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Kailey R. Meacham
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INVESTIGATION OF THE HABITAT AND CLIMATE DRIVERS OF COLLARED PIKA
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A THESIS APPROVED FOR THE
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BY THE COMMITTEE CONSISTING OF

Dr. Hayley Lanier, Chair

Dr. Katharine Marske

Dr. Cameron Siler

ABSTRACT

As environmental conditions continue to change at a rapid rate, understanding habitat requirements and climate vulnerabilities is critical for species conservation. The collared pika (*Ochotona collaris*), an alpine specialist found in Alaska and northern Canada, faces potential threats from climate change, yet its habitat requirements and responses to environmental change remain poorly understood. In this study, we use existing spatial data, combined with observations from new survey efforts, to 1) identify regional variation in collared pika habitat preferences and climate response, and 2) assess the climate change vulnerability of collared pikas and predict changes in distribution linked to future climate scenarios. To identify habitat preferences, we used a model selection approach, comparing climate and habitat characteristics at known collared pika occurrences to those at surrounding areas. Our analysis indicated that collared pika occurrence is primarily driven by the presence of talus, proximity to the talus edge (with pikas preferring areas closer to vegetation), and talus patch size (with pikas preferring small patches). The rangewide model indicated that collared pika occurrence was positively correlated with maximum winter temperature and negatively correlated with maximum summer temperature, annual precipitation, and solar radiation. While preferences for talus characteristics remained consistent rangewide, the effect of climate variables including precipitation and maximum summer temperature varied regionally. To assess climate vulnerability, we combined trait-based and correlative modeling approaches, with the results suggesting the species has high vulnerability to climate change. Our trait-based assessment indicated that collared pikas are moderately susceptible to climate change due to high exposure to changing conditions, high sensitivity to climatic variables, and low adaptive capacity. To predict future changes in distribution, we employed a presence-background species distribution modeling technique to identify the current climatic niche and projected this model into future climate scenarios. Our models suggest a loss of ~55-70% of climatically suitable areas by 2080. Together, these results inform conservation status and strategies for this species and highlight the importance of conducting regional and species-specific analyses.

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Chapter 1: Slopes and edges: Identifying regional variation in collared pika habitat preferences and climate response

ABSTRACT

Conserving and sustaining viable populations of species of concern requires knowledge of habitat requirements and use. Despite fine-scale variation in species ecologies throughout the distribution, many management efforts apply studies from other regions or closely related species to develop local action plans, leading to a mismatch between idealized outcomes and realities. The collared pika (*Ochotona collaris*; found in Alaska and northern Canada) is considered a species of concern due to its reliance on specialized alpine habitat and presumed susceptibility to climate change. However, little is known about specific habitat requirements for the species and generalizations are often made, presuming that collared pikas have the same needs and threats as other pika species such as the American pika. Here, we analyze habitat preferences across the species' range by comparing the environmental conditions of pika occurrence points to the environmental conditions of surrounding available area to assess regional differences in habitat use and climate response. As part of this effort, we developed a novel landcover map, which classifies landcover relevant to alpine mammals with ~15% greater accuracy and talus, specifically, with 9-15% more accuracy than existing landcover surfaces. Our habitat preference analysis indicates a range-wide preference for small talus patches, areas close to the talus edge, areas that receive warmer winter temperatures, cooler summer temperatures, less solar radiation, and less annual precipitation. While landcover level preferences remain constant geographically, climate preferences vary regionally. Northern populations exhibit a negative relationship between occurrence and high summer temperature and positive relationship to precipitation. In contrast, central populations exhibit a negative relationship to precipitation and southern populations exhibit a negative relationship to both precipitation and high summer temperatures. Our results indicate key differences in habitat preference and climatic threats compared to other pika species and between collared pika populations. This study is the first to analyze regional variation in habitat use of the collared pika, finding evidence that different regions have different habitat preferences and climatic drivers. We also identify key differences in habitat requirements and climatic threats between collared and American pikas, highlighting the importance of conducting species and region-specific studies to inform conservation goals.

INTRODUCTION

Species worldwide are experiencing increasing habitat loss and fragmentation due to human activities, including landcover change and climate-induced habitat degradation (McCarty 2001, Walther et al. 2002, Young et al. 2016). In the face of these global pressures, understanding the habitat requirements and distribution of species of concern is essential for predicting habitat loss and guiding effective management to preserve suitable areas. However, this task is often complicated for rare and understudied species, as data deficiencies frequently limit the scope of habitat studies (Marcer et al. 2013). This challenge is further compounded by the fact that many

species of concern are inherently data deficient (Borgelt et al. 2022), often for the same reasons they are at risk. As environmental conditions continue to shift, identifying and understanding the habitat needs of these species is of profound importance for conservation.

Pikas—small, alpine-associated lagomorphs are often considered an indicator species for climate change due to their preference for fragmented talus habitats and general intolerance to high temperatures (Hafner 1994, Beever et al. 2003, Rodhouse et al. 2018). Their inability to survive prolonged exposure to high temperatures restricts them to talus slopes where they can behaviorally thermoregulate in cooler interstitial spaces between rocks in the summer and benefit from thermal insulation under the snowpack in the winter (MacArthur and Wang 1973, Smith 1974). While the magnitude of threat warming temperatures may pose on pikas has been called into question (Smith 2020), and many pika populations have experienced no changes associated with climate (Millar and Westfall 2010), others have experienced declines. For example, the Ili pika, endemic to northwest China, is considered endangered due to population declines associated with climate change and increased grazing pressure (Li and Smith 2005). Seven additional Asian pika species are projected to experience habitat loss due to changing temperatures (Leach et al. 2015), yet further evidence shows that one of those species, Royle's pika, is more impacted by precipitation than warming (Bhattacharyya et al. 2019). These differences within and among species underscore the need to thoroughly evaluate each pika species separately, and not simply assume that the stressors which apply to one population or species are universally problematic. Further, as the potential threat of a changing climate grows, it becomes increasingly important to understand species-specific and regional variation in pika habitat preference for management and conservation planning.

The greatest body of research on pika habitat preferences and climate responses has focused on the American pika, a species found in the continental United States and southern Canada. Populations of American pikas have shown upslope retractions in response to warming temperatures in some regions (Beever et al. 2003, Moritz et al. 2008), yet others seem to be thriving in areas outside their perceived niche (Shinderman 2015, Smith and Nagy 2015). However, the directionality of effect of many of these habitat variables appears to vary throughout the range (Beever et al. 2016, Millar et al. 2016). For example, American pika occupancy decreases with high summer temperatures in areas which are drier but increases with higher summer temperatures in wetter regions (Jeffress et al. 2013). In at least one region, elevation is a strong predictor of pika abundance (Shinderman 2015); yet, in others American pikas show no preference towards higher elevations (Millar and Westfall 2010, Erb et al. 2011, Varner et al. 2016). Thus, our ability to predict if and where range reductions will occur, and which habitats will represent suitable climate refugia into the future, relies on our knowledge of habitat usage across the range.

The collared pika, inhabiting Alaska and northwest Canada, is by far the lesser studied of the two North American pika species. Despite being classified as Vulnerable throughout all four

states or territories encompassed by their range (NatureServe 2016) and the recent designation as a species of conservation concern in the Canada (COSEWIC 2011), the species is not generally considered globally threatened (Lanier and Hik 2016, NatureServe 2016). This is in part due to the broad estimated range for the species, which likely includes many regions of unsuitable nonhabitat, and the relatively little knowledge we have about collared pika occurrence or population trends (Lanier and Olson 2013, Lanier and Hik 2016). We also lack fundamental ecological data on habitat preferences, dispersal distances, or ecological differences among regions. As a result, many authors make at least some inference regarding habitat preferences based upon studies conducted in American pikas (e.g., Lanier et al. 2015). This is potentially problematic for two reasons. First, the literature suggests important distinctions between the ecologies of American and collared pikas. Second, due to Arctic amplification climate change is occurring far more rapidly at higher latitudes (Serreze and Barry 2011). As a result, it is increasingly important to devote more focus to better understanding collared pika habitat requirements.

This shortfall in our comparative knowledge of collared pikas is not due to lack of interest. The short field season and lack of road-accessibility of collared pika habitats has limited the scope and breadth of studies. As a result, much previously published research has focused on either a small portion of the collared pika range (Horn 2013, Kukka et al. 2020) or features broad habitat descriptions across the range based upon coarse climatic predictors (MacDonald and Jones 1987). The longest-running and most influential set of ecological research on collared pikas has focused on a population in the southeastern region of the range (Morrison and Hik 2007, Morrison et al. 2009, Trefry and Hik 2009). Here, collared pikas exhibit a preference for larger, more continuous talus patches, which may offer greater protection from predators (Franken and Hik 2004). Research from these populations also highlight critical differences between American and collared pika ecology. For example, the average dispersal distance of collared pikas is 5x greater than the average juvenile dispersal distance of American pikas with a mean of 536 meters for collared pikas and 90 meters for American pikas (Peacock and Smith 1997, Zgurski and Hik 2012). Collared pikas seem to prefer southwest-facing talus, which receive more direct sunlight and have a longer growing season (Renee J. Franken and Hik 2004), while southwest-facing talus are barriers to American pikas (Castillo et al. 2014). These differences highlight the importance of increasing our understanding of collared pikas specifically, as opposed to assuming similar densities, limitations, and preferences apply to both species. Recent revisions of the Committee on the Status of Endangered Wildlife in Canada have resulted in listing collared pikas as a species in special need of conservation action in the Canadian portion of their range (COSEWIC 2011). The recently released management action plan highlights the importance of identifying and protecting suitable habitat to act as a safe harbor for this species as environmental conditions change (Environment and Climate Change Canada 2023), yet we generally lack sufficient knowledge of the parameters that shape suitable habitat across most of their range.

Here, we address that gap by identifying preferred habitat features and mapping collared pika habitat suitability across their range. We rely on pika occurrence data from iNaturalist and recent museum records to (1) evaluate preferences for landscape features relative to their local availability and (2) highlight the importance of evaluating species and regional differences in habitat use. Our results provide guidance on prioritizing areas for management action and inform future directions for collared pika conservation.

STUDY AREA

Our study area covers 435,441 km² of northwest Canada and Alaska, including portions of the Alaska Range, Chugach Mountains, Wrangell-St. Elias/Coast Mountains, Mackenzie Mountains, Richardson Mountains, and the Yukon-Tanana Uplands using data points ranging from 2000 to 2024. Elevation in the study area ranged from 0 to 5195 m. Annual precipitation ranged from 213 to 1568 mm. Average summer high temperatures ranged from -10.5 to 20°C; average winter high temperatures ranged from -25 to -2.6°C. Our regional analysis focuses on three distinct geographic regions, the Yukon Tanana Uplands, Alaska Range, and the Wrangell-St. Elias/Coast Mountains. The northernmost region, the Yukon Tanana Uplands, is characterized by lower elevations, hotter summer temperatures, and colder winter temperatures. The Alaska Range, which is centrally situated within the collared pika range, is home to the tallest mountains on the continent and experiences comparatively moderate temperatures and precipitation. The Wrangell St. Elias/Coast Mountains, situated at the southern extent of the collared pika range along the Gulf of Alaska, receive considerable rainfall and solar radiation and experience moderate temperatures.

METHODS

Occurrence data

To obtain a set of current occurrence points, we downloaded all research-grade iNaturalist records for collared pikas. These occurrence points were combined with museum records amassed using VertNet. To reduce spatial bias and avoid repeat observations of one individual, we subsampled our records to limit the number of points within 2 km of another individual (Boria et al. 2014). While pikas are territorial, male/female or female/offspring territories often exhibit some degree of overlap (Zgurski and Hik 2012). To account for the possibility of territory overlap, we permitted four observations within the territory range of another observation. To better understand regional variation in habitat preferences, presence points were also separated by major geographic regions: the Alaska range, Wrangell St. Elias/Coast Mountains, Mackenzie Mountains, Richardson Mountains, and Yukon-Tanana Uplands following Lanier et al. 2013.

Because our occurrence data only reflect presence locations, we generated random pseudo-absence or background points for spatial comparison (Figure 1.1). This is a well-

established practice in many species-distribution and habitat preference studies (Phillips et al. 2009, Whitford et al. 2024). For each presence point we generated 10 background points to identify habitats which should be accessible to collared pikas based upon their current occurrence, but they may not be selecting (i.e., pseudoabsences). Here, we defined available area as anywhere within 30 km of a collared pika occurrence record. This reflects a maximum estimate of collared pika dispersal (Lanier, unpublished data). To identify preference for certain habitat features, the distribution of presence points was compared to the random distribution of our background points, allowing us to detect any specific habitat features used out of proportion with their availability.

Environmental predictors

We assessed 10 environmental predictors: summer high temperature, winter low temperature, annual precipitation, solar radiation, elevation, aspect, slope, talus patch size, distance to talus edge, and landcover type in our occurrence models (Table 1.1). Climate variables were downloaded from Worldclim 2.1 (Frick and Hijmans 2017) and reflect averages over the years 1970–2000. A digital elevation model was used to calculate aspect and slope using the corresponding functions in Google Earth Engine (Danielson and Gesch 2011).

While climate and geophysical predictor data were readily available, accurate landcover data at a fine-enough scale to classify talus and within talus meadows had to be generated using Google Earth Engine. All clear satellite images from Landsat 8 and 9 from 2020-2024 were combined into one composite image to reflect the recent average conditions in the study area. To classify landcover type, we calculated the Normalized Difference Vegetation Index (NDVI) and the Normalized Difference Water Index (NDWI). Areas with NDWI greater than 0 were classified as water or snow/ice. Areas with low NDVI, less than 0.2, were classified as talus. Areas with moderate NDVI, between 0.2 and 0.4, were classified as herbaceous vegetation. Areas with high NDVI, greater than 0.4, were classified as dense vegetation. This new landcover map was used to calculate the patch size and distance to talus edge for each occurrence and background point. To assess the accuracy of the new habitat classification and compare existing models, 250 validation points were randomly generated in a 35x25 km region of the range. Each point was given a true landcover class assignment based on satellite imagery and prior knowledge of the testing region. Each point's landcover type was classified by the new classification map, the most recent National Land Cover Database (NLCD) map (Jin et al. 2017), and the most recent GAP/LANDFIRE land cover classification map (U.S. Geological Survey Gap Analysis Project 2016) from 2016 and 2011, respectively. A confusion matrix was generated for the new classification model, NLCD, and GAP/LANDFIRE to evaluate overall accuracy, talus-specific accuracy, and Kappa coefficients.

Modelling approach

All continuous variables were extracted for each point's location using the `extract` function from the `Terra` package in *R* (Hijmans et al. 2022). Correlation of each variable was assessed using Pearson's Correlation and Variance Inflation Factor (VIF). All variables had a Pearson's correlation index below the accepted threshold of .7 and a VIF below 5, meaning they are not significantly correlated and can be included simultaneously in models without deleterious effects.

We used a model selection method to determine which environmental characteristics best predict collared pika occurrence. We evaluated the effect of each predictor on occurrence to identify preferred habitat features. The following combinations of environmental predictors were assessed: geomorphic model (elevation, aspect, and slope), climate model (maximum summer temperature, maximum winter temperature, annual precipitation, and solar radiation), American pika model (landcover type, aspect, maximum summer temperature, and precipitation), collared pika model (landcover type, patch size, maximum summer temperature, maximum winter temperature, annual precipitation, and aspect), collared pika summer stress model (landcover type, patch size, maximum summer temperature, annual precipitation, and aspect), collared pika winter stress model (landcover type, patch size, maximum winter temperature, annual precipitation, and aspect), habitat model (landcover type, distance to talus edge, and patch size), climate and habitat model (landcover type, edge distance, patch size, maximum summer temperature, maximum winter temperature, solar radiation, and precipitation). The species-specific models were chosen based on previous studies on environmental factors shaping pika occurrence. The variations of the collared pika model are included to determine if summer temperatures, winter temperatures, or both are more influential to pika occurrence. Each model was fitted as a generalized linear model (GLM) and assessed based on Akaike Information Criteria and area under the curve to determine the model of best fit.

Regional assessment

Because populations in different regions have different evolutionary histories and experience vastly different environmental regimes, we do not expect pikas in each region to exhibit the same habitat preferences. To identify regional variation, we grouped occurrence points by regions consistent with naming used in Lanier, 2015. Each occurrence model was fitted to the Yukon Tanana Uplands, Alaska Range, and Wrangell St. Elias/Coast Mountains separately. The remaining regions, the Richardson, Mackenzie, and Chugach Mountains, did not contain sufficient data points for robust modeling, and so were excluded from the regional study. The included populations each represent one of the three distinct genetic lineages that were isolated ~148 and 52 kya (Lanier et al. 2015). The Yukon-Tanana Uplands represent the northern lineage, which inhabits lower elevations with hotter summers, colder winters, and less rainfall. The Alaska Range represents the southwestern lineage, which inhabits high elevation areas that receive average temperatures and precipitation. The Wrangell St. Elias/Coast Mountains

represent the most distinct and longest diverged lineage, which inhabits high elevation, coastal areas with high precipitation and solar radiation.

RESULTS

We combined new survey data, occurrence points from iNaturalist, and museum records for our analysis of habitat preference. We downloaded locality information of 828 collared pika museum specimens from VertNet and an additional 256 observations from iNaturalist. Our survey efforts in the Alaska Range resulted in 36 additional occurrence points. After filtering out non-georeferenced localities, 356 recent records remained for analysis.

Landcover classification

Our new classification of landcover, using updated satellite imagery and NDVI metrics, correctly classified 82.8% of test points and it was 96.9% accurate at classifying talus, with a kappa statistic of 0.7565. In contrast, NLCD correctly classified 68.4%, with only 88.4% accuracy on talus and a Kappa statistic of 0.537. The GAP/LANDFIRE dataset correctly classified the smallest percentage of test points (66.8%) and had 78.8% accuracy for talus and a kappa statistic of 0.516 (Table 1.2). Of the misclassified points in the new classification, 69.7% were misclassifications of vegetation type, with herbaceous vegetation being misclassified as dense vegetation or vice versa.

Global occurrence models and habitat preferences

Range-wide, the best fit regression model was the climate and habitat model, which included landcover type, edge distance, patch size, summer high, winter high, solar radiation, and precipitation as predictors of collared pika occurrence. This model had an AIC score of 2794, which was 68.2 lower than the next best fit model (Table 1.3), and an AUC value of 0.8216. This means that the model was able to predict the occurrence of 82.16% of test points. In this model, maximum summer temperature ($P = 0.006$, estimate = -0.221), maximum winter temperature ($P \leq 0.001$, estimate = 0.398), solar radiation ($P \leq 0.001$, estimate = -0.370), annual precipitation ($P = 0.001$, estimate = -0.303), presence of talus ($P = 0.002$, estimate = 2.230), distance to talus edge ($P \leq 0.001$, estimate = -0.694), and talus patch size ($P \leq 0.001$, estimate = -0.404) were significant predictors of collared pika occurrence (Figure 1.3). Across the range, collared pikas seemed to prefer talus, areas closer to the talus edge, smaller talus patches, areas that receive warmer winter temperatures, cooler summer temperatures, less solar radiation, and less annual precipitation (Figure 1.4).

Regional occurrence models and habitat preference

Collared pika occurrence in both the Alaska Range and the Wrangell St. Elias/Coast Mountains was best predicted by the global model: the habitat and climate model (Table 1.4). In the Alaska Range, the habitat and climate model had an AIC score of 889.51, with the next-best

model having a DAIC of 10, and an AUC of 0.7361. In this model, patch size ($P \leq 0.001$, estimate = -0.359), distance to talus edge ($P = 0.011$, estimate = -0.378), and annual precipitation ($P = 0.025$, estimate = -0.571) were significant predictors of collared pika occurrence. In contrast to the global model, maximum summer temperature and solar radiation were no longer significant predictors of occurrence. In the Wrangell St. Elias/Coast Mountains, the habitat and climate model had an AIC score of 764.86, a DAIC of 11.45 from the next best model, and an AUC of 0.8839. Here, patch size ($P \leq 0.001$, estimate = -0.379), distance to talus edge ($P \leq 0.001$, estimate = -1.581), average maximum summer temperature ($P = 0.009$, estimate = -0.578), and average annual precipitation ($P = 0.002$, estimate = -0.748) were significant predictors of collared pika occurrence. In contrast to the global model, solar radiation and maximum winter temperature were not significant predictors of occurrence.

Collared pika occurrence in the Yukon Tanana Uplands was best predicted by the collared pika summer stress model. This model had an AIC score of 302.23, a DAIC of 7.1 to the next best model, and an AUC of 0.8921. Here, patch size ($p\text{-value} \leq 0.001$, estimate = -0.549), maximum summer temperature ($P \leq 0.001$, estimate = -2.042), and south-facing aspects ($P = 0.024$, estimate = 2.440) were significant predictors of collared pika occurrences. Notably, in contrast to the global and other regional models, precipitation does not appear to have a significant effect on occurrence in the Yukon-Tanana Uplands.

DISCUSSION

Our results highlight the critical role of both landcover and climate in shaping collared pika distribution, with talus characteristics emerging as the strongest predictors of occurrence across the range and in two of the regions. Generally, the locations of pika occurrences suggested a preference for small talus patches and areas near talus edges, underscoring the need for accurate mapping of this habitat type, which has historically been challenging. While talus remains a dominant driver, climatic variables—particularly temperature and precipitation—also play a significant role, with regional differences in the drivers of pika occurrence. Our findings suggest that populations in the core of the range exhibit weaker responses to climatic factors, while those at the range periphery, particularly in the Yukon-Tanana Uplands, may have stronger responses to temperature and precipitation extremes. Additionally, our results suggest a complex relationship between precipitation and pika occurrence, with varying effects across the range coinciding with the precipitation gradient. Taken together, these findings emphasize the need for species and lineage-specific research to accurately assess conservation threats, particularly as climate change alters habitat suitability.

Given that talus is a defining habitat feature for pikas, it is unsurprising that our results indicate talus characteristics as the most influential predictors of their occurrence. These findings align with a well-established body of North American pika research demonstrating the species' reliance on talus for cover, foraging, and thermal buffering (MacArthur and Wang 1973, Smith 1974a, Franken and Hik 2004, Morrison et al. 2009, Millar et al. 2016). Studies of American

pika occurrence have found consistent results, with talus characteristics having more explanatory power on distribution and occurrence than broad climate factors (Millar et al. 2016, Billman et al. 2021). However, despite its ecological importance, talus has been historically difficult to map due to the lack of high-resolution, border-agnostic spatial resources spanning Alaska and Canada. This limitation has hindered range-wide assessments of habitat availability and connectivity, particularly for species like the collared pika that inhabit specialized terrain. Our improved talus landcover model helps bridge this gap by providing a more comprehensive and consistent dataset for assessing alpine habitat across the collared pika range. This tool not only enhances our ability to locate pika habitat but also supports broader conservation efforts for other talus specialists, such as marmots, sheep, and alpine-obligate plant species. While our model represents a significant advancement, further work is needed to refine remote sensing approaches for assessing talus rock size and structure to improve our ability to characterize habitat remotely.

While collared pika occurrence was most strongly explained by talus characteristics, climatic variables provided significant explanatory contributions with smaller overall magnitude. Our global model indicates preference towards areas that experience cooler summers, warmer winters, and lower solar radiation, yet the relationship between lineages and climatic conditions varies across the collared pika range (Figure 1.4). Generally, these findings align with the sensitivity to thermal stress notable in American pikas (MacArthur and Wang 1973, Smith 1974a). However, differences among lineages also suggest variability in the seasonality and intensity of temperature stress. For example, populations in the Alaska range, which lies in the core of the collared pika range, do not exhibit a significant relationship with summer high temperatures but exhibit significant preference towards areas with warmer winter temperatures. This suggests that extreme cold overwinter, not summer heat stress, may be a limiting thermal factor in these habitats. Thus, as global temperatures continue to rise, the Alaska range may offer a thermal haven for this species, but future climate modeling will be needed to assess this relationship. Conversely, populations in the Yukon-Tanana uplands in the northern-edge of the range are significantly negatively impacted by high summer temperatures. Populations in these areas generally occupy warmer, lower elevation sites (note, higher elevation habitat is not available in this region), making them particularly vulnerable to summer heat. This variability in signatures of summer heat stress across the range, with stability in the core and avoidance of hot areas along the range boundary, aligns with previous findings that marginal populations occupying climatic niche limits are likely the first areas in a range to experience retractions and extirpations (Parmesan et al. 1999, Walther et al. 2002, Wilson et al. 2007). These results signify that collared pikas are significantly impacted by temperature as often thought, but regional complexity and differential seasonal effects need to be considered.

The relationship between precipitation and regional habitat models is of particular note, with a variable response between precipitation and collared pika occurrence along the precipitation gradient. Our range-wide habitat model suggests a significant negative effect of precipitation. Regionally, the strongest negative effect of precipitation is seen in the southern,

coastal parts of the collared pika range where rainfall is most abundant. Here, it is possible that precipitation acts as a behavioral limitation, possibly reducing time available for foraging, which is an essential component of overwinter survival (Morrison et al. 2009). In this region, pikas are also negatively associated with maximum summer temperatures although this region experiences similar summer temperatures to the Alaska range, where summer temperature does not significantly impact pika occurrence. This could indicate that high temperatures are most limiting when pikas are experiencing compounding stress from precipitation. Conversely, pikas in the drier northern region exhibit a positive relationship with precipitation, preferring areas that receive more rainfall. Here, positive local precipitation effects may be indicative of higher forage quality or improved winter snowpack, both of which have been shown to be important ecological drivers of overwinter survival (Morrison and Hik 2007, Morrison et al. 2009). While our results indicate that preference towards precipitation varies across the range, the behavioral response to precipitation is not fully understood. More work is needed to determine the physiological and behavioral effects of seasonal precipitation and identify the threshold at which precipitation becomes limiting.

Our work also highlights the importance of species-specific research when identifying ecological patterns and regional threats. In the lack of contrary data, scientists often make the simplifying assumption that most pika species share ecologies and habitat needs (e.g., Lanier et al. 2015). In pikas, this decision is often out of necessity—the greatest body of research on pikas focuses on the American pika, and generalizations from these works are often applied to under-represented pika species. While this approach can facilitate analyses on understudied species, key differences between collared pikas and American pikas suggest that there is more variation in climate response and habitat use within this genus than is often considered. For example, American pikas exhibit a preference for north facing aspects, which receive less direct sunlight (Castillo et al. 2016). When considered across all collared pika occurrence points, there was no significant preference towards any aspect, with occurrences distributed equally across available aspects (Figure 1.5). However, in the northern portion of their range (i.e., Yukon-Tanana Uplands) pika occurrences are associated with south-facing aspects. Similarly, sites with a south-facing aspect were more likely to be recolonized in a study occurring in the Wrangell-St. Elias/Coast Mountains lineage (Franken and Hik 2004). Because south-facing slopes receive greater sunlight, experience earlier seasonal snowmelt, they seem to support a longer foraging season and thus correlate with overwinter success (Morrison and Hik 2007, Morrison et al. 2009). This difference between American and collared pikas suggests a difference in ecological limitations; while American pika aspect preference is driven by avoidance of heat stress (Castillo et al. 2014), collared pika aspect preference is driven by increased foraging stress due to the shorter growing season at high latitudes. Similarly, our study indicates collared pika preference for small talus patches, while American pika occupancy is associated with larger talus patches (Billman et al. 2021). This may reflect the heightened need for forage access in collared pikas, with shorter summers and longer winters, or may simply reflect our method of delineating talus size through remote sensing techniques. Additional field-based surveys united with remotely

sensed data could provide important insights into the talus-size relationship. Overall, our results feed into a growing body of literature that indicates collared pikas face different environmental challenges than American pikas and thus need more ecological work to characterize the range of climatic limitations and responses to change. The differences in genetic diversity (with far more genetic variation in American pikas compared to collared pikas), and thus potential differences in adaptability, between the two North American pika species (Lanier and Olson 2013) combined with differing regional environmental threats, further underscore the needs to develop species-specific management plans.

Moving forward, it will be important to monitor populations on the periphery of the range where temperature and precipitation stress are more evident. Future climate projections indicate an increase in precipitation as well as warming temperatures across the collared pika range (O'Neill et al. 2016, Frick and Hijmans 2017). This may significantly impact populations at the southern margin, where precipitation is already limiting occurrence. More work is also needed to delimit this species' climatic niche and evaluate the risk of habitat loss associated with projected climate change. Many of the occurrence data used in this study came from opportunistic sampling, which is a great tool to expand sampling area but lacks information about temporality and changes in population dynamics. To better understand collared pika dynamics, regular monitoring of sites in key areas is recommended, especially in the Mackenzie, Chugach, and Richardson Mountains where data availability limited our ability to assess regional habitat use and climate response. Data limitations often constrain robust modeling efforts in rural or hard to access locations (Boakes et al. 2010, Bowler et al. 2022, Guerts et al. 2023), calling for more targeted efforts by local habitat and wildlife managers to assess areas beyond the public sphere where opportunistic observations are common. Because climate response varies geographically, survey efforts should strive to encompass the greatest range of environmental conditions and managers should carefully evaluate results from other regions before applying them locally.

Understanding the habitat needs and environmental sensitivities of rare and remote species is critical for effective conservation and management, particularly as climate change and development continue to reshape ecosystems, but these data can often be difficult to accumulate. Collared pikas exemplify the challenges of studying species that occupy difficult-to-access, rugged environments, where long-term monitoring is often logistically challenging and resource intensive. Similar biases are evident in studies of Chinese pikas, where understudied and threatened pika species are often ignored in favor of data-rich species (Lambert et al. 2023). Our findings underscore the value of leveraging broad-scale spatial data and community-sourced records to fill knowledge gaps, allowing researchers to make significant contributions to species conservation at relatively little cost while identifying regions where increased monitoring efforts would be most effective. This approach is especially important for understudied taxa, such as invertebrates and small mammals, which play vital roles in ecosystem function but often receive less attention than larger, more charismatic species (Clark and May 2002, Boakes et al. 2010, Troudet et al. 2017). By integrating targeted ecological studies with emerging remote sensing

tools and large-scale community datasets, we can improve habitat assessments, identify at-risk populations, and develop more effective conservation strategies for a wide range of species. Moving forward, continued investment in species-specific research, coupled with regional assessment and increased monitoring, will be essential for ensuring that conservation efforts extend beyond well-studied organisms to the many lesser-known species that support ecosystem stability.

TABLES

Table 1.1. Variables included as predictors of occurrence, source, and justification of their ecological impact.

Predictor	Source	Justification
Elevation	USGS Digital Elevation Model (Danielson and Gesch 2011)	Elevation found to be an important predictor of American pika (Shinderman 2015) and collared pika (Cannings et al. 2019) occurrence
Aspect	Derived from USGS DEM, using Google Earth Engine (Danielson and Gesch 2011)	SW- facing aspect found to be a significant predictor of site persistence in collared pikas (Franken and Hik 2004) and a barrier to dispersal for American pikas (Castillo et al. 2014)
Slope	Derived from USGS DEM, using Google Earth Engine (Danielson and Gesch 2011)	Slope hypothesized to be a partial predictor of habitat suitability for American pikas, corresponding with vegetation and soil properties (Varner et al. 2016)
Landcover Type	Derived from Landsat 8 and 9 (Earth Resources Observation and Science (EROS) Center. 2020)	Vegetation characteristics and access to forage identified as important predictors of collared pika occurrence (Franken and Hik 2004, Morrison et al. 2009)
Distance to Talus Edge	Derived from Landsat 8 and 9, calculated via Google Earth Engine (Earth Resources Observation and Science (EROS) Center. 2020)	Access to forage determines overwinter success of American (Dearing 1997) and collared pikas (Morrison et al. 2009)
Talus Patch Size	Derived from Landsat 8 and 9, calculated via Google Earth Engine (Earth Resources Observation and Science (EROS) Center. 2020)	Larger patches associated with increased occupancy of collared and American pikas (Franken and Hik 2004, Billman et al. 2021)
Average Summer High Temperature	WorldClim 2.1 (Frick and Hijmans 2017)	High temperatures associated with thermal stress and reduced activity of collared and American pikas, found to be a predictor of occurrence for American pikas (MacArthur

		and Wang 1973, Billman et al. 2021a, Harrison 2023)
Average Winter High Temperature	WorldClim 2.1 (Frick and Hijmans 2017)	Collared pika persistence overwinter is influenced by snowpack, which high winter temperatures may influence (Morrison et al. 2009)
Annual Precipitation	WorldClim 2.1 (Frick and Hijmans 2017)	Collared pikas rely on winter precipitation for insulation (Morrison et al. 2009), extirpations of American pikas have been observed in areas with little rainfall (Erb et al. 2011)
Annual Solar Radiation	WorldClim 2.1 (Frick and Hijmans 2017)	Solar radiation found to cause physiological stress in American pikas (Smith 1974a) and strongly impacts temperatures of talus and microclimates (Varner and Dearing 2014)

Table 1.2. The new landcover layer generated with Google Earth Engine is ~15% more accurate at classifying all habitat types and ~8% more accurate at classifying talus than existing landcover resources.

Classifier	Kappa	Overall Accuracy	Talus Accuracy
New Classification	0.7565	82.8%	96.9%
NLCD	0.5369	68.4%	88.4%
GAP/LANDFIRE	0.5158	66.8%	78.8%

Table 1.3. A comparison of regression models by Akaike's Information Criterion and AUC for each generalized regression model. Range-wide, the Climate and Habitat model is the best-fitting model and predicts occurrence with 82% accuracy.

Regression Model Predictors	ΔAIC	AUC
Climate and Habitat: landcover type, edge distance, patch size, summer high, winter high, solar radiation, precipitation	0	0.8216
Habitat: landcover type, edge distance, patch size	68.2	0.7642
Collared Pika Max Temp Stress: landcover type, patch size, summer high, winter high, annual precipitation, aspect	86.6	0.8161
Collared Pika Summer Stress: landcover type, patch size, summer high, annual precipitation, aspect	118.1	0.7863
Collared Pika Winter Stress: landcover type, patch size, winter high, annual precipitation, aspect	123.8	0.8353
Climate: precipitation, solar radiation, summer high, winter low	356.8	0.6758
American Pika: landcover type, aspect, max summer high, precipitation	372.7	0.6496
Geomorphic: elevation, aspect, slope	383.2	0.6019

Table 1.4. A comparison of regression models for each region. Occurrence points in the Alaska Range and Wrangell St. Elias Mountains are best predicted by the climate and habitat model, whereas occurrence points in the Yukon Tanana Uplands are best predicted by the collared pika summer stress model.

Region	Model	Δ AIC	AUC
Alaska Range	Climate and Habitat: landcover type, edge distance, patch size, summer high, winter high, solar radiation, precipitation	0	.7361
	Habitat: landcover type, edge distance, patch size	10	.7018
	Collared Pika Max Temp Stress: landcover type, patch size, summer high, winter high, annual precipitation, aspect	17.32	.7815
	Collared Pika Summer Stress: landcover type, patch size, summer high, annual precipitation, aspect	22.49	.7462
	Collared Pika Winter Stress: landcover type, patch size, winter high, annual precipitation, aspect	16.97	.8106
	Climate: precipitation, solar radiation, summer high, winter low	67.83	.6208
	American Pika: landcover type, aspect, max summer high, precipitation	70.3	.7037
	Geomorphic: elevation, aspect, slope	57.65	.7421
Wrangell St. Elias/ Coast Mountains	Climate and Habitat: landcover type, edge distance, patch size, summer high, winter high, solar radiation, precipitation	0	.8839
	Habitat: landcover type, edge distance, patch size	11.45	.8937
	Collared Pika Max Temp Stress: landcover type, patch size, summer high, winter high, annual precipitation, aspect	48.3	.8184
	Collared Pika Summer Stress: landcover type, patch size, summer high, annual precipitation, aspect	52.73	.8102
	Collared Pika Winter Stress: landcover type, patch size, winter high, annual precipitation, aspect	72.56	.8507

	Climate: precipitation, solar radiation, summer high, winter low	125.02	.6142
	American Pika: landcover type, aspect, max summer high, precipitation	128.85	.6768
	Geomorphic: elevation, aspect, slope	102.25	.7054
Yukon Tanana Uplands	Climate and Habitat: landcover type, edge distance, patch size, summer high, winter high, solar radiation, precipitation	7.55	.8274
	Habitat: landcover type, edge distance, patch size	14.62	.9136
	Collared Pika Max Temp Stress: landcover type, patch size, summer high, winter high, annual precipitation, aspect	7.1	.8796
	Collared Pika Summer Stress: landcover type, patch size, summer high, annual precipitation, aspect	0	.8921
	Collared Pika Winter Stress: landcover type, patch size, winter high, annual precipitation, aspect	27.59	.951
	Climate: precipitation, solar radiation, summer high, winter low	51.63	.7116
	American Pika: landcover type, aspect, max summer high, precipitation	44.84	.8098
	Geomorphic: elevation, aspect, slope	31.72	.8422

FIGURES

Figure 1.1. Map of known collared pika occurrence points relative to region (regions named consistent with Lanier 2015). Inset map depicts bounded background sampling method; random points were generated within a 30 km buffer of each occurrence point to sample environmental conditions around each known occurrence.

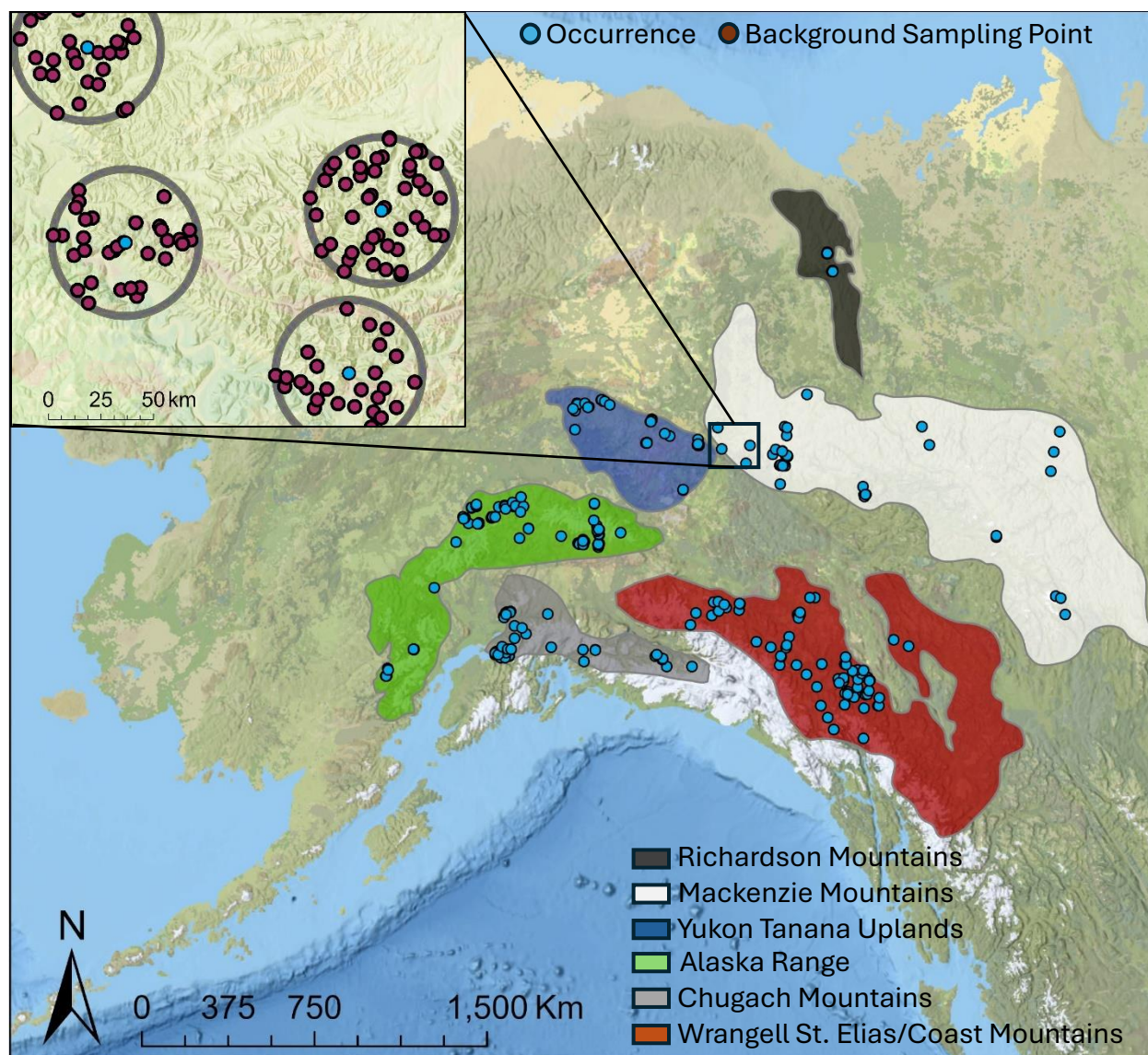


Figure 1.2. (A) The extent and classification of the new land cover map relative to the NLCD 2016, and the GAP/LANDFIRE 2011 layers. The latter only provide coverage of the Alaskan portion of the collared pika range, while the new classification scheme includes habitats in Canada. (B) Test regions and validation points used in the accuracy assessment. Although NLCD and GAP both contain more descriptive classification and a greater number of habitat types, it appears they are not accurate in classifying potential pika habitat at a meaningful scale for population-level analyses.

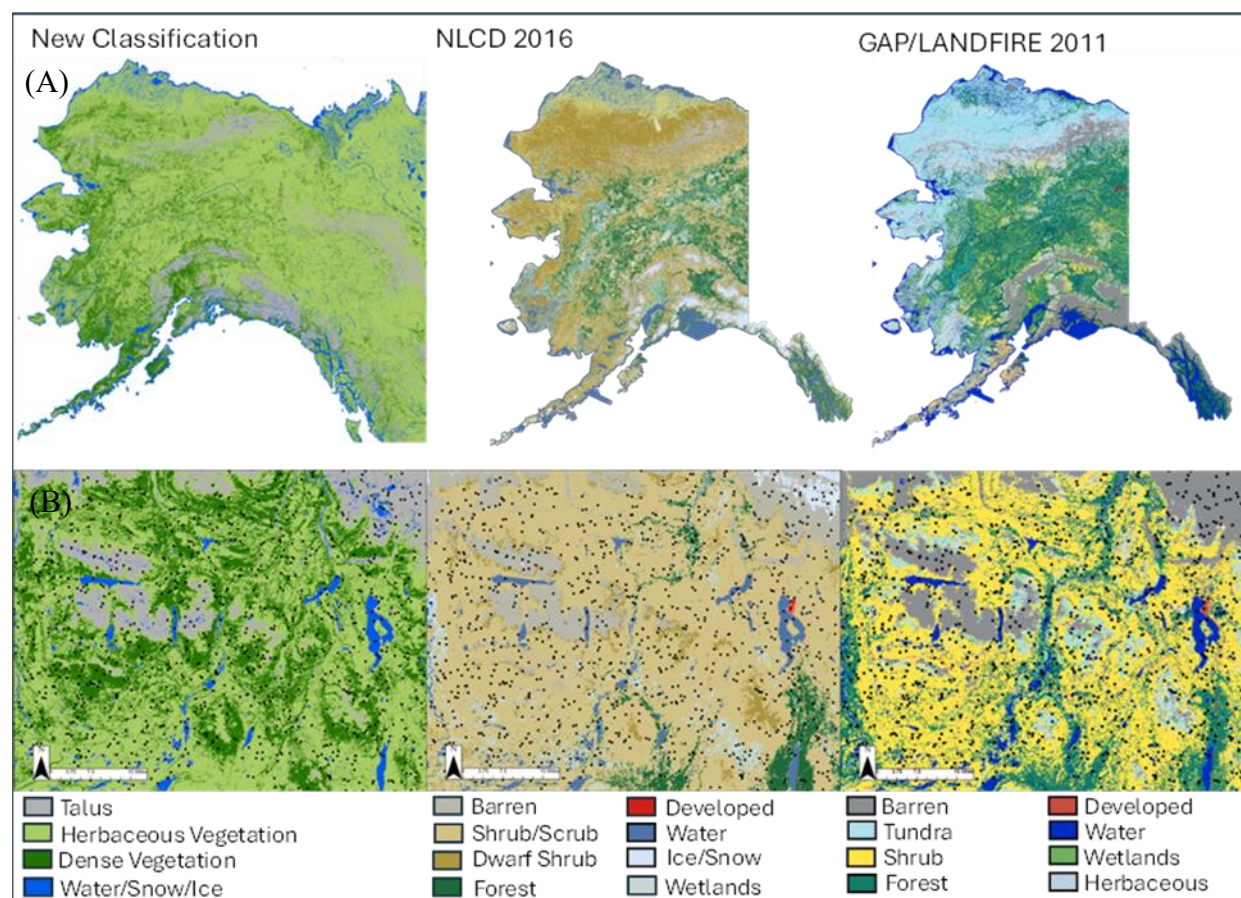


Figure 1.3. Partial effects plots showing the effects of each predictor variable in the best-fit global model on collared pika occurrence. Shaded areas represent 95% confidence intervals.

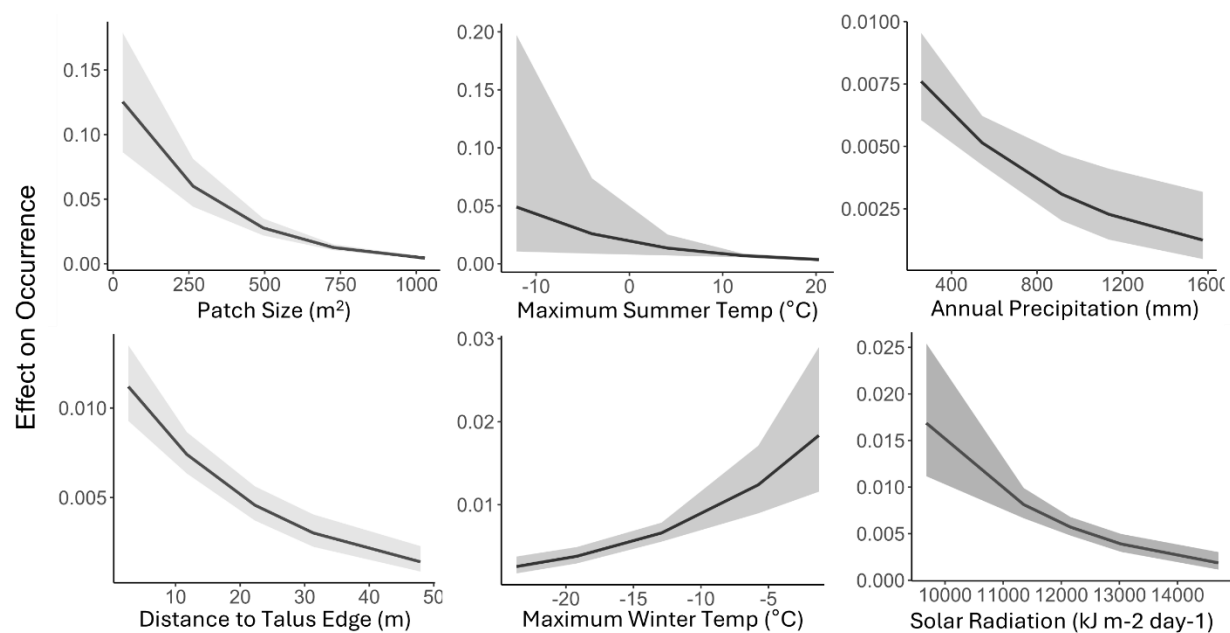


Figure 1.4. Coefficient plots showing the effect of predictors on collared pika occurrence globally (black), in the Wrangell-St. Elias/Coast Mountains (red), in the Yukon Tanana Uplands (blue) and the Alaska Range (green). Open circles represent non-significant relationships. Error bars represent 95% confidence intervals.

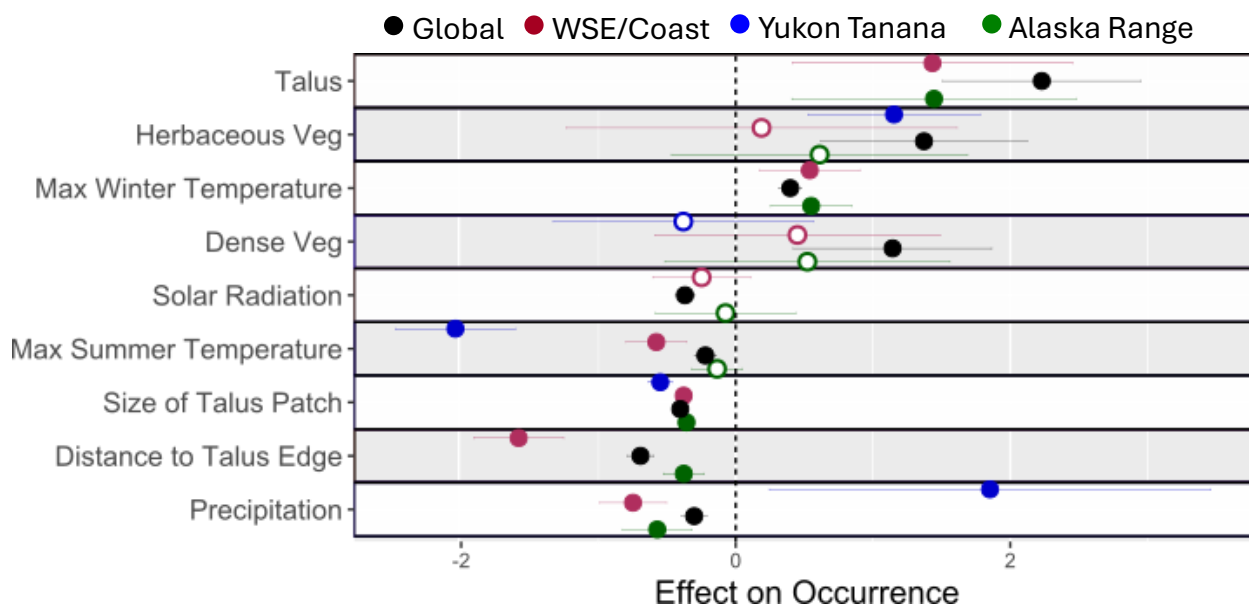
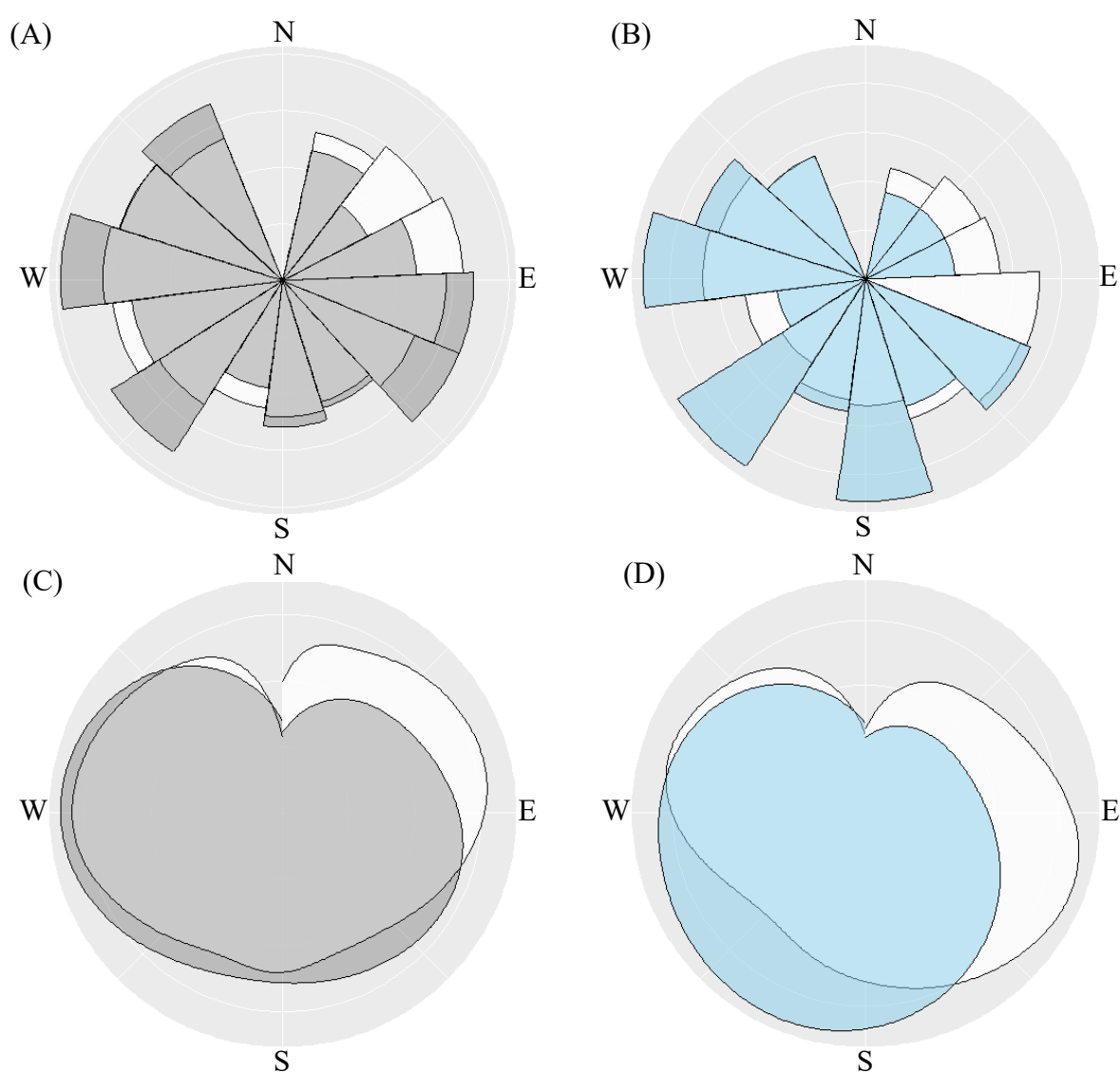


Figure 1.5. (A) Rose plot showing aspects of rangewide occurrence points (gray) over expected distribution based on available aspects (white). (B) Rose plot showing aspects of Yukon Tanana occurrence points (blue) over expected distribution based on available aspects (white). (C) Density plot showing aspects of rangewide occurrence points (gray) over expected distribution based on available aspects (white). (D) Density plot showing aspects of Yukon Tanana occurrence points (blue) over expected distribution based on available aspects (white). While both rangewide and Yukon Tanana occurrence points seem to disproportionately occur on SW-facing aspects, the relationship is only significant in the Yukon Tanana Uplands.



SUPPLEMENTAL FIGURES

Figure 1.6. Maps of climatic variables with regions and occurrence points overlaid. Climate data (provided from WorldClim) represents averaged over the years 1970–2000. Regions included in region-specific analysis are labeled and outlined in bold.

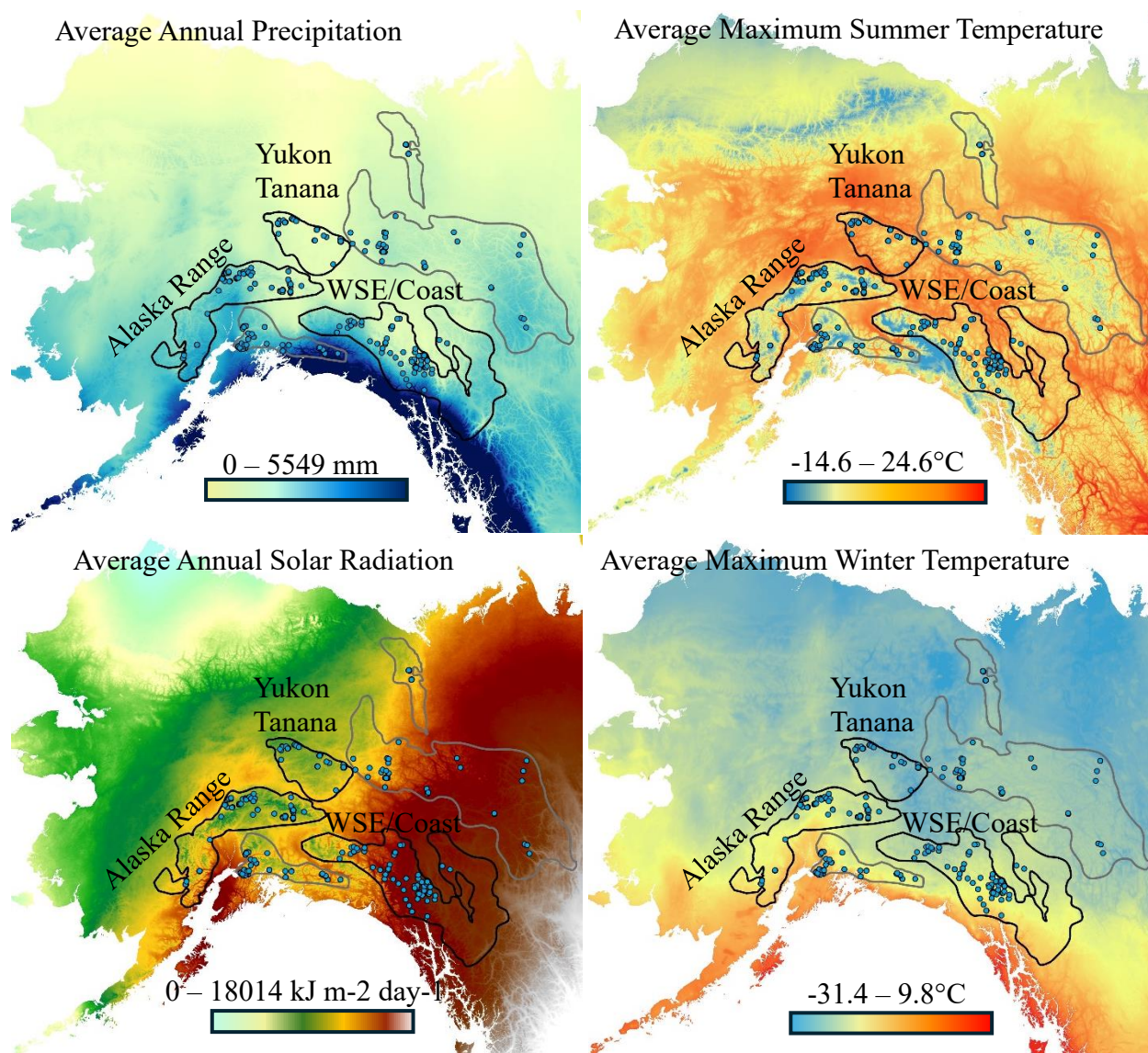
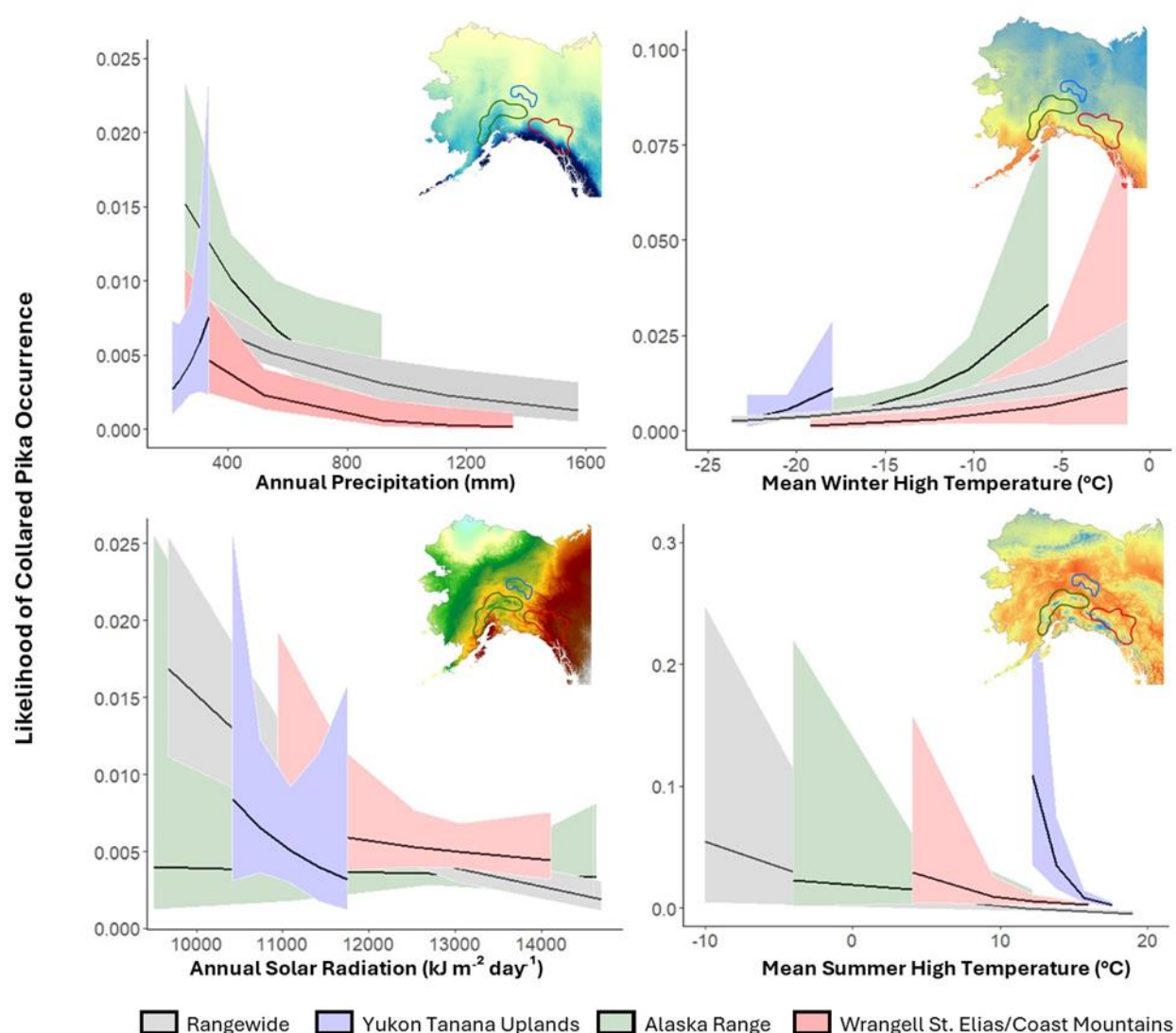


Figure 1.7. Partial effects plots of each climate variable with the response of each region plotted concurrently. Our results suggest that the relationship between pika occurrence and climatically suitable space in the Yukon Tanana Uplands (blue), often differs in direction and magnitude, from the Alaska Range (green), the Wrangell St. Elias/Coast Mountains (red), or the global model (gray). Map insets show climate variability among regions with each region outlined in its respective color.



Chapter 2: Assessing the climate change vulnerability of the collared pika

ABSTRACT

Recently, shifts in global climate have had significant impacts on species' distributions and ecologies. Alpine species, like the collared pika (*Ochotona collaris*) face unique challenges in responding to climate change due to their naturally fragmented distributions and limited dispersal opportunities. Using a combined trait-based and correlative approach, we aimed to assess the climate change vulnerability of the collared pika, identify key climatic drivers of current distribution, and predict changes in available habitat over time. Our trait-based assessment of collared pika climate vulnerability, using the NatureServe Climate Change Vulnerability Index tool, resulted in a vulnerability score between 5.31 and 6.09, a classification of Moderately Vulnerable. We employed a presence-background species distribution technique to identify the current climatic niche, determining a strong relationship between mean temperature of the driest quarter, maximum temperature of the warmest month, and precipitation of the warmest quarter with probability of occurrence. To assess changes in future distribution, we projected this model into predicted climate conditions for 2021-2040, 2041-2060, and 2061-2080 of global scenarios 370 and 585 of global circulation model MPI-ESM1-2-HR. We predict a loss of between 56.1 and 67.7% of climatically suitable area within the range by 2080. Our adaptive capacity assessment suggests a limited ability for persistence, while future modeling indicates minimal suitable habitat for spatial shifts. Given these characteristics, we recommend further monitoring efforts be put in place, particularly in vulnerable portions of the species' range. This work underscores the importance of continual review of species' needs and conservation plans as environmental conditions continue to rapidly change.

INTRODUCTION

Over the past century, unprecedented shifts in climate normals have led to significant changes in species' ecologies and ranges, altering community dynamics and distributions. Many species have been extirpated from areas that have become unsuitable due to rising temperatures, shifting precipitation, and increased frequency of extreme weather events (McCarty 2001, Walther et al. 2002, Walther 2010). Numerous plant and animal taxa have exhibited poleward range shifts as they track cooler climates (Parmesan et al. 1999, Hickling et al. 2006). Alpine species face unique challenges in responding to climate change due to their naturally fragmented distributions and limited dispersal opportunities. Unlike species in lowland environments, which can shift latitudinally to maintain their climatic niche, alpine organisms are often confined to isolated mountain peaks, leaving them with no option but to move upslope in search of suitable conditions (Pounds et al. 1999, Wilson et al. 2007, Freeman et al. 2018). This vertical retreat not only reduces the total area available for occupation but also increases population isolation, which can lead to reduced gene flow, increased genetic drift, and an elevated risk of local extinction (Rubidge et al. 2012, Robson et al. 2016, Polechová 2018). As habitable zones shrink and populations become increasingly isolated, the long-term viability of many alpine species remains

uncertain, emphasizing the urgent need for conservation efforts that incorporate both habitat protection and climate adaptation strategies. Thus, identifying sensitive species and key populations to target within those species is increasingly important.

Pikas—small, alpine-associated lagomorphs—are widely regarded as indicator species for climate change due to their reliance on fragmented talus habitats and their limited tolerance for high temperatures (Hafner 1994, Beever et al. 2003, Rodhouse et al. 2018). Their survival depends on access to cool microhabitats, as prolonged exposure to high temperatures can be fatal (MacArthur and Wang 1973, Smith 1974a). During the summer, pikas thermoregulate behaviorally by retreating into the cooler interstitial spaces between talus rocks, while in winter, they rely on the insulating properties of the snowpack for protection against extreme cold (Morrison and Hik 2007, Beever et al. 2010, 2016). Although responses to climate change vary among pika populations and species, recently documented population declines linked to shifting environmental conditions are becoming increasingly concerning (Li and Smith 2005, Lambert et al. 2023). These declines may often be most pronounced at the edges of their range, where populations may already be living near their physiological limits (Wilkening et al. 2015). As climate change continues to alter alpine ecosystems, the loss of peripheral populations could signal broader impacts on alpine biodiversity, highlighting the vulnerability of these high-elevation communities.

The collared pika (*Ochotona collaris*), which inhabits alpine regions of Alaska and northwestern Canada, may face heightened risk compared to other pikas due to Arctic amplification—a process in which the loss of sea ice substantially accelerates the pace of climate change (Serreze and Barry 2011). In recognition of these threats, the Committee on the Status of Endangered Wildlife in Canada has identified the collared pika as a species of conservation concern (COSEWIC 2011), a process which has triggered a new management plan calling for the identification and protection of critical habitat (Environment and Climate Change Canada 2023). Likewise, the state of Alaska has classified the species as Vulnerable (NatureServe 2016). Although the IUCN currently classifies collared pikas as a species of Least Concern (Lanier and Hik 2016), based largely on the large estimated species' range, little comprehensive data exists on population status or regional outlook under climate change. This species has historically been understudied, largely due to the challenges of accessing the remote and rugged landscapes it occupies. As climate change continues to reshape alpine ecosystems, particularly at higher latitudes, further research is needed to clarify the collared pika's population trends, habitat requirements, and long-term resilience to environmental change to understand the relationship between collared pikas and climate change (Environment and Climate Change Canada 2023).

To assess the risks posed by climate change, it is essential to understand the relationship between a species' distribution and the environmental variables that shape its habitat. Species distribution models (SDMs) use environmental data from known occurrence locations to identify key climate variables influencing occupancy and to map the species' range (Elith and Leathwick

2009). By incorporating these relationships, SDMs provide a valuable tool for understanding habitat suitability and forecasting potential range shifts under changing conditions (Elith and Leathwick 2009, Miller 2010). While SDMs are predictive in nature, they can offer valuable insight into not only where a species is likely to be found but also how changes in environmental conditions can affect a species distribution (Guisan and Thuiller 2005, Elith and Leathwick 2009). Although the actual magnitude of future climate change is unknown, it can be represented by multiple models, each based on different scenarios of carbon emissions modeled in Coupled Model Intercomparison Project 6 (CMIP6, O'Neill et al. 2016). These projections offer insights into potential environmental conditions, allowing researchers to predict how plant and animal species may respond to shifting climates. By integrating current distribution patterns with future climate scenarios, SDMs can help anticipate range contractions (Vieilledent et al. 2013), expansions (Ancillotto et al. 2016), and shifts (Chen et al. 2011), informing conservation strategies aimed at mitigating climate change impacts on biodiversity.

Previous efforts to model the distribution of the collared pika have primarily focused on identifying responses to historical climates (Lanier and Olson 2013, Lanier et al. 2015) or have included collared pika as one of a series of species within studies with broader taxonomic scopes and thus focused less on species-specific outcomes (Hope et al. 2015, Leach et al. 2015). Here, we aim to refine and enhance these models by incorporating up-to-date, georeferenced presence data to more accurately circumscribe the species' climatic niche and updated current climate data (Frick and Hijmans 2017), to assess the risk of climate change to collared pikas. Our objectives are to (1) model the current distribution of the collared pika, (2) identify key climatic drivers of occupancy, (3) predict changes in distribution and available habitat over time, and (4) assess the overall climate change vulnerability of this species by evaluating data on adaptive capacity alongside projections of climatic niche space. By improving species distribution models with high-quality occurrence data, this study will provide a more robust understanding of not only which areas are currently climatically suitable but how climate change may impact the collared pika in the future, thus informing conservation status and strategies for this alpine species.

METHODS

To evaluate climatic niche and future vulnerability of the collared pika, we combined two common approaches to conducting climate change vulnerability assessments (CCVAs): trait-based and correlative analysis (Foden et al. 2019). First, we conducted a trait-based analysis using the NatureServe Climate Change Vulnerability Index (Release 4.0, Lyons et al. 2024). Trait-based approaches assess species vulnerability by evaluating the relationships between biological traits and climate change impacts, considering factors such as exposure, sensitivity, and adaptive capacity (Young et al. 2012, Thurman et al. 2020). Second, we implemented a correlative species distribution modeling approach following guidelines outlined in Foden et al. 2019. Correlative models quantify the correlation between a species' distribution and climatic conditions (Pacifici et al. 2015). Because trait-based approaches lack geographic specificity in

identifying areas most affected by climate change, and correlative approaches rely on assumptions (e.g., a species distribution is determined solely by climatic variables and current sampling breadth is representative of the entire climatic niche), combining these approaches strengthens our ability to predict vulnerability and inform conservation decisions (Willis et al. 2015).

Trait-based vulnerability assessment

We used NatureServe's Climate Change Vulnerability Index tool (CCVI, Lyons et al. 2024) to estimate the trait-based vulnerability of collared pikas based on exposure to climate threat, sensitivity to environmental change, and adaptive capacity to handle novel conditions. The CCVI tool has been used by dozens of state agencies/conservation organizations to assess climate vulnerability (Young et al. 2014) and thus provides a way to contextualize vulnerability of a given species according to criteria that are broadly understood and applicable across taxa. The tool consists of 5 modules that guide assessors through evaluations of projected moisture and temperature changes, landscape context, natural history traits, and documented or modeled response to climate change. We evaluated each trait by conducting a literature search to determine the collared pika's vulnerability index score.

Occurrence points and sampling region

We combined opportunistic citizen-science records with validated museum specimen locations to estimate the current collared pika distribution. To accurately characterize the species' bioclimatic tolerances, we took steps to ensure accuracy of occurrence data. The citizen-science records, consisting of research-grade observations of collared pikas from iNaturalist, were verified to ensure proper species identification and plausible georeferencing before inclusion in the study. Museum records were amassed using the VertNet database, filtered to exclude specimen records prior to January 2000, and each point was mapped and examined to assess accuracy. Because citizen science and museum records are biased towards areas with higher sampling effort or accessibility (e.g., field sites, trails and roadways, national parks), spatial bias is inherent to many occurrence datasets (Boakes et al. 2010, Guerts et al. 2023). To reduce spatial bias and reduce overfitting, we employed a spatial filtering approach (Boria et al. 2014), removing occurrence points within 5 km from others using the *R* package *spThin* (Aiello-Lammens et al. 2015) as implemented in Wallace EcoMod (Kass et al. 2023). All *R*-based analyses were run in *R* version 4.1.2 (R Core Team, 2023).

Because our data reflects only presence locations, we employed presence-background modeling (Phillips et al. 2009), estimating suitable habitat by comparing environmental characteristics at known locations to randomly sampled background conditions throughout the region (Guillera-Aroita et al. 2015). Defining the extent of the background sampling region has important implications for the model's ability to predict areas of suitable habitat (Foden et al. 2019). To encompass the entirety of the species' niche breadth and include sufficient accessible

areas that could feasibly become suitable, we limited our sampling region to areas within a 3-degree buffer around each presence location (Barve et al. 2011, Fourcade et al. 2014, Whitford et al. 2024). We generated 10,000 random background points within our sampling region to adequately represent available environmental conditions based on best-practice recommendations (Fourcade et al. 2014, Grimmer et al. 2020, Whitford et al. 2024).

Environmental data

We assessed eight climatic variables (Table 2.1): mean diurnal range (bio1), max temperature of warmest month (bio5), min temperature of coldest month (bio6), mean temperature of wettest quarter (bio8), mean temperature of the driest quarter (bio9), annual precipitation (bio12), precipitation of the warmest quarter (bio18), and precipitation of the driest quarter (bio19). Climate variables were downloaded from Worldclim 2.1 (Frick and Hijmans 2017) and reflect averages over the years 1970–2000 at a resolution of 2.5 arcmin. To reduce collinearity in predictor variables, we selected only candidate variables with plausible ecological roles on our study species (Dormann et al. 2013, Foden et al. 2019). We selected these ten variables as they have been shown to influence haying ability, overwinter survival, and thermal stress of collared and American pikas (MacArthur and Wang 1973, Smith 1974a, Morrison et al. 2009, Erb et al. 2011, Beever et al. 2016, Billman et al. 2021).

To evaluate persistence of suitable habitat in future climatic conditions, we used the Max Planck Institute Earth System Model (MPI-ESM1-2-HR; Müller et al. 2018), accessed from WorldClim’s Coupled Model Intercomparison Project 6 (CMIP6) downscaled future climate projections. We selected this global circulation model (GCM) because MPI models have outperformed other models over Alaska (Walsh et al. 2008). Each GCM models future climates according to several carbon emission scenarios, referred to as shared socioeconomic pathways (SSP), designed to capture the uncertainty inherent in climate projections (O’Neill et al. 2016). We selected SSP 370, which presumes steady maintenance of current emission trends, and SSP 585, which represents increased emissions driven by an energy-intensive fossil fueled economy, to model collared pika distribution under two likely global scenarios (Raupach et al. 2007, O’Neill et al. 2016).

Modelling approach

To generate distribution models, we used the application Wallace v2.1.3, which provides an accessible and reproducible platform for ecological niche modeling (Kass et al. 2023). Before generating models, we divided occurrence points into training and testing data to validate the predictive ability of our models to classify withheld data. We used a spatial partitioning method, dividing our occurrences into 4 equal blocks based on geographic proximity, with the R package ENMeval (Muscarella et al. 2014). It is generally recommended to use spatial partitioning methods as they increase the transferability of model results and better assess the ability of the model to predict across the entire range (Randin et al. 2006, Wenger and Olden 2012). Models

were generated using the Maxent algorithm (Phillips et al. 2006), allowing for all four feature classes (L-Linear, Q-Quadratic, H-Hinge, and P-Product) to provide maximum model complexity. We generated five candidate models, with regularization multipliers (higher values implement higher penalties of complexity on the model) ranging from 1 to 5, with a step value of 1, to parameterize model complexity (Warren and Seifert 2011, Radosavljevic and Anderson 2014). Models were evaluated based on corrected Akaike Information Criterion, Omission Rates, and Continuous Boyce Index. The model with the lowest AICc was considered the best performing model, as this metric consistently outperforms others at selecting models that accurately estimate habitat suitability and relative importance of predictors (Warren and Seifert 2011).

Estimating future range loss and gain

We projected our best fit model into projected climate conditions for 2021-2040, 2041-2060, and 2061-2080 of global scenarios 370 and 585 of global circulation model MPI-ESM1-2-HR. To estimate range changes, our resulting models of future habitat suitability were classified into binary predictors of absence or presence at a threshold of 10 percentile training presence (Kass et al. 2023), so we could compare area of suitable habitat across scenarios and time periods. Because our models include climatically suitable habitat that is unlikely to be colonized due to the limited dispersal ability of collared pikas (Zgurski and Hik 2012), we bounded our loss/gain analysis within the realized range of the species using an adjusted range polygon.

Refining range map

To better track range expansions and understand current occurrence, we created a more reliable range map for collared pikas, modified from the existing IUCN range map (Lanier and Hik 2016). The existing polygon for the species was overlayed with a map of talus (see Chapter 1) and a map of climate suitability (developed in this study). Areas with overlap of all three layers were extracted into a new polygon layer. All known occurrence points were overlayed and portions of continuous area without occurrence points were removed from the polygon layer. The resulting range map (Figure 2.1) encompasses all known localities of collared pikas, making it a meaningful update on the existing map (Lanier and Olson 2013, Baltensperger and Huettmann 2015), and is more representative of the true range because it incorporates talus availability and climate suitability.

RESULTS

Trait-based vulnerability assessment

Our assessment of collared pika climate change vulnerability resulted in a vulnerability score between 5.31 and 6.09, leading to a classification of the species as Moderately Vulnerable (Table 2.3). We assessed traits corresponding to 10 categories found to influence climate change vulnerability: threat of climate exposure, adaptive capacity based on distribution, movement,

evolutionary potential, ecological role, abiotic niche, life history, demography, change in vulnerability based on threat multipliers, and change in vulnerability based on documented/modeled response to climate change (Table 2.2). Collared pikas ranked relatively low for climate exposure under RCP 4.5 with a ranking of 0.36 and high for climate exposure under RCP 8.5 with a ranking of 0.56. The species ranked moderately low for adaptive capacity, with a score of 3.55, based on low evolutionary potential, narrow abiotic niche, and limited dispersal ability (Figure 2.2). Threat multipliers such as movement barriers, land-use change, and anthropogenic threats did not have a large impact on collared pika vulnerability, with a threat multiplier of 0.2. Based on this study, the species ranked 0.33, Moderately Vulnerable, in the documented/modeled response to climate change module.

Predictors of species distribution

The best-fitting SDM showed reliable predictive performance according to the omission rate (OR < 0.10) and continuous Boyce index (CBI > 0.85) metrics (Table 2.3), meaning that the model predicted ~90% of withheld occurrence data as presence locations and performed better at predicting occurrences than would be expected by chance. Maximum temperature of the warmest month had the highest contribution to the climatic niche (25.6%), with warmer temperatures having a positive effect on suitability until reaching ~20°C. Mean temperature of the driest quarter had the second highest contribution to the climatic niche (25.1%), with suitability decreasing as temperatures increased above 0°C. Precipitation of the warmest quarter had the next highest contribution (21.2%), where suitability increased with higher precipitation. Minimum temperature of the coldest month had the next highest contribution (17.9%) with warmer temperatures having a positive effect on suitability. The niche suitability increased with mean diurnal ranges between -10 and 0°C (4.5%), decreased with higher mean temperatures of the wettest quarter (2.9%), decreased with annual precipitation (2.8%), and increased with precipitation of the coldest quarter (<1%, Figure 2.3).

The model overpredicted the collared pika range, identifying climatically suitable habitat in areas with no previous records of collared pika occurrence (Figure 2.4), particularly in the northwestern portion of Alaska. This is expected, as this species has a notably short dispersal range (Zgurski and Hik 2012). The model prediction was clipped to the current known extent, estimating a total area of 409,911.14 km² accessible, climatically suitable habitat. The potential distribution decreased significantly under both modeled emissions scenarios (Table 2.4). Under SSP 370, the area of climatically suitable habitat decreased by 42.5% by 2060 and 56.1% by 2080. Under SSP 585, the area of climatically suitable habitat decreased by 47.7% by 2060 and 67.7% by 2080. In both scenarios, ranges retracted towards higher elevations and expanded poleward (Figure 2.5).

DISCUSSION

We evaluated climate vulnerability of the collared pika through trait-based and climate correlative assessment, providing baseline evidence of high climate vulnerability, highlighting the need for increased monitoring of this at-risk species. Our adaptive capacity assessment suggests a limited ability to persist through changing climates, based on low evolutionary potential, narrow abiotic niche, and limited dispersal ability. Likewise, future modeling indicates loss of ~55-70% of suitable area in the current range as well as minimal suitability for shifting to track newly available areas. When faced with novel unsuitable conditions, a species can either “persist in place” or “shift in place” (Thurman et al. 2020). Our results indicate that collared pikas are limited in their capacity for either, and thus are highly vulnerable to projected climate change.

Conducting an assessment of trait-based vulnerability has been identified as a top priority to collared pika conservation (Environment and Climate Change Canada 2023) to better inform how key climatic variables affect this species across the range. Our trait-based assessment indicates variable exposure to climate change with low adaptive capacity and high sensitivity to climatic changes, resulting in a NatureServe CCVI rank of Moderately Vulnerable. The assessment of adaptive capacity focused on traits associated with the ability to adjust to novel conditions genetically, behaviorally, and spatially, resulted in a ranking of 3.55 (out of 10) and a classification of Moderately Low. This classification is largely driven by the assessment of evolutionary potential, where collared pikas score low in all three traits. This species is known to have relatively low genetic diversity (Lanier and Olson 2013), meaning there is little chance for genetic variation allowing for adaptation to changing conditions. Likewise, the species occurs in low densities (Broadbooks 1965, Morrison and Hik 2007, Horn 2013), limiting the allelic options for adaptation in an area. The evidence for low evolutionary potential is strong, with supporting studies occurring across the range. The other most influential trait sets, reflecting the ability to spatially or behaviorally adapt to changing conditions, are less supported by empirical studies. For example, collared pikas score low on movement traits, yet the majority of studies on their dispersal are limited to one study site in the southeastern portion of the range. Here, recorded dispersal events were limited by size of the study site, and instances of dispersal beyond 2 km would not have been detected. Preliminary data from another region, the Alaska Range, suggests that further dispersal may be possible, with evidence of population connectivity between two populations ~30 km apart (Lanier, unpublished data). Our lack of knowledge of dispersal across the range may impede our assessment of dispersal distance, high site fidelity, and age-restricted dispersal. More work is needed to understand collared pika movement rangewide to provide more information on how well this species will be able to track suitable environmental conditions. The ability to behaviorally adapt to changing conditions (represented in the abiotic niche module) is similarly understudied and regionally-biased, with evidence of low physiological tolerances and seasonal physiology from American pikas and single study sites of collared pikas informing adaptive capacity rangewide (MacArthur and Wang 1973, Morrison et

al. 2009), although recent works have strived to fill gaps in our understanding of environmental effects on behavior across the broader range (Harrison 2023). A study of adaptive capacity in American pikas found differences in vulnerability within clades occupying different regions (Beever et al. 2023). This is likely the case in collared pikas as well, due to differing climatic drivers of occurrence (see Chapter 1) and differences in environment (e.g., elevational and precipitation gradients). However, as most of the detailed ecological studies on collared pikas behavior originate from a single study site (Pika Camp; e.g., Franken and Hik 2004, Trefry and Hik 2009, Zgurski and Hik 2012), more foundational work is necessary to describe differences in behavioral response to adverse conditions across the range to inform regional adaptive capacity. Based on current available information, it seems likely that this species will be challenged to adapt to forecasted climate changes beyond their niche.

Our species distribution model indicates a complex relationship between precipitation, temperature, and the collared pika climatic niche. Maximum temperature of warmest month, mean temperature of driest quarter, precipitation of warmest quarter, and minimum temperature of coldest month explained ~90% of the variability in collared pika distribution. Importantly, our results suggest that collared pikas are more likely to be found in areas that experience drier conditions in the winter. Although collared pikas are known to rely on winter precipitation for insulative snowpack (Morrison and Hik 2007), rain-on-snow events can substantially decrease the insulative capacity of the snowpack (Pauli et al. 2013). These events have increased in modern times and are projected to continue to increase across the range of collared pikas (Du et al. 2025), likely increasing winter thermal stress. Our results also reflect the tenuous balance between environmental conditions producing quality forage and thermal stress. Likelihood of pika occurrence increases with maximum temperature of the warmest month, which likely reflects more suitable growing conditions for forage. However, probability of occurrence decreases over 20°C, which may reflect the upper limit of temperature suitability. We recognize that microclimates within talus are critical for pikas' ability to persist through unfavorable conditions (Sakiyama and Molinos 2025), but broad-scale surface temperatures influence these microclimates which have experienced warming in tandem with ambient-air temperatures (Monk and Ray 2022). Our results suggest that beyond ~20°C ambient temperature, the cooler interstitial spaces within the talus may no longer provide efficient thermal refuges for collared pikas. We see a similar balancing act regarding precipitation, where probability of occurrence increases with precipitation of the warmest quarter, likely linked to forage quality, yet decreases with annual precipitation, likely linked to thermal stress and reduced foraging time to avoid unfavorable conditions. Taken together, these results highlight the dual, and sometimes opposing, climate pressures which result in a relatively narrow climatic niche of the collared pika.

Our species distribution model also suggests drastic changes to the collared pika distribution, with projections indicating a 55–70% range contraction by the end of the century. Binary suitability classification maps projected range loss under both the SSP 370 and 585 scenarios, with upslope movement and northward expansion predicted under both scenarios.

These results are consistent with previous observations showing poleward movements in response to climate change (Parmesan et al. 1999, Hickling et al. 2006). Northward expansion appears to be limited to the Richardson mountains in the northern Yukon territory, where talus habitat exists beyond currently suitable areas, while northward expansion in other regions is constrained by talus availability. Unbounded habitat suitability models based on present day conditions indicate climatic suitability in the western portion of the Brooks Range (Figure 2.4), which has no documented occurrences of collared pikas. Although appearing suitable, this mountain range remains currently disconnected to current populations by lowland areas lacking appropriate talus cover. Our models indicate the potential for colonization of the Brooks range northwest of the extent of the current range as favorable climates move poleward. Beyond the northern limit, there is little predicted latitudinal shifting of the distribution with favorable conditions moving upslope rather than poleward. The Yukon Tanana Uplands, a relatively low elevation area in the center of the current range, experiencing the most extreme modern temperatures, is at great risk of total population loss due to the lack of upslope colonization ability. Our models indicate loss of between 92.4 and 97.4% of suitable area within this portion of the species' range. While upslope and poleward shifts have not been documented in this species, these predictions of future changes in distribution generally align with reports of documented upslope retraction in other pika species (Beever et al. 2003, Moritz et al. 2008, Robson et al. 2016, Billman et al. 2021*b*) and alpine species in general (Pounds et al. 1999, Polechová 2018). Similar studies have projected between a 22–73% (Calkins et al. 2012) and 25% (Leach et al. 2015) loss in suitable area for the closely related American pika. Our results indicate that collared pikas are likely to experience greater loss of suitable area than the American pika, underscoring the importance of increasing focus on this species as climate change occurs more rapidly within their range (Serreze and Barry 2011).

Climate relationships are complex and vary across space, so results of any correlative climate vulnerability model should be interpreted cautiously. However, the results of our trait-based analysis support the likelihood of population loss and habitat reductions exhibited by our models. This assessment of high climate change vulnerability supports the need for increased monitoring of this species. In the absence of refined population and abundance data, it is challenging to assess projected loss of habitat and corroborate models of distribution shifts. Conservation organizations should prioritize establishing long-term monitoring sites to identify any distribution/population shifts, particularly in the northern extent of the range in the northern Yukon Territory where expansion is projected to occur and in the Yukon-Tanana uplands of central Alaska where the most significant loss of habitat is predicted. Additionally, encouraging public participation in collared pika conservation efforts is of high priority to expanding collared pika conservation efforts (Environment and Climate Change Canada 2023). Portions of the core collared pika range are well-sampled (e.g., Denali National Park, Chugach State Park, Tombstone Provincial Park, and Kusawa Territorial Park, and Kluane National Park) with many recent recorded observations on iNaturalist. Systematic, sustained monitoring plans across the range, paired with a broader push for community contributed datasets of pika occurrence at more

marginal locations (e.g., iNaturalist or Pika Watch observations) are recommended for tracking predicted retractions. By establishing long-term monitoring and encouraging the use of community-science, we can fill in critical gaps in our knowledge of collared pika distribution and population trends.

This work further underscores the importance of continual review of species' needs and conservation plans. Many climate change assessments are conducted in rapid, batch-style to meet the needs of agencies evaluating concern for Wildlife Action Plans (Droghini et al. 2022) or to assess entire regions simultaneously (Hope et al. 2015, Leach et al. 2015). These works are important to evaluate system-wide risk in a timely manner, but there is merit in re-analyzing a target species with a more fine-scale approach. Even species-specific niche-models (e.g., Lanier and Olson 2013) should be re-conducted in a timely manner, as more occurrence data and refined modeling methods become available. Here, our species-specific focus allowed us to (1) parameterize our models with variables directly relevant to our single species and (2) focus more on the drivers of distribution as they relate to our target species' ecology. With growing concern for species' ability to persist through changing climates, species-specific analyses incorporating trait-based and modelled assessments are important endeavors, and provide essential data for developing a better understanding of vulnerability on a changing planet.

Ultimately, this research contributes to the growing body of evidence indicating that alpine and cold-adapted species like the collared pika are particularly vulnerable to climate change, both from direct climatic shifts and the compounded effects of habitat isolation and limited adaptive capacity. Similar to trends observed in the American pika and other alpine specialists, collared pikas face a narrowing window of climatic suitability, restricted movement options, and limited capacity for evolutionary or behavioral adjustment. More broadly, this study highlights the importance of integrating trait-based vulnerability assessments with climate-correlative models to better anticipate the fates of data-deficient, range-restricted species under climate change. As climate change continues to alter high-latitude and alpine systems more rapidly than many other ecosystems, this study of the collared pika serves as an example of the challenges facing cold-adapted species globally. Continued research, targeted monitoring, and public engagement will be essential not only for conserving collared pikas but also for informing conservation strategies for other alpine species facing similar threats.

TABLES

Table 2.1. Climatic variables and their proposed influence on collared pika ecology. Variables were accessed from WorldClim and represent averages over the years 1970–2000.

Name	Description	Potential Ecological Impact
Bio1	Mean Diurnal Range	Thermal stress, overwinter survival, forage quality and haying
Bio5	Maximum Temperature of the Warmest Month	Thermal stress, forage quality and haying
Bio6	Minimum Temperature of the Coldest Month	Thermal stress, overwinter survival
Bio8	Mean Temperature of the Wettest Quarter	Forage quality, overwinter survival
Bio9	Mean Temperature of the Driest Quarter	Thermal stress, forage quality
Bio12	Annual Precipitation	Forage quality and haying, overwinter survival
Bio18	Precipitation of Warmest Quarter	Thermal stress, forage quality and haying
Bio19	Precipitation of Coldest Quarter	Thermal stress, overwinter survival

Table 2.2. Assessment of collared pika traits and their implications for climate vulnerability following NatureServe recommendations.

Trait	Ranking	Reasoning
Threat of Climate Exposure		
Exposure to Sea Level Rise	Neutral	Species is distributed in inland, mountainous habitats (Broadbooks 1965)
Adaptive Capacity based on Distribution		
Extent of Occurrence (EOO)	High	Total area encompassing entire range >20,000 km ²
Area of Occurrence (AOO)	High	>2,000 km ² of range is occupied
Habitat Specialization (HS)	Low	>85% of occurrences contained in talus habitat (MacDonald and Jones 1987)
Commensalism with Humans (CH)	Moderate	Related species known to utilize semi-natural landscapes (e.g., artificial rock piles, roadsides, Smith 1974b)
Geographic Rarity (GR)	Moderately High	Species broadly distributed with sparse or isolated populations (Lanier and Olson 2013)
Adaptive Capacity based on Movement		
Dispersal Syndrome (DS)	Low	Dispersal generally limited to juveniles with few recorded instances of adult dispersal (Franken and Hik 2004, Zgurski and Hik 2012)
Dispersal Distance (DD)	Moderately High	Individuals disperse average of 500-539 m (Franken 2002)
Dispersal Phase (DP)	Low	Dispersal associated with juvenile life stage (Franken 2002, Zgurski and Hik 2012)
Site Fidelity (SF)	Moderate	No reliable ratio of “stayers” to “strayers”, juvenile site fidelity is dependent on habitat quality and availability (Franken 2002)
Adaptive Capacity based on Evolutionary Potential		
Genetic Diversity (GD)	Low	Low within-population genetic variability and low genetic variation compared to other pika species (Lanier and Olson 2013)
Population Size (PS)	Low	Low local abundance of individuals (Broadbooks 1965, Morrison and Hik 2007, Horn 2013)
Hybridization Potential (HP)	Low	No range overlap with other pika species
Adaptive Capacity based on Ecological Role		
Enemies (E)	Unknown	Possible increased competition with marmots (Morrison et al. 2009) as forage quantity decreases (Droghini et al. 2022)
Diet Breadth (DB)	High	Species known to select broad range of forage (Morrison et al. 2004)

Diversity of Obligate Species (DOS)	High	No obligate interactions with other species
Adaptive Capacity based on Abiotic Niche		
Seasonal Phenology (SP)	Low	Dependent on seasonal environmental cues for hay piling and foraging (Morrison et al. 2009:200)
Climatic Niche Breadth (CNB)	Low	Species restricted to a particular climatic condition that could be lost because of climate change
Physiological Tolerances (PT)	Low	Range of novel conditions known to cause lethal effects (MacArthur and Wang 1973)
Behavioral Regulation of Physiology (BRP)	Moderate	Species reduces above-ground activity (e.g., foraging, haying) during unfavorable conditions (Harrison 2023)
Disturbance Tolerance (DT)	Moderate	Changes in intensity, frequency, and severity of droughts, wildfires, and disease outbreaks are likely to have moderate impacts on the species
Adaptive Capacity based on Life History		
Reproductive Phenology (RP)	Low	Dependence on seasonal cues like loss of snowpack to cue reproduction (Renee J. Franken and Hik 2004)
Reproductive Mode (RM)	High	Species is viviparous
Mating System (MS)	High	Species is polygynandrous; individuals of both sexes have multiple mating partners (Zgurski and Hik 2012)
Fecundity (F)	Moderate	Litter size ranges from 1-4 (MacDonald and Jones 1987, R. J. Franken and Hik 2004)
Parity (P)	High	Species has multiple reproductive cycles throughout lifespan (Franken 2002)
Sex Ratio (SR)	High	Species has balanced sex ratio (Franken 2002)
Sex Determination (SD)	High	Species has chromosomal sex determination
Parental Investment (PI)	Low	Juveniles require parental care at birth
Adaptive Capacity based on Demography		
Life Span (LS)	Moderately High	Average lifespan is within 1-10 years (Franken 2002)
Generation Time (GT)	Moderately High	1-2 years average time between two consecutive generations (Franken and Hik 2004)
Age of Sexual Maturity (ASM)	High	Individuals reach sexual maturity at 1 year (Franken 2002, R. J. Franken and Hik 2004)
Age Structure (AS)	Moderate	Balanced age classes found in closely related species (Millar and Zwickel 1972)
Recruitment (R)	Low	Low juvenile overwinter survival (Franken 2002)
Change in Vulnerability based on Threat Multipliers		
Topographic Barriers	Greatly Increase	Distribution limited by availability of talus habitat, associated with alpine environments (MacDonald and Jones 1987)

Anthropogenic Barriers	Neutral	Significant anthropogenic barriers do not exist for this species
Land-use Change	Neutral	Species' habitat at low risk of agricultural or urban development
Other Anthropogenic Threats	Neutral	Harvest, by-catch, pollution, and disturbance not expected to cause a population decrease of >10%
Other Biological Threats	Neutral	Species not expected to be significantly impacted by an invasive species because of climate change
Change in Vulnerability based on Documented/Modeled response to Climate Change		
Documented Response to Climate Change	Unknown	No data on overall population trends of the species
Modeled Future Change in Range Size	Increase	Predicted range represents 56-67% decrease relative to current range
Overlap of Modeled Future Range with Current Range	Somewhat Increase	Predicted future range overlaps with current range by 30.99-43.17%
Occurrence of Protected Areas in Modeled Future	Neutral	~40% of future distribution is encompassed by protected areas

Table 2.3. CCVI results report of collared pika climate vulnerability under representative concentration pathway 4.5 (representing a medium-low emissions scenario) and 8.5 (representing a high-emissions scenario).

	RCP 4.5	RCP 8.5
Climate Exposure (Module A)	0.36	0.56
<i>Exposure Category</i>	Relatively Low	High
Exposure to Sea Level Rise (Module B)	0	0
Adaptive Capacity Score (sum of Modules C – I)	3.55	
<i>Adaptive Capacity Category</i>	Moderately Low	
Threat Multipliers (Module J)	0.2	
<i>Vulnerability Score</i>	5.31	6.09
Documented Response	0.33	
Documented Response Category	Moderately Vulnerable	
<i>Overall CCVI Category</i>	Moderately Vulnerable	

Table 2.3. Model evaluation table showing each model's omission rate of withheld presence locations outside of the minimum training presence threshold, continuous Boyce index, and AICc.

Feature Class	Regularization Multiplier	Omission Rate (MTP)	Continuous Boyce Index	Δ AICc
LQHP	1	0.08	0.89	0
LQHP	2	0.09	0.87	39.60
LQHP	3	0.07	0.86	61.52
LQHP	4	0.06	0.85	75.17
LQHP	5	0.06	0.85	83.90

Table 2.4. Predicted loss in climatically suitable areas under SSP 370 (continuing current emission trends) and SSP 585 (increased demand for fossil-fueled energy consumption) by 2060 and 2080.

SSP	Current climatically suitable area (km ²)	Future suitable area (km ²)		Potential net range gain/loss	
		2060	2080	2060	2080
370	409,911.15	235,775.29	179,896.97	-42.5%	-56.1%
585	409,911.14	214,533.88	132,247.31	-47.7%	-67.7%

FIGURES

Figure 2.1. (A) Map of the study region including the current IUCN range map and all known occurrences. (B) Map using the suggested revised range map, which contains all known occurrence points and accounts for habitat availability and climatic suitability.

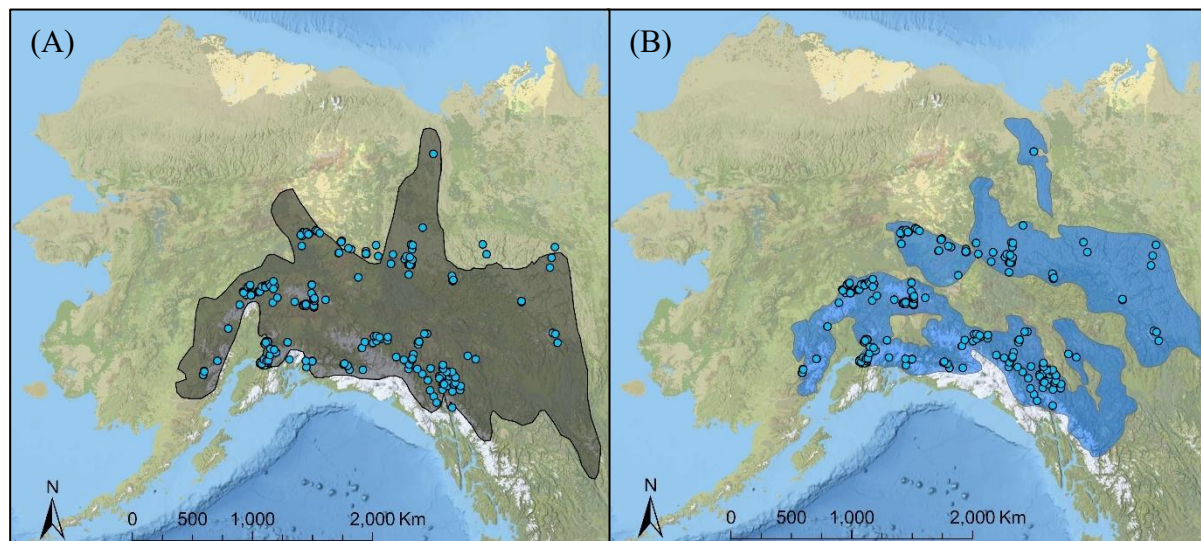


Figure 2.2. Collared pika adaptive capacity represented by the 37 NatureServe assessment factors, color-coded by level of adaptive capacity. Low adaptive capacity of collared pikas is primarily driven by low evolutionary potential and low physiological tolerance.

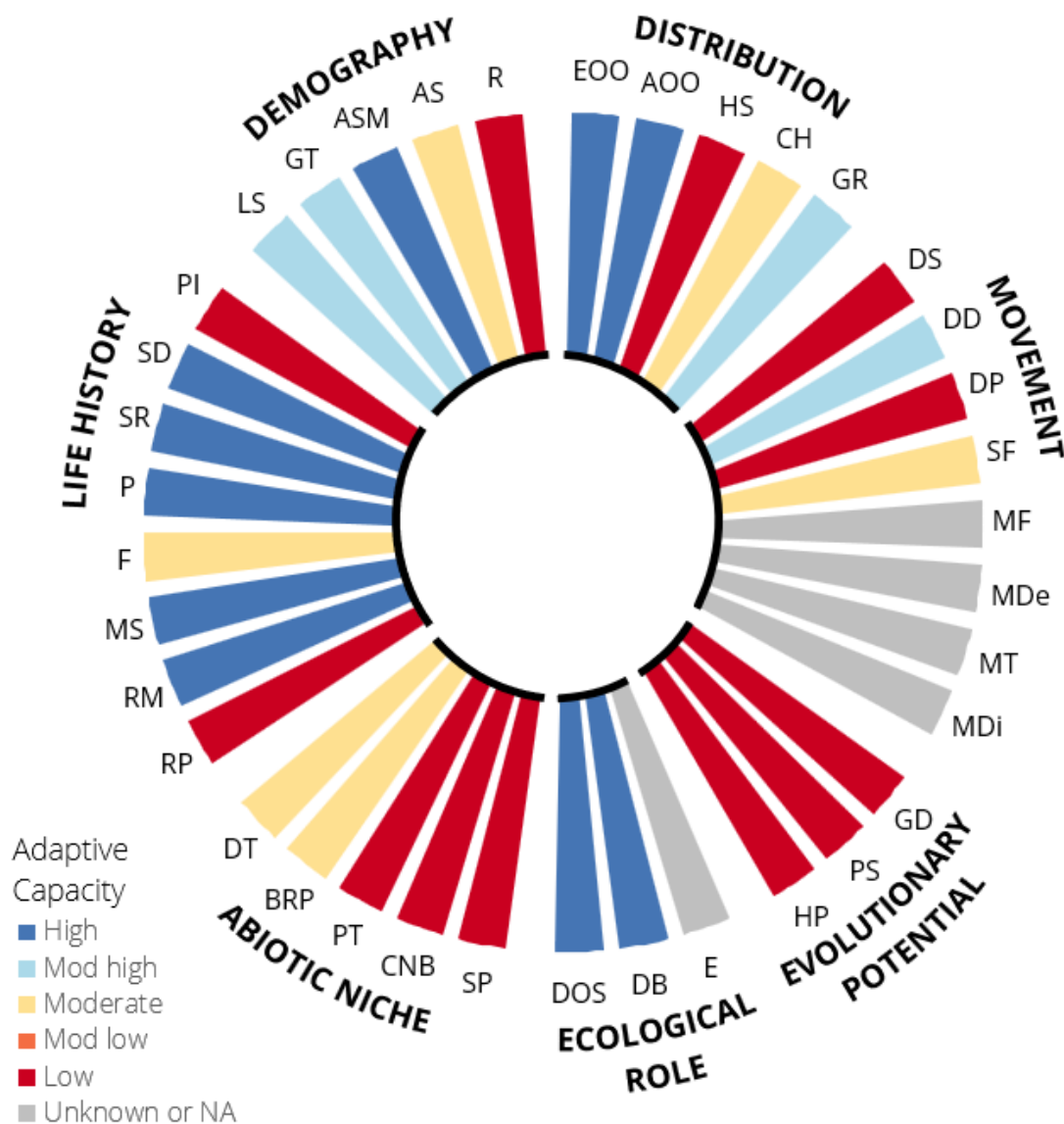


Figure 2.3. Relative importance of each climate variable on collared pika distribution. Maximum temperature of warmest month, mean temperature of driest quarter, precipitation of warmest quarter, and minimum temperature of the coldest month accounted for ~90% of the model's prediction.

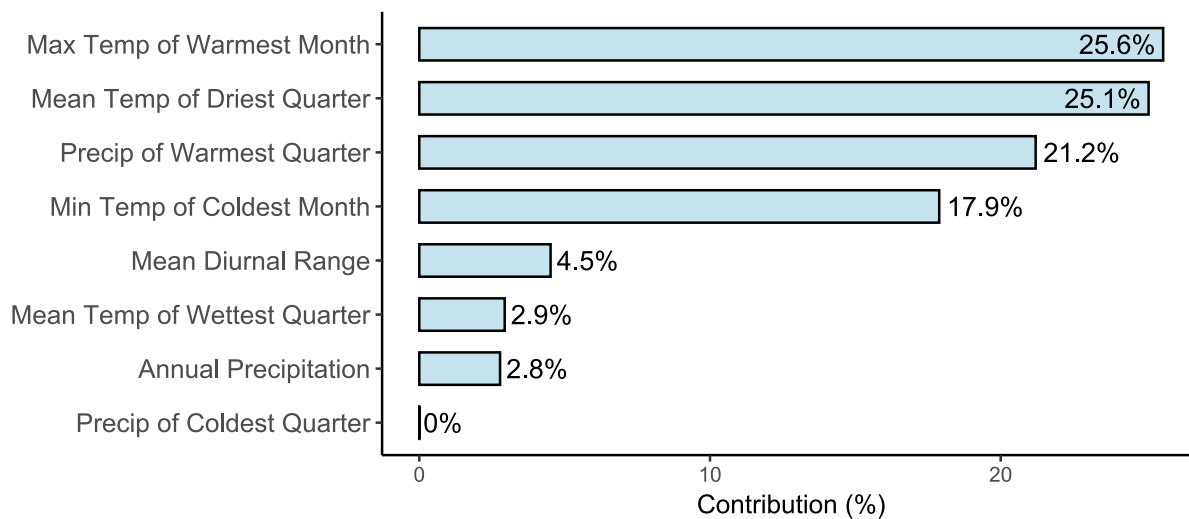


Figure 2.4. Partial dependence plots for each climate variable ordered by relative influence on collared pika distribution.

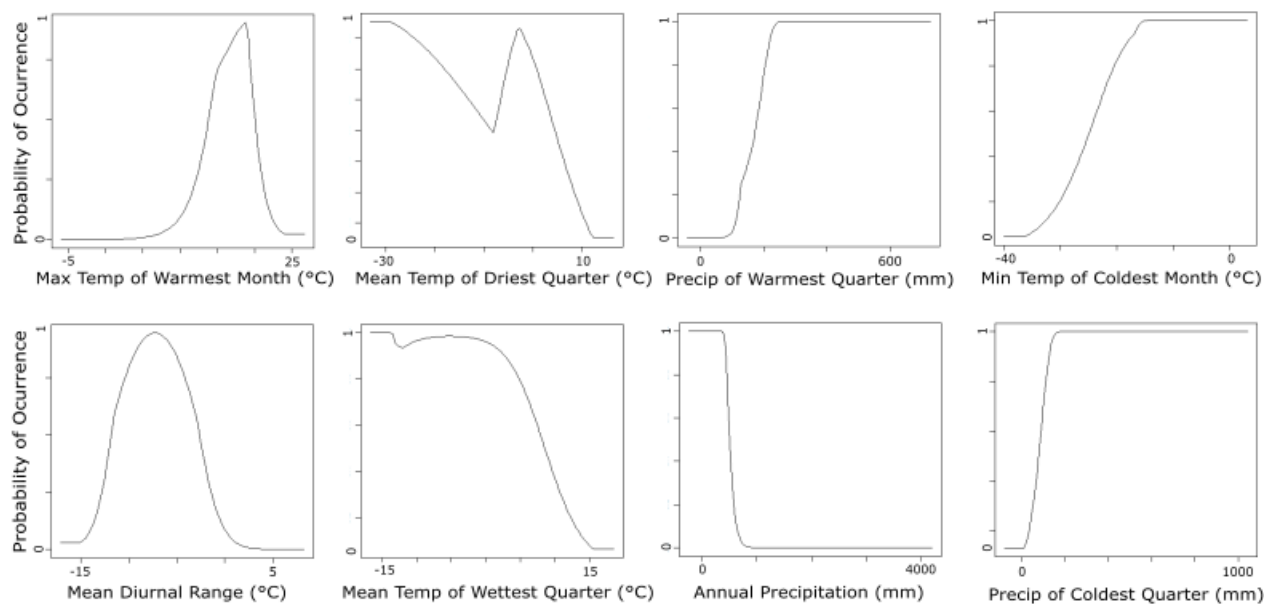


Figure 2.5. Model prediction of current climatically suitable areas for collared pikas with suggested revised range map (Fig. 2.1) overlaid in white.

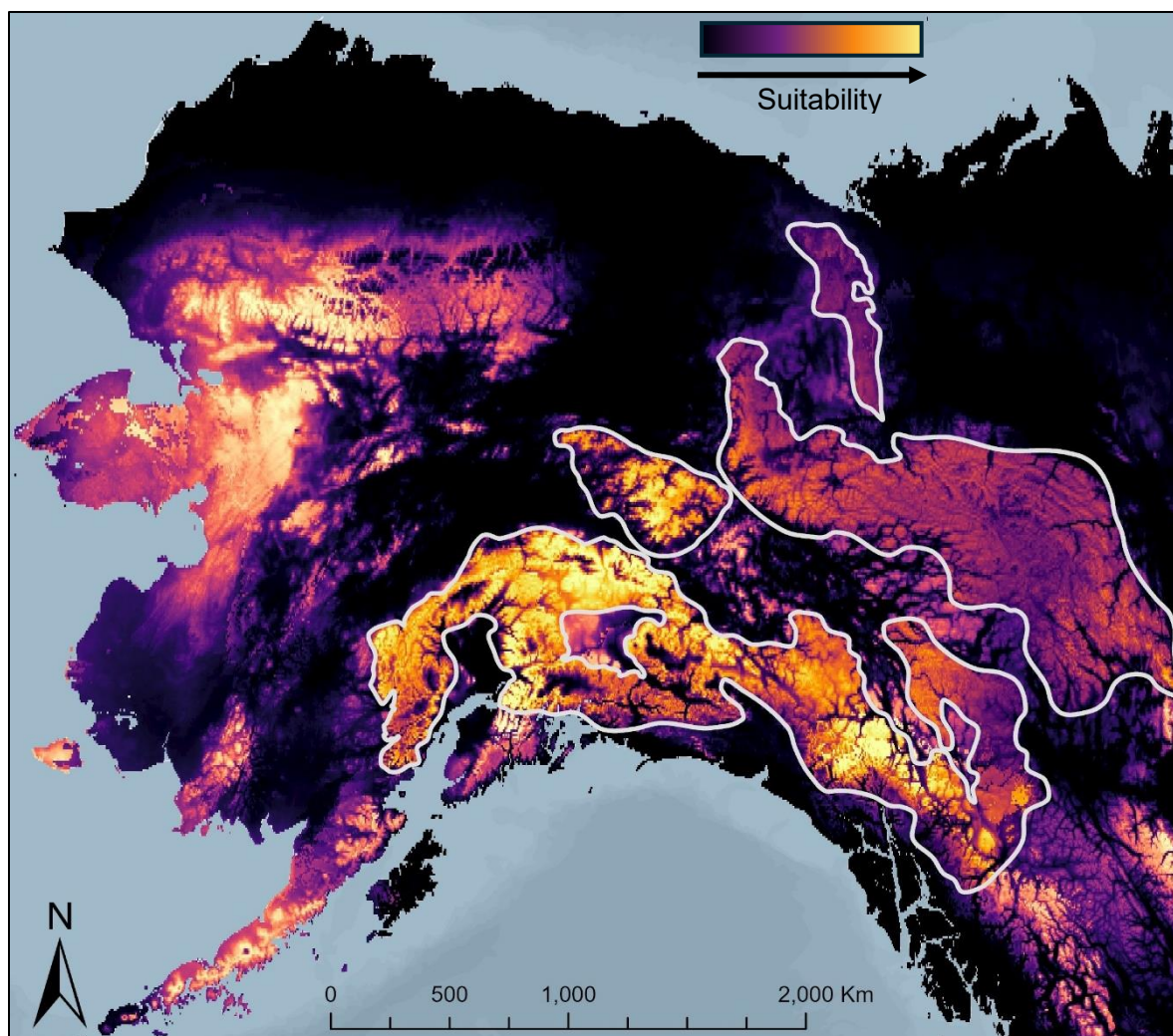
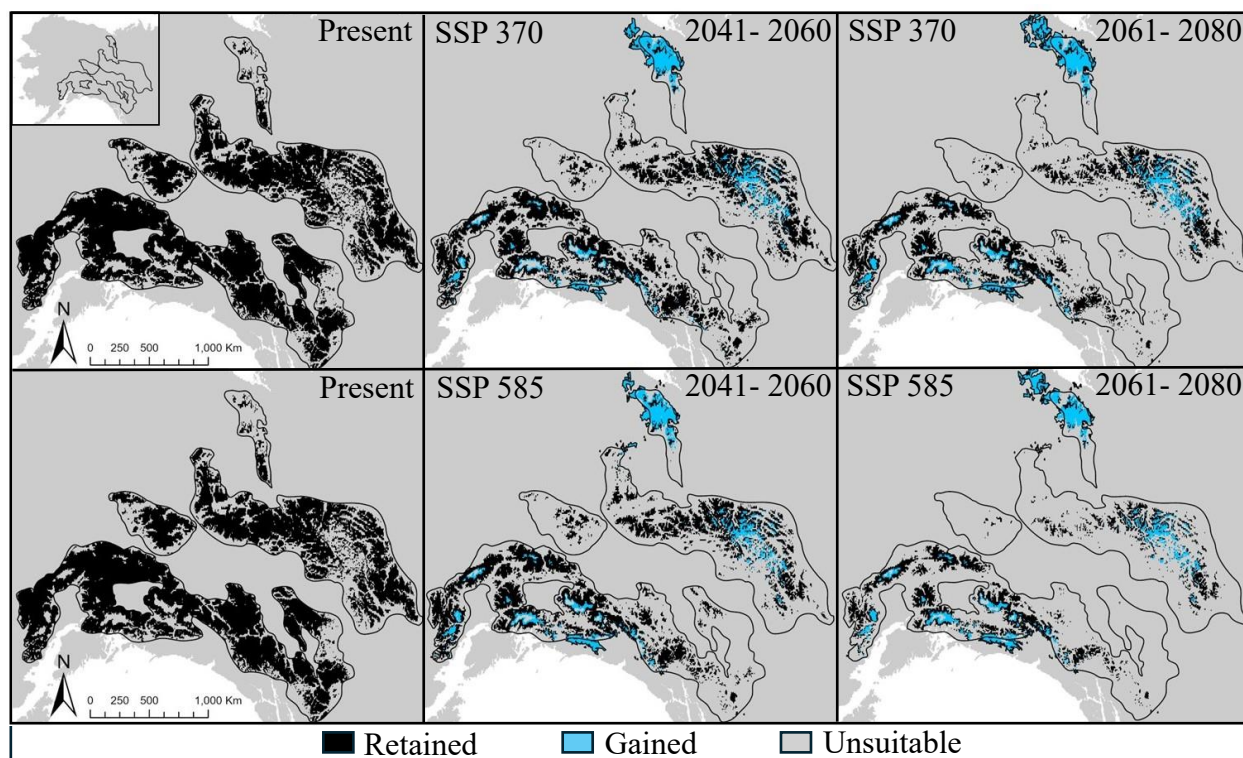


Figure 2.6. Retention (black), gain (blue), and loss (gray) of climatically suitable habitat for collared pikas in 2041-2060 and 2061-2080 under predicted climate scenarios 370 (continued rate of current emissions) and 585 (increased carbon emissions).



REFERENCES

- Aiello-Lammens, M. E., R. A. Boria, A. Radosavljevic, B. Vilela, and R. P. Anderson. 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* 38:541–545.
- Ancillotto, L., L. Santini, N. Ranc, L. Maiorano, and D. Russo. 2016. Extraordinary range expansion in a common bat: the potential roles of climate change and urbanisation. *The Science of Nature* 103:15.
- Baltensperger, A. P., and F. Huettmann. 2015. Predictive spatial niche and biodiversity hotspot models for small mammal communities in Alaska: applying machine-learning to conservation planning. *Landscape Ecology* 30:681–697.
- Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S. P. Maher, A. T. Peterson, J. Soberón, and F. Villalobos. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling* 222:1810–1819.
- Beever, E. A., P. E. Brussard, and J. Berger. 2003. Patterns of apparent extirpation among isolated populations of pikas (*Ochotona princeps*) in the Great Basin. *Journal of Mammalogy* 84:37–54.
- Beever, E. A., J. D. Perrine, T. Rickman, M. Flores, J. P. Clark, C. Waters, S. S. Weber, B. Yardley, D. Thoma, T. Chesley-Preston, K. E. Goehring, M. Magnuson, N. Nordensten, M. Nelson, and G. H. Collins. 2016. Pika (*Ochotona princeps*) losses from two isolated regions reflect temperature and water balance, but reflect habitat area in a mainland region. *Journal of Mammalogy* 97:1495–1511.
- Beever, E. A., C. Ray, P. W. Mote, and J. L. Wilkening. 2010. Testing alternative models of climate-mediated extirpations. *Ecological Applications* 20:164–178.
- Beever, E. A., J. L. Wilkening, P. D. Billman, L. L. Thurman, K. A. Ernest, D. H. Wright, A. M. Gill, A. C. Craighead, N. A. Helmstetter, L. K. Svancara, M. J. Camp, S. Bhattacharyya, J. Fitzgerald, J. M. R. Hirose, M. L. Westover, F. D. Gerraty, K. B. Klingler, D. A. Schmidt, D. K. Ryals, R. N. Brown, S. L. Clark, N. Clayton, G. H. Collins, K. A. Cutting, D. F. Doak, C. W. Epps, J. E. Foley, J. French, C. L. Hayes, Z. A. Mills, L. Moyer-Horner, L. B. Nichols, K. B. Orlofsky, M. M. Peacock, N. C. Penzel, J. Peterson, N. Ramsay, T. Rickman, M. M. Robinson, H. L. Robison, K. M. C. Rowe, K. C. Rowe, M. A. Russello, A. B. Smith, J. A. E. Stewart, W. W. Thompson, J. H. Thorne, M. D. Waterhouse, S. S. Weber, and K. C. Wilson. 2023. Geographic and taxonomic variation in adaptive capacity among mountain-dwelling small mammals: Implications for conservation status and actions. *Biological Conservation* 282:109942.
- Billman, P. D., E. A. Beever, D. B. McWethy, L. L. Thurman, and K. C. Wilson. 2021a. Factors influencing distributional shifts and abundance at the range core of a climate-sensitive mammal. *Global Change Biology* 27:4498–4515.
- Billman, P. D., E. A. Beever, D. B. McWethy, L. L. Thurman, and K. C. Wilson. 2021b. Factors influencing distributional shifts and abundance at the range core of a climate-sensitive mammal. *Global Change Biology* 27:4498–4515.
- Boakes, E. H., P. J. K. McGowan, R. A. Fuller, D. Chang-qing, N. E. Clark, K. O'Connor, and G. M. Mace. 2010. Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data. *PLOS Biology* 8:e1000385.
- Borgelt, J., M. Dorber, M. A. Høiberg, and F. Verones. 2022. More than half of data deficient species predicted to be threatened by extinction. *Communications Biology* 5:679.

- Boria, R. A., L. E. Olson, S. M. Goodman, and R. P. Anderson. 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling* 275:73–77.
- Bowler, D. E., C. T. Callaghan, N. Bhandari, K. Henle, M. Benjamin Barth, C. Koppitz, R. Klenke, M. Winter, F. Jansen, H. Bruelheide, and A. Bonn. 2022. Temporal trends in the spatial bias of species occurrence records. *Ecography* 2022:e06219.
- Broadbooks, H. E. 1965. Ecology and distribution of the pikas of Washington and Alaska. *The American Midland Naturalist* 73:299–335.
- Calkins, M. T., E. A. Beever, K. G. Boykin, J. K. Frey, and M. C. Andersen. 2012. Not-so-splendid isolation: modeling climate-mediated range collapse of a montane mammal *Ochotona princeps* across numerous ecoregions. *Ecography* 35:780–791.
- Cannings, S. G., T. S. Jung, J. H. Skevington, I. Duclos, and S. Dar. 2019. A reconnaissance survey for Collared Pika (*Ochotona collaris*) in northern Yukon. *The Canadian Field-Naturalist* 133:130–135.
- Castillo, J. A., C. W. Epps, A. R. Davis, and S. A. Cushman. 2014. Landscape effects on gene flow for a climate-sensitive montane species, the American pika. *Molecular Ecology* 23:843–856.
- Castillo, J. A., C. W. Epps, M. R. Jeffress, C. Ray, T. J. Rodhouse, and D. Schwalm. 2016. Replicated landscape genetic and network analyses reveal wide variation in functional connectivity for American pikas. *Ecological Applications* 26:1660–1676.
- Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science* 333:1024–1026.
- Clark, J. A., and R. M. May. 2002. Taxonomic Bias in Conservation Research. *Science* 297:191–192.
- COSEWIC. 2011. COSEWIC Assessment and Status Report on the Collared Pika (*Ochotona collaris*) in Canada. Committee on the Status of Endangered Wildlife in Canada, Canadian Wildlife Service, Ottawa, ON.
- Danielson, J. J., and D. B. Gesch. 2011. Global multi-resolution terrain elevation data 2010 (GMTED2010). Open-File Report, USGS Numbered Series.
- Dearing, M. D. 1997. The Function of Haypiles of Pikas (*Ochotona princeps*). *Journal of Mammalogy* 78:1156–1163.
- Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46.
- Droghini, A., K. S. Christie, R. R. Kelty, P. A. Schuette, and T. Gotthardt. 2022. Conservation status, threats, and information needs of small mammals in Alaska. *Conservation Science and Practice* 4:e12671.
- Du, J., P. B. Kirchner, C. G. Pan, J. D. Watts, and J. S. Kimball. 2025. Assessing rain-on-snow event dynamics over Alaska using 30 year satellite microwave observations. *Environmental Research Letters* 20:034048.
- Earth Resources Observation and Science (EROS) Center. 2020. Landsat 8-9 Operational Land Imager / Thermal Infrared Sensor Level-2, Collection 2 [dataset]. U.S. Geological Survey. <<https://www.usgs.gov/centers/eros/science/usgs-eros-archive-landsat-archives-landsat-8-9-olitis-collection-2-level-2>>. Accessed 20 Mar 2025.

- Elith, J., and J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics* 40:677–697.
- Environment and Climate Change Canada. 2023. Management Plan for the Collared Pika (*Ochotona collaris*) in Canada. Species at Risk Act Management Plan Series. featured articles. <<https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/management-plans/collared-pika-2023.html>>. Accessed 3 Sep 2024.
- Erb, L. P., C. Ray, and R. Guralnick. 2011. On the generality of a climate-mediated shift in the distribution of the American pika (). *Ecology* 92:1730–1735.
- Foden, W. B., B. E. Young, H. R. Akçakaya, R. A. Garcia, A. A. Hoffmann, B. A. Stein, C. D. Thomas, C. J. Wheatley, D. Bickford, J. A. Carr, D. G. Hole, T. G. Martin, M. Pacifici, J. W. Pearce-Higgins, P. J. Platts, P. Visconti, J. E. M. Watson, and B. Huntley. 2019. Climate change vulnerability assessment of species. *WIREs Climate Change* 10:e551.
- Fourcade, Y., J. O. Engler, D. Rödder, and J. Secondi. 2014. Mapping Species Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias. *PLOS ONE* 9:e97122.
- Franken, R. J. 2002. Demography and metapopulation dynamics of collared pikas (*Ochotona collaris*) in the Southwest Yukon. M.Sc Thesis, University of Alberta.
- Franken, Renee J., and D. S. Hik. 2004. Influence of Habitat Quality, Patch Size and Connectivity on Colonization and Extinction Dynamics of Collared Pikas *Ochotona collaris*. *Journal of Animal Ecology* 73:889–896.
- Franken, R. J., and D. S. Hik. 2004. Interannual variation in timing of parturition and growth of collared pikas (*Ochotona collaris*) in the southwest Yukon. *Integrative and Comparative Biology* 44:186–193.
- Freeman, B. G., M. N. Scholer, V. Ruiz-Gutierrez, and J. W. Fitzpatrick. 2018. Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the National Academy of Sciences* 115:11982–11987.
- Frick, S. E., and R. J. Hijmans. 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37:4302–4315.
- Grimmett, L., R. Whitsed, and A. Horta. 2020. Presence-only species distribution models are sensitive to sample prevalence: Evaluating models using spatial prediction stability and accuracy metrics. *Ecological Modelling* 431:109194.
- Guerts, E. M., J. D. Reynolds, and B. M. Starzomski. 2023. Turning observations into biodiversity data: Broadscale spatial biases in community science. *Ecosphere* 14.
- Guillera-Aroita, G., J. J. Lahoz-Monfort, J. Elith, A. Gordon, H. Kujala, P. E. Lentini, M. A. McCarthy, R. Tingley, and B. A. Wintle. 2015. Is my species distribution model fit for purpose? Matching data and models to applications. *Global Ecology and Biogeography* 24:276–292.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993–1009.
- Hafner, D. J. 1994. Pikas and Permafrost: Post-Wisconsin Historical Zoogeography of *Ochotona* in the Southern Rocky Mountains, U.S.A. *Arctic and Alpine Research* 26:375–382.
- Harrison, L. A. 2023. How Climate Influences Occupancy and Behavior of Pikas in Alaska. M.S., University of Idaho, United States -- Idaho.

- Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology* 12:450–455.
- Hijmans, R. J., R. Bivand, K. Forner, J. Ooms, E. Pebesma, and M. D. Summer. 2022. Package ‘terra’. Maintainer: Vienna, Austria.
- Hope, A. G., E. Waltari, J. L. Malaney, D. C. Payer, J. A. Cook, and S. L. Talbot. 2015. Arctic biodiversity: increasing richness accompanies shrinking refugia for a cold-associated tundra fauna. *Ecosphere* 6:art159.
- Horn, H. L. 2013. The role of habitat quality and climate in the dynamics of occupancy and survival of a population of collared pikas (*Ochotona collaris*) in the Ruby Range, Yukon Territory. M.S., University of Alberta (Canada), Canada -- Alberta, CA.
- Jin, S., L. Yang, Z. Zhu, and C. Homer. 2017. A land cover change detection and classification protocol for updating Alaska NLCD 2001 to 2011. *Remote Sensing of Environment* 195:44–55.
- Kass, J. M., G. E. Pinilla-Buitrago, A. Paz, B. A. Johnson, V. Grisales-Betancur, S. I. Meenan, D. Attali, O. Broennimann, P. J. Galante, B. S. Maitner, H. L. Owens, S. Varela, M. E. Aiello-Lammens, C. Merow, M. E. Blair, and R. P. Anderson. 2023. wallace 2: a shiny app for modeling species niches and distributions redesigned to facilitate expansion via module contributions. *Ecography* 2023:e06547.
- Kukka, P. M., J. P. Thomas, J. E. Benjamin, and T. S. Jung. 2020. Rapid assessment of site occupancy by collared pika (*Ochotona collaris*) at the leading edge of their range. *European Journal of Wildlife Research* 66:64.
- Lambert, J. P., X. Zhang, K. Shi, and P. Riordan. 2023. The pikas of China: a review of current research priorities and challenges for conservation. *Integrative Zoology* 18:110–128.
- Lanier, H. C., R. Massatti, Q. He, L. E. Olson, and L. L. Knowles. 2015. Colonization from divergent ancestors: glaciation signatures on contemporary patterns of genomic variation in Collared Pikas (*Ochotona collaris*). *Molecular Ecology* 24:3688–3705.
- Lanier, H. C., and L. E. Olson. 2013. Deep barriers, shallow divergences: reduced phylogeographical structure in the collared pika (Mammalia: Lagomorpha: *Ochotona collaris*). *Journal of Biogeography* 40:466–478.
- Lanier, H., and D. Hik. 2016. *Ochotona collaris*. IUCN Red List of Threatened Species. <<https://www.iucnredlist.org/en>>. Accessed 24 Feb 2025.
- Leach, K., R. Kelly, A. Cameron, W. I. Montgomery, and N. Reid. 2015. Expertly Validated Models and Phylogenetically-Controlled Analysis Suggests Responses to Climate Change Are Related to Species Traits in the Order Lagomorpha. *PLOS ONE* 10:e0122267.
- Li, W.-D., and A. T. Smith. 2005. Dramatic decline of the threatened Ili pika *Ochotona iliensis* (Lagomorpha: Ochotonidae) in Xinjiang, China. *Oryx* 39:30–34.
- Lyons, M. P., J. R. Stevenson, L. L. Thurman, and B. E. Young. 2024. Guidelines for Using the NatureServe Climate Change Vulnerability Index. Release 4.0. Arlington, VA: NatureServe.
- MacArthur, R. A., and L. C. H. Wang. 1973. Physiology of thermoregulation in the pika, *Ochotona princeps*. *Canadian Journal of Zoology* 51:11–16.
- MacDonald, S. O., and C. Jones. 1987. *Ochotona collaris*. Pages 1–4 in. *Mammalian Species*. Volume 281.

- Marcer, A., L. Sáez, R. Molowny-Horas, X. Pons, and J. Pino. 2013. Using species distribution modelling to disentangle realised versus potential distributions for rare species conservation. *Biological Conservation* 166:221–230.
- McCarty, J. P. 2001. Review: Ecological Consequences of Recent Climate Change. *Conservation Biology* 15:320–331.
- Millar, C. I., and R. D. Westfall. 2010. Distribution and Climatic Relationships of the American Pika (*Ochotona princeps*) in the Sierra Nevada and Western Great Basin, U.S.A.; Periglacial Landforms as Refugia in Warming Climates. *Arctic, Antarctic, and Alpine Research* 42:76–88.
- Millar, C. I., R. D. Westfall, and D. L. Delany. 2016. Thermal Components of American Pika Habitat—How does a Small Lagomorph Encounter Climate? *Arctic, Antarctic, and Alpine Research* 48:327–343.
- Millar, J. S., and F. C. Zwickel. 1972. Determination of age, age structure, and mortality of the pika, *Ochotona princeps* (Richardson). *Canadian Journal of Zoology* 50:229–232.
- Miller, J. 2010. Species Distribution Modeling. *Geography Compass* 4:490–509.
- Monk, E. M., and C. Ray. 2022. Revisiting talus and free-air temperatures after 50 years of change at an American pika (*Ochotona princeps*) study site in the Southern Rockies. *PLOS Climate* 1:e0000049.
- Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impact of a Century of Climate Change on Small-Mammal Communities in Yosemite National Park, USA. *Science* 322:261–264.
- Morrison, S., L. Barton, P. Caputa, and D. S. Hik. 2004. Forage selection by collared pikas, *Ochotona collaris*, under varying degrees of predation risk. *Canadian Journal of Zoology* 82:533–540.
- Morrison, S. F., and D. S. Hik. 2007. Demographic Analysis of a Declining Pika *Ochotona collaris* Population: Linking Survival to Broad-Scale Climate Patterns via Spring Snowmelt Patterns. *Journal of Animal Ecology* 76:899–907.
- Morrison, S. F., G. Pelchat, A. Donahue, and D. S. Hik. 2009. Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. *Oecologia* 159:107–116.
- Müller, W. A., J. H. Jungclaus, T. Mauritsen, J. Baehr, M. Bittner, R. Budich, F. Bunzel, M. Esch, R. Ghosh, H. Haak, T. Ilyina, T. Kleine, L. Kornblueh, H. Li, K. Modali, D. Notz, H. Pohlmann, E. Roeckner, I. Stemmmler, F. Tian, and J. Marotzke. 2018. A Higher-resolution Version of the Max Planck Institute Earth System Model (MPI-ESM1.2-HR). *Journal of Advances in Modeling Earth Systems* 10:1383–1413.
- Muscarella, R., P. J. Galante, M. Soley-Guardia, R. A. Boria, J. M. Kass, M. Uriarte, and R. P. Anderson. 2014. ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution* 5:1198–1205.
- NatureServe. 2016. *Ochotona collaris*. NatureServe Network Biodiversity Location Data accessed through NatureServe Explorer [web application]. NatureServe Explorer. <https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.100243/Ochotona_collaris>. Accessed 24 Feb 2025.
- O'Neill, B. C., C. Tebaldi, D. P. van Vuuren, V. Eyring, P. Friedlingstein, G. Hurtt, R. Knutti, E. Kriegler, J.-F. Lamarque, J. Lowe, G. A. Meehl, R. Moss, K. Riahi, and B. M. Sanderson.

2016. The Scenario Model Intercomparison Project (ScenarioMIP) for CMIP6. *Geoscientific Model Development* 9:3461–3482.
- Pacifici, M., W. B. Foden, P. Visconti, J. E. M. Watson, S. H. M. Butchart, K. M. Kovacs, B. R. Scheffers, D. G. Hole, T. G. Martin, H. R. Akçakaya, R. T. Corlett, B. Huntley, D. Bickford, J. A. Carr, A. A. Hoffmann, G. F. Midgley, P. Pearce-Kelly, R. G. Pearson, S. E. Williams, S. G. Willis, B. Young, and C. Rondinini. 2015. Assessing species vulnerability to climate change. *Nature Climate Change* 5:215–224.
- Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. J. Tennent, J. A. Thomas, and M. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–583.
- Pauli, J. N., B. Zuckerberg, J. P. Whiteman, and W. Porter. 2013. The subnivium: a deteriorating seasonal refugium. *Frontiers in Ecology and the Environment* 11:260–267.
- Peacock, M. M., and A. T. Smith. 1997. The effect of habitat fragmentation on dispersal patterns, mating behavior, and genetic variation in a pika (*Ochotona princeps*) metapopulation. *Oecologia* 112:524–533.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- Phillips, S. J., M. Dudik, J. Elith, C. H. Graham, A. Lehmann, J. Leathwick, and S. Ferrier. 2009. Sample Selection Bias and Presence-Only Distribution Models: Implications for Background and Pseudo-Absence Data. *Ecological Applications* 19:181–197.
- Polechová, J. 2018. Is the sky the limit? On the expansion threshold of a species' range. *PLOS Biology* 16:e2005372.
- Pounds, J. A., M. P. L. Fogden, and J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. *Nature* 398:611–615.
- Radosavljevic, A., and R. P. Anderson. 2014. Making better Maxent models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography* 41:629–643.
- Randin, C. F., T. Dirnböck, S. Dullinger, N. E. Zimmermann, M. Zappa, and A. Guisan. 2006. Are niche-based species distribution models transferable in space? *Journal of Biogeography* 33:1689–1703.
- Raupach, M. R., G. Marland, P. Ciais, C. Le Quéré, J. G. Canadell, G. Klepper, and C. B. Field. 2007. Global and regional drivers of accelerating CO₂ emissions. *Proceedings of the National Academy of Sciences* 104:10288–10293.
- Robson, K. M., C. T. Lamb, and M. A. Russello. 2016. Low genetic diversity, restricted dispersal, and elevation-specific patterns of population decline in American pikas in an atypical environment. *Journal of Mammalogy* 97:464–472.
- Rodhouse, T. J., M. R. Jeffress, K. R. Sherrill, S. R. Mohren, N. J. Nordensten, M. L. Magnuson, D. Schwalm, J. A. Castillo, M. Shinderman, and C. W. Epps. 2018. Geographical variation in the influence of habitat and climate on site occupancy turnover in American pika (*Ochotona princeps*). *Diversity and Distributions* 24:1506–1520.
- Rubidge, E. M., J. L. Patton, M. Lim, A. C. Burton, J. S. Brashares, and C. Moritz. 2012. Climate-induced range contraction drives genetic erosion in an alpine mammal. *Nature Climate Change* 2:285–288.

- Sakiyama, T., and J. G. Molinos. 2025. Mapping fine-scale distribution of the northern pika *Ochotona hyperborea* considering duality in microhabitat thermal conditions. *Frontiers of Biogeography* 18.
- Serreze, M. C., and R. G. Barry. 2011. Processes and impacts of Arctic amplification: A research synthesis. *Global and Planetary Change* 77:85–96.
- Shinderman, M. 2015. American pika in a low-elevation lava landscape: expanding the known distribution of a temperature-sensitive species. *Ecology and Evolution* 5:3666–3676.
- Smith, A. T. 1974a. The Distribution and Dispersal of Pikas: Influences of Behavior and Climate. *Ecology* 55:1368–1376.
- Smith, A. T. 1974b. The Distribution and Dispersal of Pikas: Consequences of Insular Population Structure. *Ecology* 55:1112–1119.
- Thurman, L. L., B. A. Stein, E. A. Beever, W. Foden, S. R. Geange, N. Green, J. E. Gross, D. J. Lawrence, O. LeDee, J. D. Olden, L. M. Thompson, and B. E. Young. 2020. Persist in place or shift in space? Evaluating the adaptive capacity of species to climate change. *Frontiers in Ecology and the Environment* 18:520–528.
- Trefry, S. A., and D. S. Hik. 2009. Eavesdropping on the Neighbourhood: Collared Pika (*Ochotona collaris*) Responses to Playback Calls of Conspecifics and Heterospecifics. *Ethology* 115:928–938.
- Troutet, J., P. Grandcolas, A. Blin, R. Vignes-Lebbe, and F. Legendre. 2017. Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports* 7:9132.
- U.S. Geological Survey (USGS) Gap Analysis Project (GAP). 2016. GAP/LANDFIRE National Terrestrial Ecosystems 2011. U.S. Geological Survey data release.
- Varner, J., and M. D. Dearing. 2014. The Importance of Biologically Relevant Microclimates in Habitat Suitability Assessments. *PLOS ONE* 9:e104648.
- Varner, J., J. J. Horns, M. S. Lambert, E. Westberg, J. S. Ruff, K. Wolfenberger, E. A. Beever, and M. D. Dearing. 2016. Plastic pikas: Behavioural flexibility in low-elevation pikas (*Ochotona princeps*). *Behavioural Processes* 125:63–71.
- Vieilledent, G., C. Cornu, A. Cuní Sanchez, J.-M. Leong Pock-Tsy, and P. Danthu. 2013. Vulnerability of baobab species to climate change and effectiveness of the protected area network in Madagascar: Towards new conservation priorities. *Biological Conservation* 166:11–22.
- Walsh, J. E., W. L. Chapman, V. Romanovsky, J. H. Christensen, and M. Stendel. 2008. Global Climate Model Performance over Alaska and Greenland. <https://doi.org/10.1175/2008JCLI2163.1>.
- Walther, G.-R. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2019–2024.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Warren, D. L., and S. N. Seifert. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications* 21:335–342.
- Wenger, S. J., and J. D. Olden. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution* 3:260–267.

- Whitford, A. M., B. R. Shipley, and J. L. McGuire. 2024. The influence of the number and distribution of background points in presence-background species distribution models. *Ecological Modelling* 488:110604.
- Wilkening, J. L., C. Ray, N. Ramsay, and K. Klingler. 2015. Alpine biodiversity and assisted migration: the case of the American pika (*Ochotona princeps*). *Biodiversity* 16:224–236.
- Willis, S. G., W. Foden, D. J. Baker, E. Belle, N. D. Burgess, J. A. Carr, N. Doswald, R. A. Garcia, A. Hartley, C. Hof, T. Newbold, C. Rahbek, R. J. Smith, P. Visconti, B. E. Young, and S. H. M. Butchart. 2015. Integrating climate change vulnerability assessments from species distribution models and trait-based approaches. *Biological Conservation* 190:167–178.
- Wilson, R. J., D. Gutiérrez, J. Gutiérrez, and V. J. Monserrat. 2007. An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology* 13:1873–1887.
- Young, B. E., K. R. Hall, E. Byers, K. Gravuer, G. Hammerson, A. Redder, and K. Szabo. 2012. Rapid assessment of plant and animal vulnerability to climate change. Pages 129–150 *in*. *Wildlife conservation in a changing climate*.
- Young, H. S., D. J. McCauley, M. Galetti, and R. Dirzo. 2016. Patterns, Causes, and Consequences of Anthropocene Defaunation. *Annual Review of Ecology, Evolution, and Systematics* 47:333–358.
- Zgurski, J. M., and D. S. Hik. 2012. Polygynandry and even-sexed dispersal in a population of collared pikas, *Ochotona collaris*. *Animal Behaviour* 83:1075–1082.