in our model suites than winter conditions (Table 3). For all responses but abundance, summer metrics collectively outcompeted winter ones. This result can be interpreted as suggesting this species is more physiologically stressed during summer months as opposed to winter months and was anticipated due to the relatively high and stable, buffering snowpack in winter in this part of the Rocky Mountains. However, over the 20th and 21st centuries, this region has experienced significantly declining snow packs across all months (Mote et al., 2018), which may expose subnivean plants and animals alike to the ambient winter conditions in the near future, especially at lower elevations. This trend of decreasing snowpack is apparent throughout the entire western United States (Mote et al., 2018) and foreshadows the risks to montane species in what are considered to be geographic refugia (Beever et al., 2011; Johnston et al., 2019).

Other species that rely on seasonal snowpacks to buffer against extreme diel fluctuations have also been documented to be more sensitive to summer conditions than winter ones (Campbell et al., 2012). Subnivean, alpine, and arctic species are typically specialized for surviving cold environments for significant portions of the year, so genetic adaptation to warmer conditions may now be lacking, as these adaptations were not needed historically (Theodoridis et al., 2018). However, winter conditions can become detrimental when species are exposed to cold stress in the absences of these insulative snowpacks (e.g. Armitage, 2013). Understanding seasonal limitations on populations can indicate which demographic processes may be most sensitive to further environmental change, which can in turn predict the future stability or extinction risk of populations (Paniw et al., 2019). Therefore, further demographic analyses using seasonal extents will be necessary to more comprehensively understand the links between species and contemporary climate change.

Conclusions

Here, we show evidence of widespread upslope retractions at the lower elevational limits of pikas that have occurred across this ecoregion in recent decades (72% of watersheds), which implies this species' geographic center is not as resilient to climate change as one would expect from classic ecological theory (e.g., the Abundant Centre Hypothesis, Sagarin & Gaines, 2002). In this region, temperatures are projected to increase into the future, spanning increases in minimum, mean, and maximum daily temperatures, and especially in summer months (Whitlock et al. 2017). This warming is likely to amplify the probability of further extirpations and extinctions. Given the prevalence of distributional shifts and population declines in response to anthropogenic climate change globally, mechanistic-based analyses are needed to identify and test the spatial and temporal scales at which species may be responding. Long-term demographic studies and physiological monitoring have the potential to continue disentangling these complex ecological relationships and will compliment studies identifying range shifts for determining where and which species will require additional conservation efforts in the face of future changes in climatic conditions.

Table 1. Top-ranked models with substantial support (ΔAIC < 2) for abundance, occupancy, upslope retraction, and the residuals of retraction, with mountain range as the random effect. Summer predictors were present in the top models for all four responses. For the occupancy results, the number of home ranges available (i.e. patch size) appeared in all top models, along with acute heat stress, indicating that greater patch size was important for persistence.

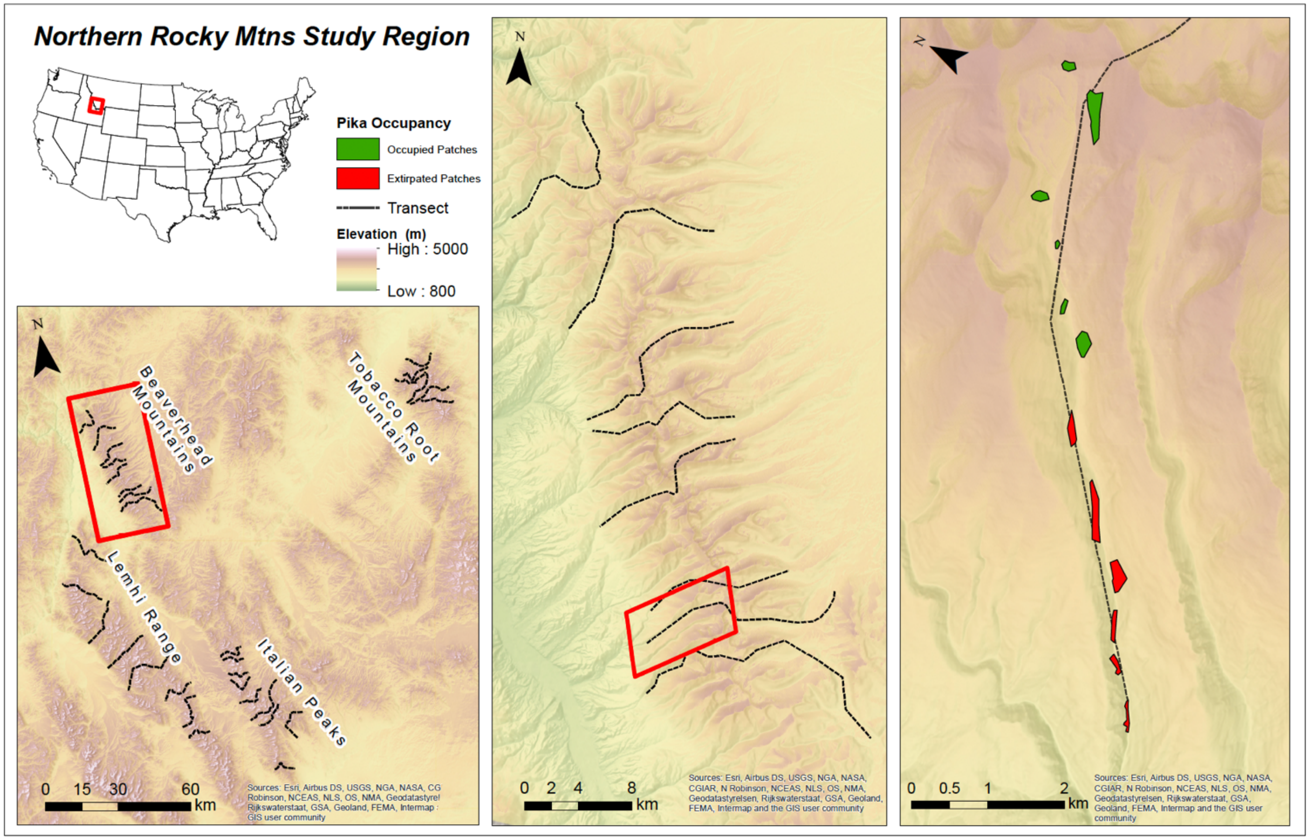
Top-Performing Models by Response	**K**	**AIC**	**ΔAIC**	**Model Likelihood**	**AIC w_i**	**Cumulative Weight**	**Log Likelihood**	**Residual Log Likelihood**	**R^2_c**	**R^2_m**
A) Occupancy										
Acute Heat Stress + Home Ranges + AET	5	774.23	0	1	0.160	0.160	-382.117	-	-	-
Acute Heat Stress + Home 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 x AET	6	775.19	0.96	0.099	0.099	0.534	-381.595	-	-	-
Acute Heat Stress + Home Ranges x AET	6	775.36	1.13	0.091	0.091	0.625	-381.682	-	-	-
Acute Heat Stress x 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	808.44	0	1	0.751	0.751	-	-397.722	0.434	0.434
Null	3	853.71	48.27	<0.001	0	1	-	-423.855	0	0
D) Retraction Residuals										
Acute Heat Stress x Summer Precipitation	6	947.31	0	1	0.351	0.351	-	-467.656	0.018	0.018
Heat Run x Summer Precipitation	6	947.67	0.36	0.837	0.294	0.645	-	-467.834	0.012	0.012
Chronic Heat Stress x Summer Precipitation	6	947.81	0.50	0.779	0.273	0.918	-	-467.907	0.012	0.012
Null	3	973.45	26.14	<0.001	0	1	-	-483.724	0	0

Table 2. Ranks of the average variable weight per model for the top five variables for each the abundance, occupancy, upslope retraction, and retraction residuals. The variable weight w_i per model was calculated by summing the model weights for models containing a particular variable by the number of models containing the variable. A full table for all predictor variables can be found in the Supplementary Material (Appendix A: Table 6).

Variable	**Cumulative Weight**	**Num. of Models In**	**Variable Weight per Model, w_j**	**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 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	0.759	2	0.380	+
Chronic Heat Stress	0.953	6	0.159	+
Summer Precipitation	0.196	7	0.028	6+, 1- (mixed)
Soil Water	0.037	3	0.012	1+, 2- (mixed)
Snow Water Equivalent	0.006	3	0.002	-
Retraction Residuals				
Summer PPT	0.931	7	0.133	+
Heat Runs	0.298	3	0.099	-
Acute Heat Stress	0.361	4	0.090	-
Chronic Heat Stress	0.328	6	0.055	5+, 1-
Chronic Cold Stress	0.047	2	0.023	+

Table 3. Model-averaged weights by season 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. Summer variables outperformed winter variables for three of the four responses, with abundance as the only response where winter was more important.

Response Type	**Season**	**Summed Weight**	**Model Averaged Weights, w_j**
Abundance	Summer	0.4137	0.0259
	Winter	0.5863	0.0838
Occupancy	Summer	1.0000	0.0625
	Winter	0.0000	0.0000
Retraction	Summer	0.9551	0.0531
	Winter	0.0449	0.0090
Retraction Residuals	Summer	0.9890	0.0550
	Winter	0.0110	0.0021



Sources: Esri, Airbus DS, USGS, NGA, NASA, CG Robinson, NCEAS, NLS, OS, NMA, Geodatastyrel Rijkswaterstaat, GSA, Geoland, FEMA, Intermap : GIS user community

Sources: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community

Sources: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community

Figure 1. Study region within the Northern Rocky Mountains of North America, illustrating the hierarchically nested design of our study. The left panel shows the four mountain ranges that we surveyed. These mountains generally span a gradient of relatively warm and dry in the west to colder and wetter in the east. Each line represents a cross-sectional transect connecting two watersheds, one on the east and one on the west. The center panel depicts a finer-scale map of a single mountain range, to better depict the transect layout among watersheds. Lastly, the right panel is an example of a single watershed that was surveyed in the Beaverhead Mountains, with each patch outlined with a polygon, and filled with the occupancy status colored accordingly.

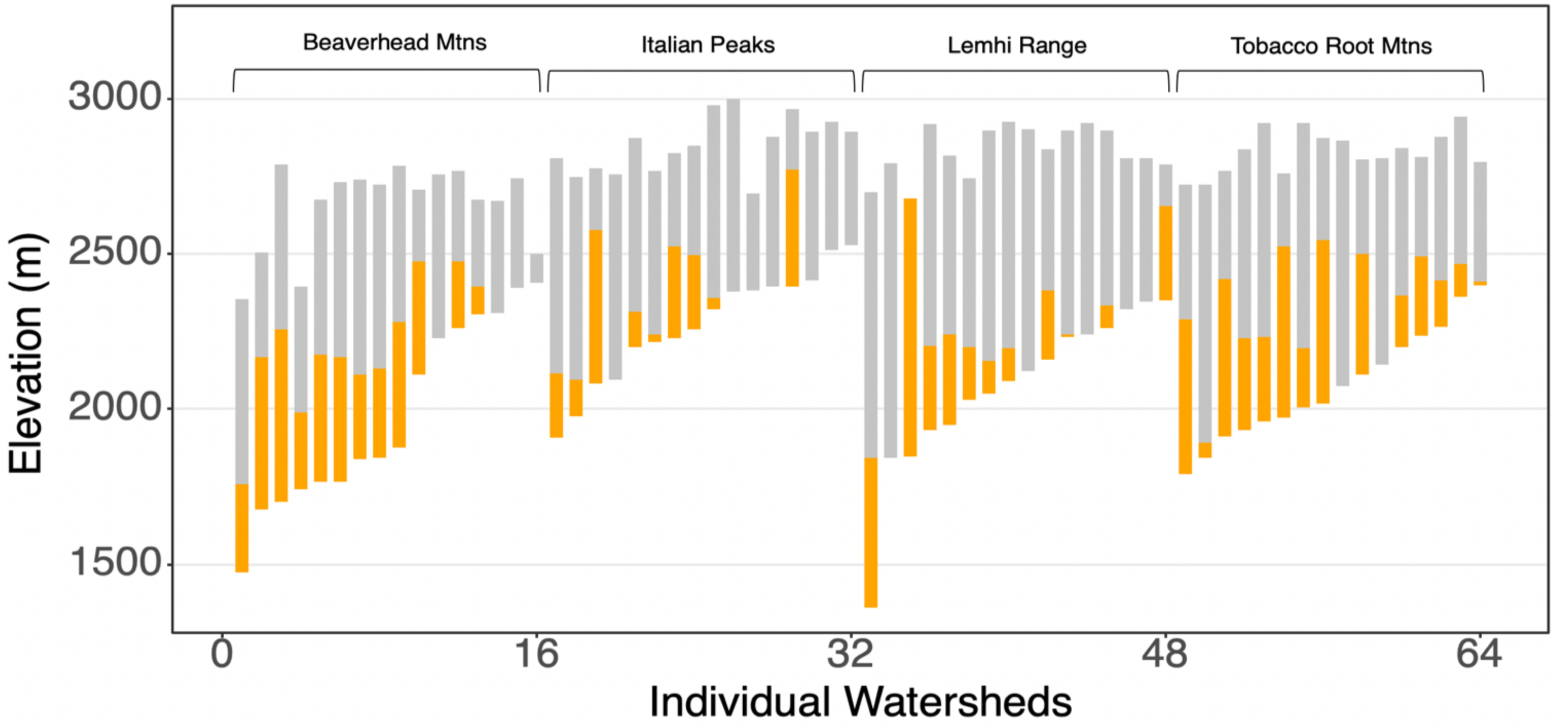


Figure 2. Elevational retractions by watershed and mountain range (four groupings) of American pikas (*O. princeps*) across the northern Rocky Mountains, North America. Shifts were documented at the lower elevational limits based on current site occupancy versus historical evidences at sites. Gray bars represent the elevational bands where pikas are currently occur within each watershed, whereas orange represents the elevational bands where pikas historically occupied (based off of detection of only old fecal pellets, old hay piles, and urine stains). However, this figure does not include orange bars at the upper elevational limits of ten watersheds that did not have pikas occupying the highest patches. We acknowledge that lower elevational extirpated sites may be recolonized for shorter or longer periods in the future. Overall, the mean lower elevational edge moved upslope 206 m across all watersheds. One watershed was entirely extirpated of pikas, except one individual at the top patch which we consider functionally extirpated.

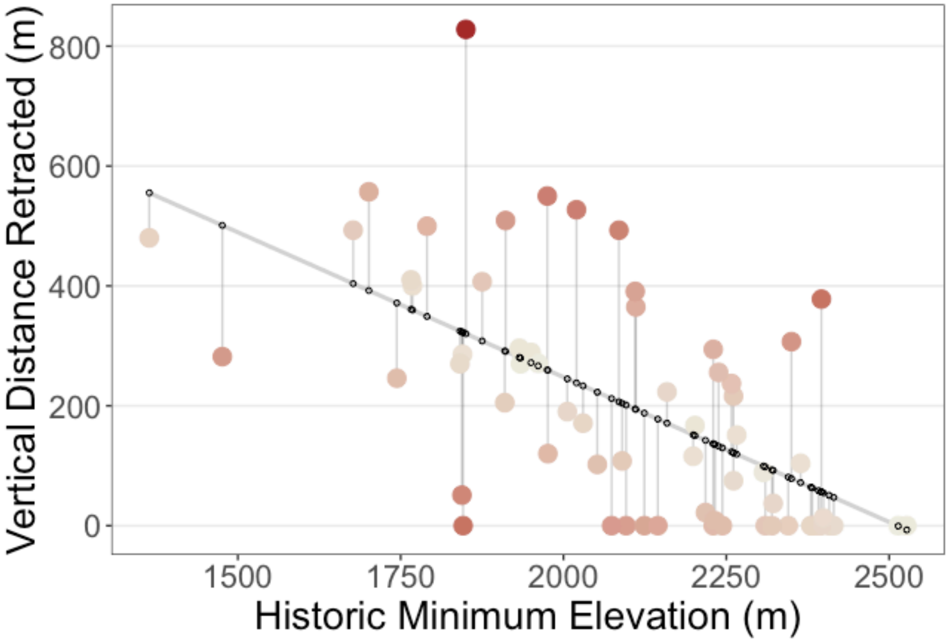


Figure 3. Plotted residuals of upslope retraction by watershed. We used the residuals of the amount of elevation retracted (in m) on the y-axis, regressed against the historic minimum elevation on the y-axis (i.e., bottom of orange or gray bar, whichever is lowest, in Figure 2). The residual represents the difference between the amount of elevation in which pika distribution retracted in each watershed and the amount that would be expected based on the historic minimum elevation of distribution in a given watershed. Saturation of residuals increase as residuals become further from the predicted regression line. Note, the residual farthest above the line is the watershed where pikas were completely extirpated in the Lemhi Range, Idaho.

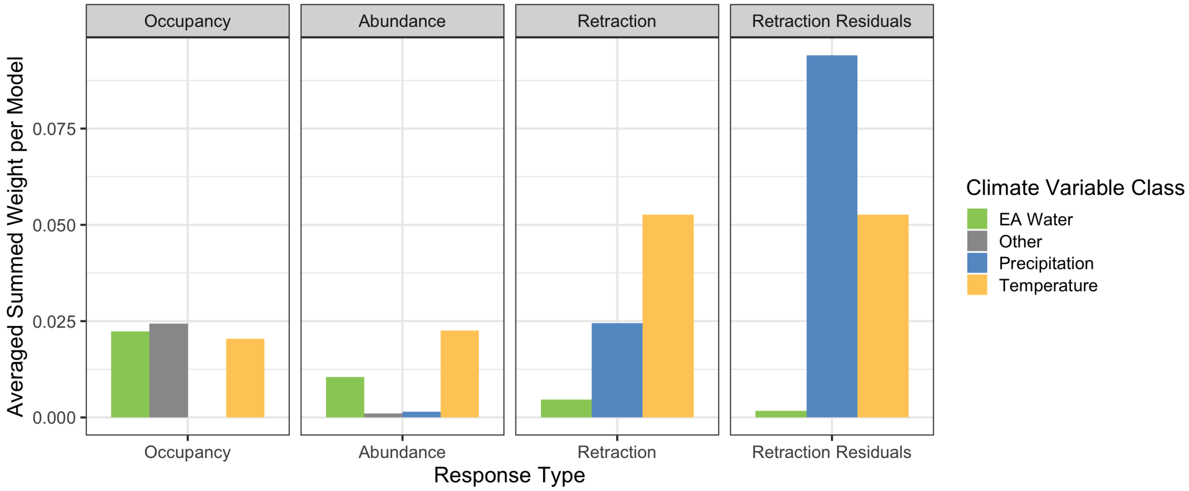


Figure 4. Average summed weight per model per climate classes, ordered on the x-axis by response type. The importance of the climate classes varies greatly among response types, suggesting results from one response type should not be interpolated to other response types. For example, although temperature metrics were the best predictors for the amount of upslope retraction in any given watershed, the residuals of retraction are best explained by precipitation metrics, suggesting that both are important for determining the amount of retraction and whether the watershed retracts more or less than expected. **EA Water** = measurements of ecologically-available water (AET, water deficit, soil moisture, and vapor pressure deficit). **Other** = non-climatic metrics (Abundance = grazing status near the patch, insolation, moss coverage, slope, grasses, and forbs; Occupancy = habitat availability, grazing status near the patch, insolation, lichen cover, moss cover, slope, grasses, and forbs)

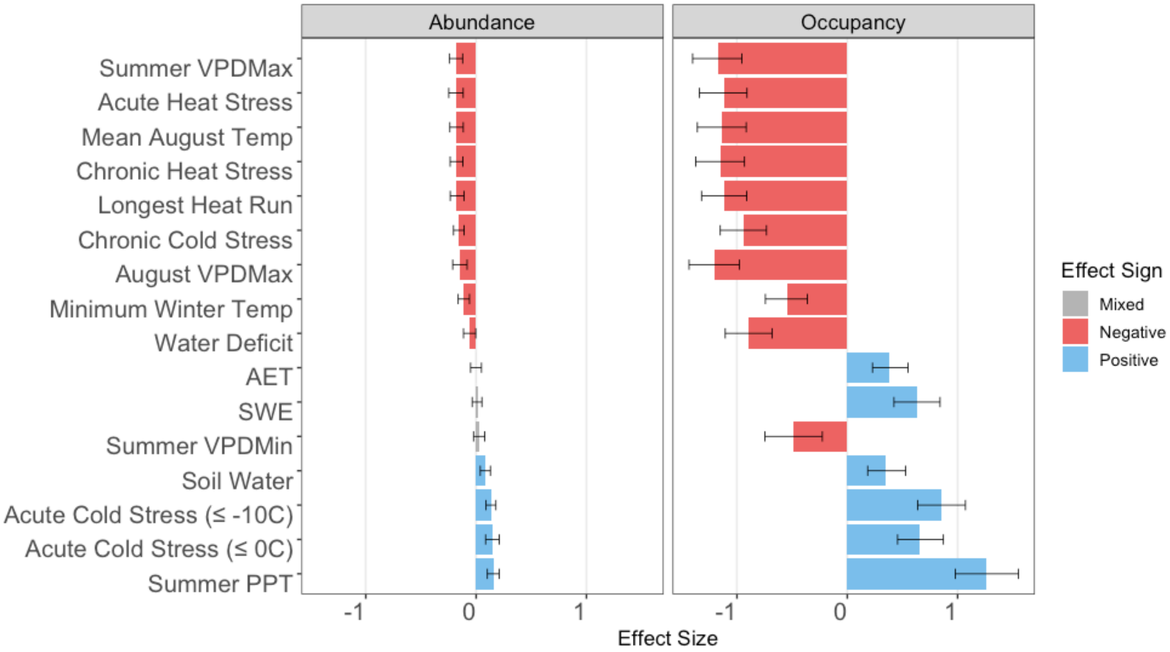


Figure 5. Standardized effect sizes for all univariate models of climatic predictors for the abundance and occupancy analyses. The signs of the predictors' coefficients were strongly aligned between the two analyses, with the exceptions of actual evapotranspiration (AET), snow water equivalent (SWE), and the summer VPD_{min}.

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APPENDIX A

ENVIRONMENTAL VARIABLES, FULL MODEL SUITES, AND FIGURES

Table 1. 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	Definition
Chronic heat	°C	Mean daily maximum temperatures for July–August (Beever et al. 2011, 2016, Stewart et al. 2015)
Acute heat	Days	Number of days with temperature ≥26°C (Beever et al. 2011, 2016, Stewart et al. 2015)
Heat run	Days	Largest number of consecutive days where temperatures were ≥ 20°C
Chronic cold	°C	mean daily minimum temperature for November–February (Beever et al. 2011, Johnston et al. 2019)
Acute cold	Days	Number of days with temperature ≤ -10°C or ≤ 0°C for September–August (Beever et al. 2011) (Johnston et al. 2019)
Winter T_{min}	°C	Mean of daily minimum temperature from Nov 1 -March 31
Summer Precipitation	mm	Sum of daily precipitation for July–September (Beever et al. 2013)
SWE	mm	Snow water equivalent mean from November 1-March 31
Actual Evapotranspiration (AET)	mm	Total daily actual evapotranspiration during late summer (Jul 01 – Aug 31)
Moisture Deficit	mm	Total daily moisture deficit during late summer (Jul 01 – Aug 31)
Soil Water	mm	Mean daily soil water storage during late summer (Jul 01 – Aug 31)
Vapor Pressure Deficit Max	kPa	Mean daily maximum VPD for June–September, or November–February (Beever et al. 2016, Millar et al. 2018, Johnston et al. 2019)
Vapor Pressure Deficit Min	kPa	Mean daily minimum VPD for June–September, or November–February (Beever et al. 2016, Millar et al. 2018, Johnston et al. 2019)
Insolation	W/m^2	Mean amount of sunlight/power hitting the patch over a year (Millar et al. 2016)
Habitat Availability	m^2	Number of total home ranges (25m diameter circles) within patch
Grasses	%	Average % of graminoid species within 15m of pika evidence, summed over pika evidences in patch
Forbs	%	Average % of forb species within 15m of pika evidence, summed over pika evidences in patch
Grass:Forb ratio		Ratio of graminoid cover to forb cover
Slope	%	Slope using a clinometer and averaged across all evidences within a patch.
Moss	%	Mean moss cover, by surface area, on talus over the patch
Lichen	%	Mean lichen cover, by surface area, on talus in the patch

Table 2: 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 = home ranges, AET = actual evapotranspiration, and SWE = snow water equivalent.

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
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
$\text{SummerVPD}_{\text{max}}$	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
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 3: Full model suite for the multiple linear regression analysis for abundance, only including the one-year lagged conditions, with mountain range as the random effect. AET = actual evapotranspiration, and SWE = snow water equivalent.

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
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 4: 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 5. 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 6. Ranks of the average variable weight per model for all variables for each the abundance, occupancy, upslope retraction, and retraction residuals. The variable weight w_j per model was calculated by summing the model weights for models containing a particular variable by the number of models containing the variable.

Variable	**Cumulative Weight**	**Num. of Models In**	**Overall Variable Weight per Model, w_j**
Occupancy			
# of days Above 26°C	0.752	11	0.068
Actual Evapotranspiration	0.355	6	0.059
Home Ranges	1.000	21	0.048
Heat Runs (20°C)	0.201	6	0.033
# 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} 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} 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 Tmin	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} Summer	0.142	3	0.047

VPD_{Max} Summer	0.027	1	0.027
Summer Mean Temp	0.246	19	0.013
Heat Runs (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 Tmin	0.001	3	0.000
Insolation	0.001	5	0.000
Snow Water Equivalent	0.001	9	0.000
August 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 Run (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 Tmin	0.000	1	0.000
# of days Below 0°C	0.000	1	0.000
VPD_{Min} Summer	0.000	1	0.000
August VPD_{Max}	0.000	1	0.000
VPD_{Max} 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 Run (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 Tmin	0.000	1	0.000
Moisture Deficit	0.000	1	0.000
Actual Evapotranspiration	0.000	1	0.000
VPD_{Max} Summer	0.000	1	0.000
August VPD_{Max}	0.000	1	0.000
VPD_{Min} Summer	0.000	1	0.000
August Mean Temp	0.000	1	0.000

Table 7. 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 (Abundance = grazing status near the patch, insolation, moss coverage, slope, grasses, and forbs; Occupancy = habitat availability, grazing status near the patch, insolation, lichen coverage, moss coverage, slope, grasses, and forbs)

Response Type	**Climate Class Metric**	**Average Variable Weight, w_j, 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

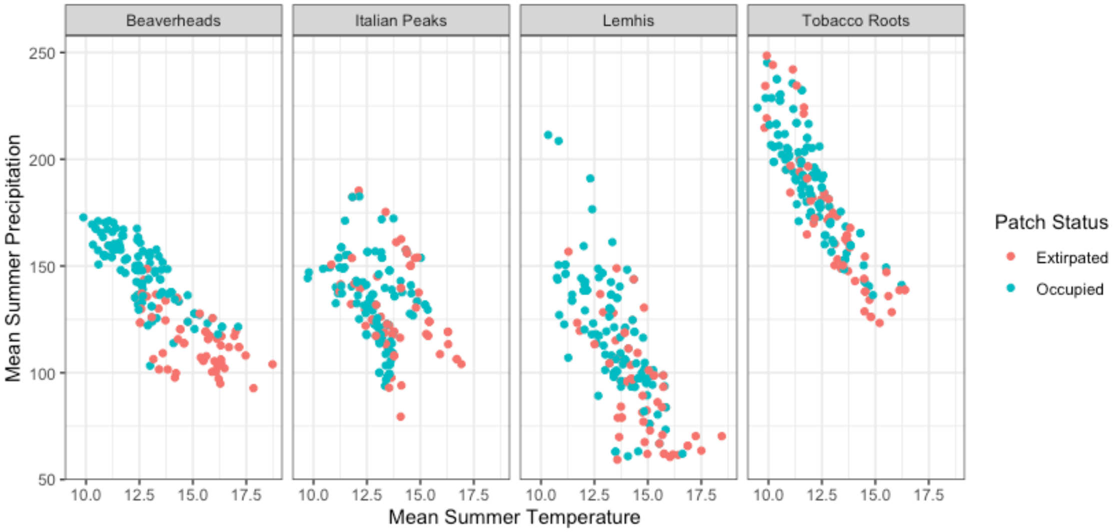

Figure 1. Scatterplot of the occupancy status of patches by mean summer temperature on the x-axis and summer precipitation on the y-axis.

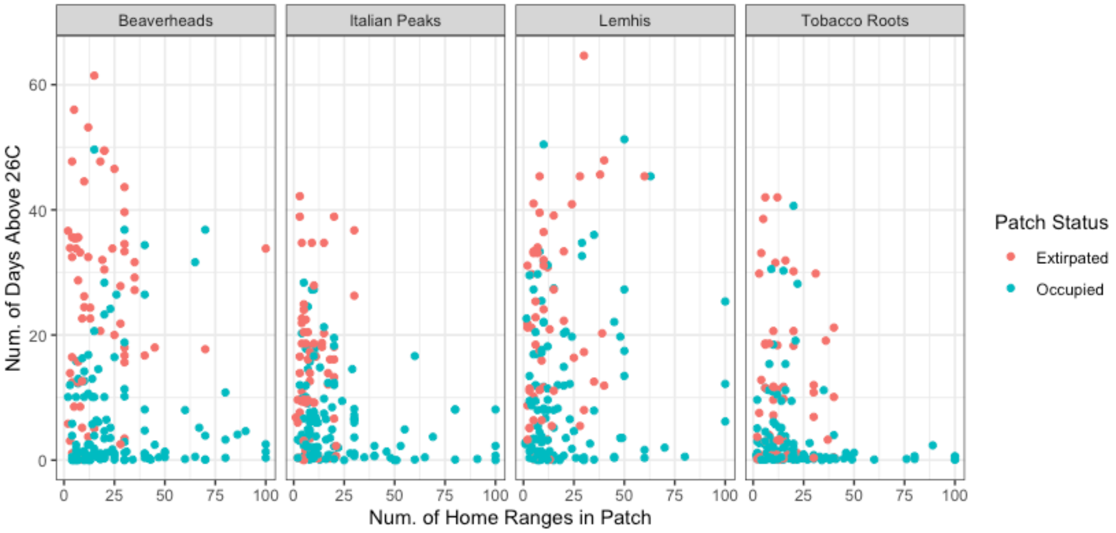

Figure 2. Scatterplot of the top model for occupancy including additive terms for habitat availability on the x-axis and acute heat stress on the y-axis, paneled by mountain range.

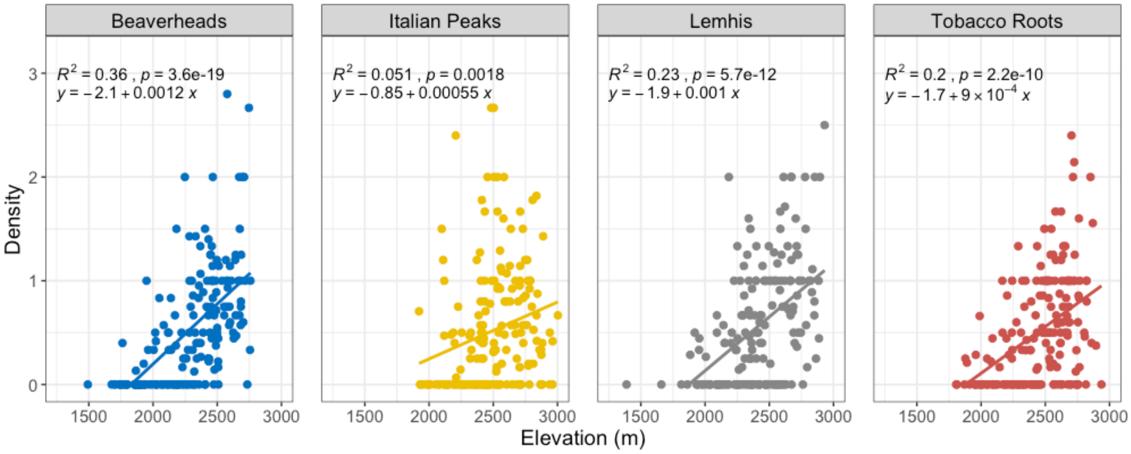

Figure 3. Scatterplot of abundance and elevation, by mountain range. Abundance appears to increase strongly with increasing elevations across all ranges in this ecoregion. However, the strength of this relationship varies, with the Italian Peaks showing the weakest relationship and the Beaverhead Mountains showing the strongest relationship.

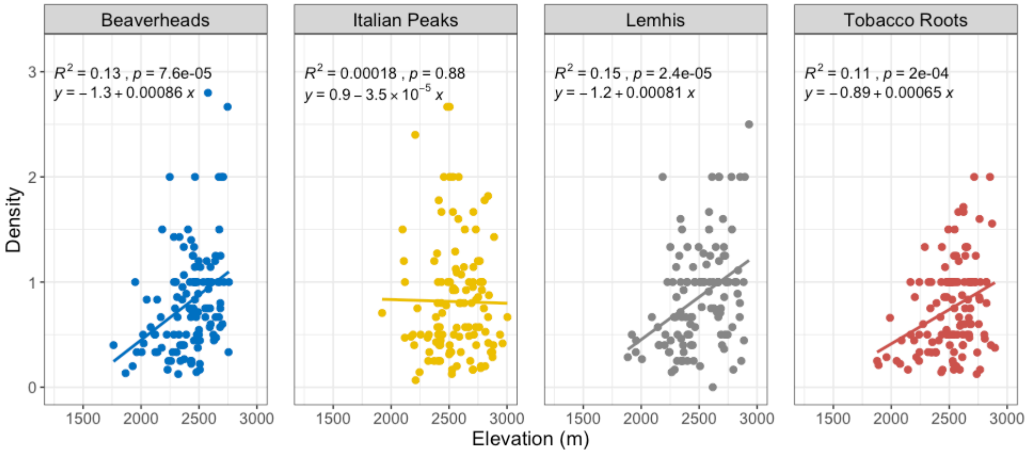

Figure 4. Scatterplot of abundance and elevation, by mountain range, after removing patches without any individuals. The strength of this relationship varies among mountain ranges, with the Italian Peaks showing no relationship, and the Lemhi Range now showing the strongest positive relationship.

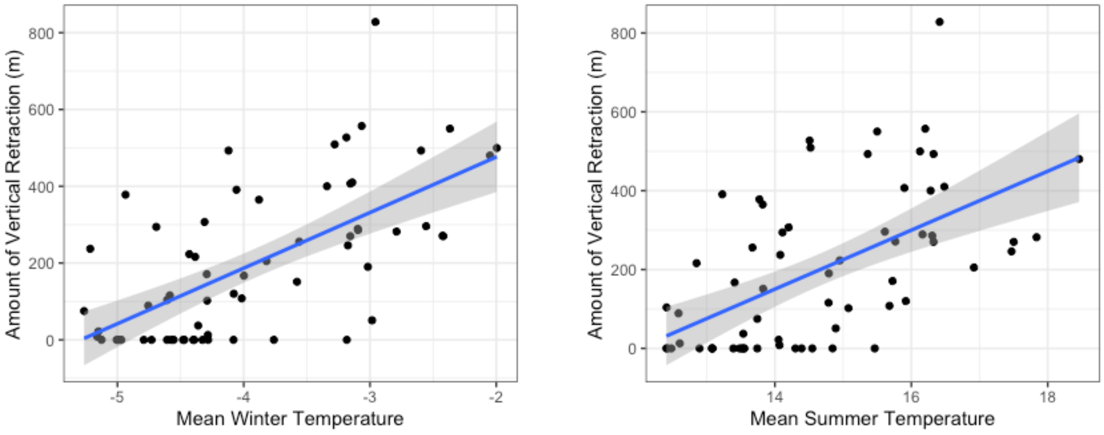

Figure 5. Scatterplots of the two variables, mean winter temperature (left) and mean summer temperature (right) in their univariate form and on their original scales. Both terms appeared in the top model predicting the total amount of vertical retraction in each watershed. The additive model had an overall good fit to the data ($r^2 = 0.434$).

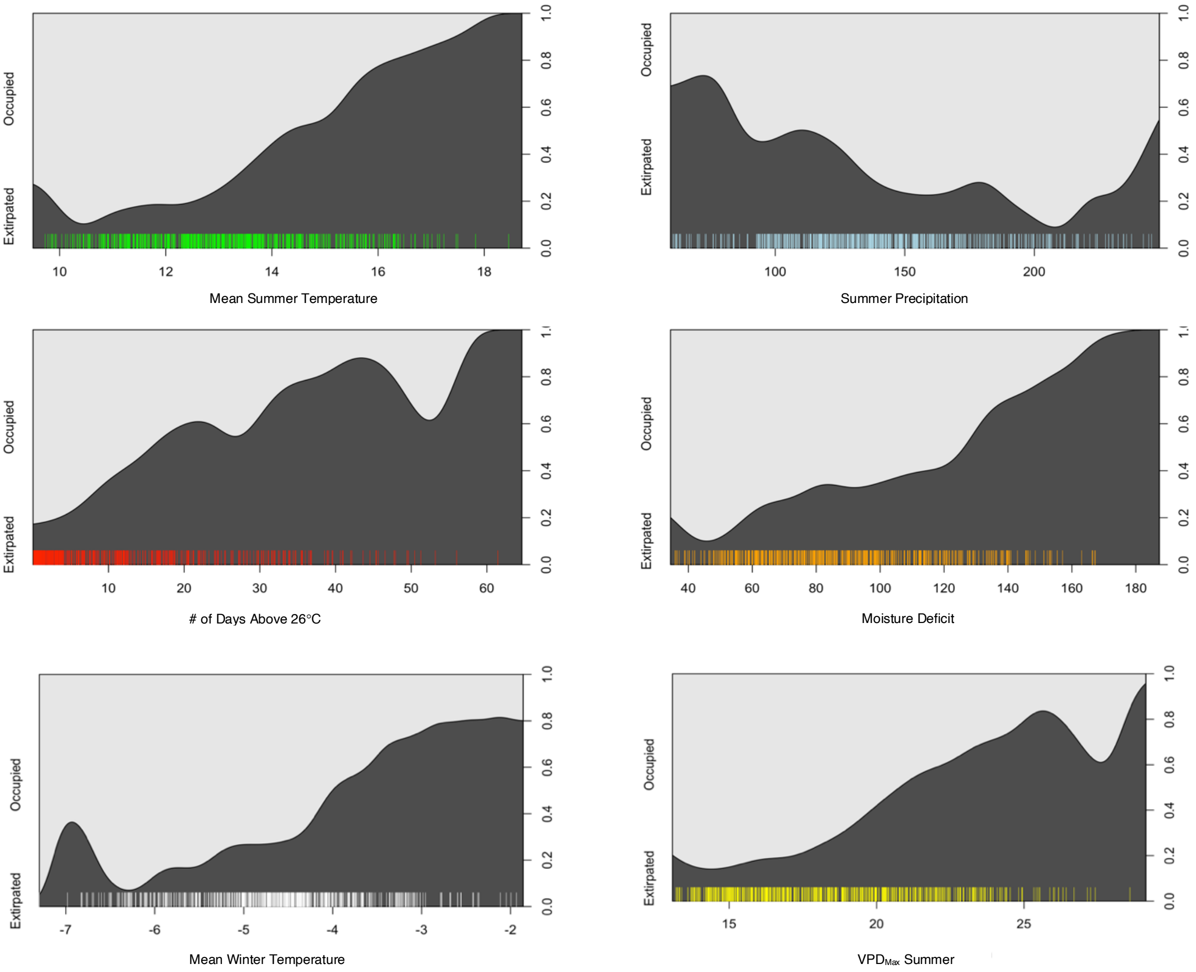

Figure 6. Conditional density plots of six prominent climate variables, predicting the likelihood of any patch given the predictor on its original scale. Tick marks on the bottom indicate individual patches.

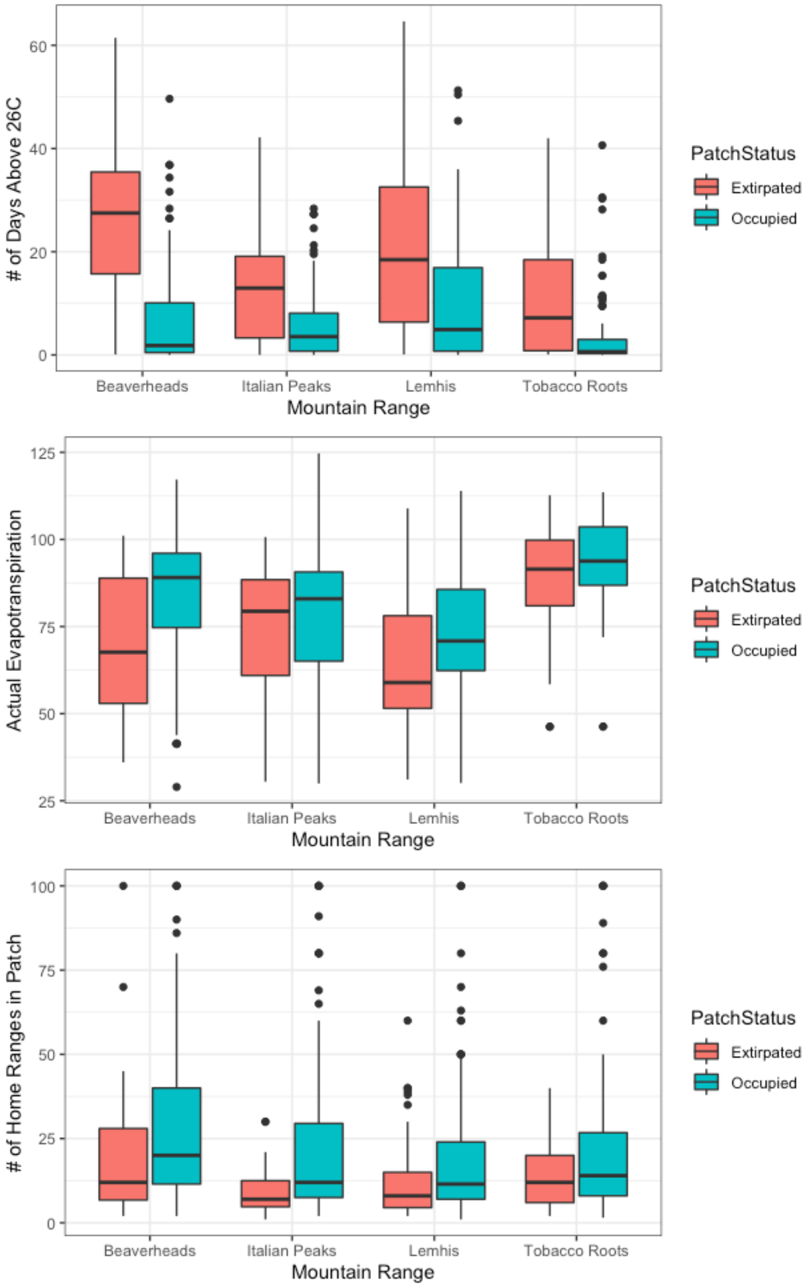

Figure 7. Boxplots of the top three variables for site occupancy in Table 2, by mountain range. First, acute heat stress represents a direct mechanism by which climate is acting on the species thermal physiological limits. Second, AET likely acts indirectly, as it is a proxy for vegetation quality and above ground biomass. Third, habitat availability shows a strong signal that smaller patches are have a higher probability of extirpation than larger patches across all four mountain ranges, hinting at an island size effect.