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The role of microclimate in maintaining species distribution under climate change: a case study of the northern pika

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Contents

Summary

Anthropogenic climate change is posing a grave threat to biodiversity around the globe. One of the widespread impacts of climate change on terrestrial ecosystems is the change in species distributions, which can bring negative consequences to interacting species as well as ecosystem functions and services. It is therefore imperative to understand how species distributions are shaped and predict how it may change under warming temperatures.

Despite the general trend of poleward and upslope shifts in species distributions, a large variation exists around these responses. Indeed, many species are found persisting at the trailing edge of the distribution, thus indicating lags in range shifts compared to the isothermal shifts. One hypothesis explaining this phenomenon is that heterogenous thermal conditions generated by complex topography enable species to persist locally while the climate changes at larger spatial scales. This perception follows the microrefugia concept, which considers that populations can persist in small habitat patches by using locally available, favorable environmental conditions even under hostile, environmental changes. Therefore, the importance of microclimate, the thermal conditions existing locally and experienced by individuals, is being increasingly recognized for maintaining species distributions under contemporary climate change. However, there are various aspects in its role that are yet to be explored.

First, few studies have assessed distribution changes in species that utilize microclimates, and therefore, the effectiveness of microclimates in maintaining species distribution remains unclear. Second, since previous studies have not assessed the relative importance of microclimate with other drivers of species distribution, the environmental context in which microclimate is important for shaping species distribution remains poorly discussed. Third, despite the development of species distribution predictions that account for microclimates, few studies have validated its accuracy in predicting range shifts over time. In this dissertation, I aimed to assess the role of microclimate in maintaining species distribution to advance the current knowledge of species range dynamics under climate change. I focused on the northern pika (*Ochotona hyperborea*), a small lagomorph species, in Hokkaido, Japan, as my subject species since thermal buffering effects have been reported in its rocky landform habitats.

In Chapter 2, I aimed to develop a foundation method for surveying the distribution of the northern pika by assessing the efficacy of aural detection methods. In particular, I compared the efficacy of auditory observation, in which naturally occurring vocalizations of

pikas are surveyed, and playback, in which acoustic cues are used to trigger vocalizations from pikas. Based on the time-wise accuracy, playback was suggested as a highly effective method for surveying site occupancy. Therefore, playback was used to survey the northern pika distribution across Hokkaido in this dissertation.

In Chapter 3, I assessed how the northern pika distribution has changed from the past (1961-2010) by conducting resurveys along a wide elevational gradient (60–2,210 m). The resurvey revealed population turnovers, shifting from past presence to current absence at low- to mid-elevations, suggesting that the Hokkaido regional population of the northern pika is becoming unstable under rising temperatures. Importantly, however, persistence of some local populations was observed in these warmer regions. As habitat size was found positively correlated with persistence, it is plausible that higher environmental heterogeneity in larger habitats, such as variations in thermal conditions, is important for maintaining the northern pika distribution over time.

In Chapter 4, by measuring habitat thermal conditions along a wide elevational gradient (350–2,200 m), I evaluated their relationships with the northern pika occupancy at two nested spatial scales. Analyses showed that rock interstice microclimate was not an important factor at both the whole-distribution and range-edge (i.e., low-elevations) scale. Instead, other factors such as ambient thermal condition and microhabitat availability influenced occupancy at the whole-distribution scale, whereas presence of human land-use was strongly important at the range edge. Although thermal measurements indicated that rock interstices effectively buffered ambient thermal conditions, these results suggest that the refugial effect of microclimates at the trailing edge could be overridden by other environmental factors due to spatial hierarchy. This implies that the environmental context in which the microclimate exists is crucial for driving species persistence at the trailing edge.

In Chapter 5, I developed a fine-scale distribution model for the northern pika by using downscaled climate data and showed that the predictive performance becomes slightly higher by considering fine-scale conditions. While the fine-scale model was originally developed based on ambient thermal conditions, accounting for rock interstice microclimates increased the predicted habitat suitability distinctively for the low- to mid-elevation areas owing to the thermal buffering effect, which also was observed in future projections. This suggests that the rock interstice microclimate may facilitate persistence if the northern pika could effectively reduce physiological stress from warming temperatures through behavioral thermoregulation.

In Chapter 6, I evaluated the accuracy of fine-scale species distribution models developed in Chapter 5 by comparing the predictions with the observed distribution in

Chapters 3 and 4. Interestingly, models incorporating rock interstice microclimate exhibited the highest accuracy in predicting the current distribution of present sites as the omission error was the smallest. This suggests that accounting for microclimate in species distribution models provides more realistic predictions than that based on coarse scales or on ambient thermal conditions as overestimation of species range shifts was prevented.

Taken together, this dissertation provides evidence that complex topographies have the potential to maintain species distributions at the trailing edge under warming trends, but the refugial effect of microclimates is likely context-dependent given the influences of other environmental factors. This reminds the importance to consider the strong relationship between species distribution and spatial scale: microclimate is an environmental condition occurring at relatively small scales, while conditions at larger scales generally exhibit stronger influence on local population dynamics. Therefore, it will be imperative to consider where microclimates fit in the hierarchical structure of how various drivers influence species distribution in understanding range dynamics. Nonetheless, this study highlights the importance of considering the contribution of microclimates when predicting future range shifts under climate change to avoid overlooking potential suitable habitats. To enhance its contribution to species persistence under climate change, it is crucial to incorporate the geological and topographical features that underlie and create microclimates into contemporary conservation planning.

Chapter 1: General Introduction

1.1 Observed shifts in species distribution under climate change

Anthropogenic climate change is posing a grave threat to biodiversity around the globe. Observed impacts include, among others, mass mortality events, ecosystem deterioration, mismatch in seasonal timings among interacting species (IPBES, 2019; Parmesan, 2006; Parmesan & Yohe, 2003). One of the most widespread and frequently reported impacts of climate change on terrestrial ecosystems is the change in species distributions. As climate change alter habitat conditions many species are observed shifting their distribution poleward and upslope to keep track of their suitable habitats (Chen et al., 2011; Lenoir & Svenning, 2015; Moritz et al., 2008; Parmesan, 2006; Parmesan & Yohe, 2003; Tingley et al., 2012). The ultimate case of this phenomenon, where a species loses its entire suitable habitat or cannot shift fast enough to compensate for it, is species extinction (Waller et al., 2017). Importantly, changes in species distributions can bring negative consequences beyond the individual species level as interacting species within the ecosystem will also be affected, which has further implications on ecosystem functioning and servicing (Kass et al., 2023; Pecl et al., 2017). It is therefore imperative to understand how species will shift their distributions in response to contemporary climate change. Moreover, species range shifts challenge the effectiveness of current area-based conservation efforts, such as protected areas, since these schemes are planned assuming that species distributions will remain static over time (Hoffmann et al., 2019; Lawler et al., 2015). In this sense, identifying areas that facilitate species persistence should help adapt current conservation measures for safeguarding biodiversity effectively (Keppel et al., 2012; Whittaker et al., 2005).

Species range shifts are induced by changes in climate. Although other parameters are also important, temperature arguably represents the main driver of species range shifts because thermal conditions influence organismal performance, such as behavior, growth, reproduction, and survival (Pörtner & Farrell, 2008), as well as population dynamics, such as growth/decline and colonization/extinction rates (Lenoir & Svenning, 2013). Thus, local shifts in thermal conditions, in theory, can trigger both individual- and population-level responses of a species at the local scale, which ultimately alters the species distribution and abundance along latitude and elevation at the broader scale (Lenoir & Svenning, 2013). Under warming conditions, in terrestrial systems, current unsuitable locations at the cold, leading edge of the distribution (i.e., higher latitudes and elevations) will become warmer and therefore suitable for populations to grow and colonize, resulting in range expansions. Conversely, current suitable locations at the warm, trailing edge of the distribution (i.e., lower latitudes and elevations) will become unsuitable for populations to persist as they turn too hot, resulting in local population declines, extinctions and ultimately range contractions (A. E. Bates et al., 2014; Lenoir & Svenning, 2013).

Despite the general pattern of range shifts towards cooler regions, there is a large variation in the magnitude and direction of these responses among species (Chen et al., 2011; Crimmins et al., 2011; Lenoir, Gégout, Guisan, et al., 2010; Rubenstein et al., 2023). For instance, some species are known for shifting towards warmer regions, but this unexpected pattern has been explained as a result of the species tracking the change in precipitation and water availability rather than temperature (Crimmins et al., 2011; Tingley et al., 2012). However, even in species responding to temperature changes, previous studies have shown that species distributions are lagging behind isothermal shifts among a wide variety of taxa including plants (Lenoir, Gégout, Dupouey, et al., 2010), invertebrates (Devictor et al., 2012), birds (Devictor et al., 2008, 2012), and mammals (Moritz et al., 2008). One of the reasons is the dispersal limitation as most species cannot keep up with the speed of the isothermal shift to expand their distribution (Lenoir, Gégout, Dupouey, et al., 2010), even in species with relatively high dispersal abilities such as butterflies and birds (Devictor et al., 2012). On the other hand, the interesting phenomenon of these lags is that these species are so far observed persisting in relatively warmer areas than their optimal condition towards the trailing edge of the distribution, with the ultimate case being no change in distribution from the past (Chen et al., 2011; Lenoir et al., 2020). Clarifying the drivers and mechanisms that lead to the emergence of such patterns has been the focus of much recent attention in the literature as it has crucial implications for improving range predictions and further conservation efforts (Rubenstein et al., 2020, 2023).

1.2 Understanding persistence at the trailing edge

One of the explanations following observations of local populations persisting at the trailing edge of the distribution is the occurrence of favorable thermal conditions existing at local scales (Chen et al., 2011; Moritz & Agudo, 2013). This is because, while a spatial hierarchy exists in the effects of environmental factors on species distribution and climate (i.e., temperature) operates at relatively larger scales (Pearson & Dawson, 2003; Willis & Whittaker, 2002), thermal conditions are known for exhibiting high heterogeneity at smaller scales and species may be experiencing thermal conditions that are locally buffered or decoupled from those prevailing at larger scales (Lenoir et al., 2017) (Fig. 1-1). Here, “scale” is defined as the physical dimension of an object and consists of “extent” and “resolution” (Noda, 2004), while extent and resolution are often commonly related in biogeographical studies (Blackburn & Gaston, 2002). Thus, while the rising temperature is a trend that is happening at larger scales (e.g., regional, continental, and global scales), species may not be affected negatively at a rate that would be expected simply from the ongoing trend at larger scales as each individual experience distinct thermal conditions existing at much smaller scales (e.g., micro, site, and local scales) (Fig. 1-1). In this study, I refer to these thermal conditions existing locally and experienced by an individual as *microclimate*. For instance, both plant and animal species occurring at the forest floor may benefit from microclimates existing under forest canopies, which are buffered from temperatures occurring at the regional scale (De Frenne et al., 2013; Stickley & Fraterrigo, 2021; Zellweger et al., 2020) (Fig. 1-1). Nonetheless, the exact definition and size of microclimates differ among studies depending on the focal species and the processes creating the microclimates (Bramer et al., 2018; Morelli et al., 2016; Shi et al., 2016). Moreover, in the case of animals, an individual may experience different microclimatic conditions as it moves around and uses various *microhabitats*, here defined as the small-scale environments that is unique in structure from its surroundings (e.g., Varner & Dearing, 2014).

So far, various types of microclimates have been reviewed or described in terrestrial ecosystems (Morelli et al., 2016), including the effects of vegetation and tree canopies (Stickley & Fraterrigo, 2021; Suggitt et al., 2011), cold-air pools (Pastore et al., 2022), topography (Suggitt et al., 2018), and rocky landforms (Shi et al., 2014; Varner & Dearing, 2014). Moreover, field-based observations have shown that microclimates can affect species behavior, distribution, and abundance, as well as compositions of biological communities in various taxa, such as plants (De Frenne et al., 2013; Maclean et al., 2015; Zellweger et al., 2020), insects (Suggitt et al., 2018), birds (Kim et al., 2022), and mammals (Shi et al., 2015). For instance, Lawson et al. (2014) has shown that a thermally-constrained butterfly species lay eggs in places with cooler microclimates generated by topography. Another study by Suggitt et al. (2015) has shown that the microclimate created by complex topography is important for the persistence of butterflies and moths. Therefore, the association between the species range shift and rising temperatures occurring at larger scales might be too simplistic and microclimate ecology has gained recent attention to consider the possibility that species may persist by utilizing local-scale thermal conditions (Kemppinen et al., 2024).

The importance of local scale environments in maintaining species distribution under climate change has gained support from palaeoecological studies investigating patterns of species range shifts following the Last Glacial Period. These palaeoecological studies have shown that, under cooler conditions during the Last Glacial Maximum (LGM), many tree species in Europe and North America responded to the formation of massive ice sheets by retreating into southern refugia. For instance, Iberian, Italian, and Balkan peninsulas are known as refugial areas as ice sheets covered northern Europe (Petit et al., 2002). However, considering their current distribution, the expansion rates and distances covered by these species following the glacial retreat are much larger than the dispersal capacity currently appreciated. To solve this contradiction, known as the Reid's paradox (Clark et al., 1998), researchers proposed the existence of small but suitable areas in northern regions that allowed the persistence of local populations throughout the LGM (J. R. Stewart & Lister, 2001). Later these areas were clarified by genetic studies (McLachlan et al., 2005; Petit et al., 2003) and this led to the perception that the current distributions are formed by short-distance dispersals from those small refugia after the glacial retreat (Provan & Bennett, 2008). Although the actual drivers and mechanisms that enabled local-scale persistence remains unclear, the distinction between these southern and northern refugia is in how species avoided negative impacts from the glacial formation. In the former, species avoided the impacts by utilizing the warm, southern climate, whereas in the latter, species avoided them by utilizing more local-scale environmental conditions, although ice sheets may have prevailed in the surroundings. Thus, considering the differences in underlying mechanisms and the overall size, these refugia are referred to as the *macrorefugia* and *microrefugia* (or cryptic refugia), respectively, (Ashcroft 2010; Rull 2009).

The whole species range dynamics in the past provide important insights for ecologists and biogeographers to predict how species will respond to contemporary climate change (Pearson, 2006). Importantly, while the spatial hierarchy is well-perceived in the relationship between species distribution and environment (Pearson & Dawson, 2003; Willis & Whittaker, 2002), these evidence in species responses to glaciation show that favorable environmental conditions at smaller spatial scales may support persistence of local populations even when unfavorable conditions prevail at larger scales. In this sense, the general pattern in the species range shifts currently observed in response to the thermal changes at relatively larger scales (i.e., upward and poleward shifts) could be perceived as the formation of the contemporary macrorefugia, while areas that local populations are persisting at the trailing edge of the distribution could be perceived as the contemporary microrefugia (Ashcroft, 2010;

Kiedrzyński et al., 2017; Moritz & Agudo, 2013; Mosblech et al., 2011; Rull, 2009). However, the validity of this perception on microrefugia formation for the trailing edge populations remains uncertain since few studies have actually investigated the contribution of microclimates on species persistence (e.g., Suggitt et al., 2018). With species ranges predicted to continue to change in the future, it is strongly needed to improve our understanding of microrefugia establishment. Moreover, identifying the potential refugial areas, both the macrorefugia and microrefugia, should help implementing strategic conservation (Keppel et al., 2012; Morelli et al., 2016, 2020).

1.3 Recent improvements in range shift predictions

One of the most widely used tools for predicting suitable habitats of a given species is the species distribution model (SDM), in which the species occurrence (presence or absence) is modeled as a function of environmental parameters to predict the habitat suitability of a given spatial area (Elith & Leathwick, 2009; Franklin, 2023; Guisan & Thuiller, 2005). Further, by inputting future climate conditions, these models also allow forecasting and identifying areas that are suitable for the species in the future. However, when compared to observed species range shifts, SDMs have shown a tendency to overpredict as locations where many species are found persisting at the trailing edge of the distribution are often predicted to be unsuitable (e.g., too warm) by these models (Maclean & Early, 2023). Long discussed following this response is the mismatch in spatial scale between the scale at which the models are developed and the typically much smaller scale at which the individual organisms are influenced by the environment. Indeed, a review by Potter et al. (2013) showed that the grid lengths of the environmental data used in previous studies were approximately 10,000 and 1,000 times larger than the body length of, respectively, the focal animal and plant species being modelled. Thus, the spatial resolution of the model is often too low to represent local-scale environmental conditions that may influence species distributions. This is problematic given that the potential benefits provided by the microclimates are not factored into the model predictions as thermal conditions at larger scales are only considered (Austin & Van Niel, 2011; Sears et al., 2011). Consequently, a typical species distribution analysis is likely simplifying potential patterns of species range shifts and rather identifying only the macrorefugia, which risks overlooking potential microrefugia under climate change (Luoto & Heikkinen, 2008; Mosblech et al., 2011; Randin et al., 2009). Therefore, it is of high necessity to enhance the ability of predicting potential refugial areas accurately.

While the field-based microclimate studies were introduced in the previous section, there have also been endeavors in SDM-based studies to analyze species distributions at high resolutions by downscaling the climate data (Franklin et al., 2013; Gillingham et al., 2012; Guisan et al., 2007; Maclean & Early, 2023; Patiño et al., 2023; Randin et al., 2009; Trivedi et al., 2008). These studies have shown that incorporation of fine-scale conditions can improve model performances relative to conventional, coarse-scale analysis (Gillingham et al., 2012; Guisan et al., 2007), and change predictions of suitable areas, thus affecting the trajectory of potential range shifts over time (Franklin et al., 2013; Patiño et al., 2023; Randin et al., 2009). For example, Maclean and Early (2023) showed that six out of 244 European plants were predicted to become extinct in the coarse-scale forecast (e.g., 5-km resolution), whereas all taxa remained extant in the fine-scale forecast (e.g., 0.1-km resolution), which was in agreement with the actual, observed status of the species distributions. Furthermore, recent studies are attempting to improve the qualities of fine-scale climate data by shifting from using downscaling techniques to generate fine scale climate data from coarse scale products, to the actual modeling system-specific microclimates (Gril et al., 2023; Kearney et al., 2020; Maclean et al., 2019; Maclean & Klinges, 2021), in order to obtain more realistic fine-scale predictions (Haesen et al., 2023; Stark & Fridley, 2022; Stickley & Fraterrigo, 2023).

Obtaining finer predictions of species distribution will be advantageous for conservation in various ways. First, since areas predicted suitable at fine-scales may be distinct from that in the coarse-scale predictions, these areas could be considered important areas for conservation. This avoids the risk of overlooking areas that will likely support species persistence and therefore contribute to conserving the focal species in larger areas (Zellweger et al., 2020). Second, microrefugia conservation may be a relatively simple and cheap measure as it basically requires protection of the underlying features that create distinct microclimates. While a strict management scheme to protect these features at larger scales may be difficult and unrealistic for implementation, restricting land conversions with attention towards maintaining microclimatic environments will likely be possible (Badgley et al., 2017). I believe that this is more advantageous than direct management of species and habitats, which are often costly and can only be applied for limited areas (Jones, 2011).

1.4 Building a holistic assessment on the role of microclimates

The importance of microclimate in species range dynamics under climate change is being increasingly recognized. However, I propose that there is still a lack in the assessment on the effectiveness of microclimates in maintaining species distributions. Here, I raise three directions of improvement to advance the knowledge of microclimate importance in shaping species distributions. In this dissertation, I aim to address these questions to assess the role of microclimate in maintaining species distributions by conducting a case study on the northern pika *Ochotona hyperborea* (introduced in the next section) (Fig. 1-2).

1. *Expanding the timeframe of microrefugia studies*. Field-based studies have assessed the importance of microclimate on current patterns of species distributions, whereas model-based studies have assessed current and future patterns. Here, there remains a lack of perspective on how microclimate has helped species to persist from the past to present under current climate change. Habitat resurvey is a field-survey framework where historical site records of species occurrences are revisited to estimate long-term changes in species distributions (Tingley & Beissinger, 2009; Verheyen et al., 2017). This survey offers opportunities to assess how species distribution is changing and the possible drivers behind those changes. In Chapter 3, I intend to use this method to assess the contribution of microclimate in maintaining the northern pika distribution from the past.
2. *Comparing the relative importance of microclimate with other environmental factors in the trailing edge populations*. While theory behind species range dynamics suggests that microclimate is particularly important at the trailing edge for the microrefugia formation (Rull, 2009), other local-scale factors such as human land-use may also have strong effects on distribution patterns (Latimer & Zuckerberg, 2017). However, most studies assessing the importance of microclimate on species distribution have focused only on its sole effect. Thus, whether the persistence of trailing edge populations is driven by microclimate or other factors remains uncertain. Clarifying this aspect has implications for conservation because the efficiency of protecting microclimates as a conservation measure may be compromised or potentiated in the future by changing conditions in other factors. In Chapter 4, I aim to analyze the importance of microclimate on the northern pika distributions in comparison with the effects of human land-use.
3. *Validating fine-scale species distribution models*. Previous studies have shown that incorporating microclimates into SDMs enhances the predictive accuracy from traditional, coarse-scale models (Gillingham et al., 2012). However, there have been very few attempts in the SDM literature to validate the accuracy of predicting ranges

shifts over time. Considering that the initial motivation of incorporating microclimate into SDMs was to address the performance issues where models frequently overestimate distribution changes (Pearson, 2006), it is important to assess whether the incorporation of microclimate is leading to more nuanced estimation of range shifts. This type of validation is possible by building the model using past distribution data, predicting the present distribution, and comparing that forecast with present distribution data, such as from occupancy surveys. In Chapters 5 and 6, I develop a fine-scale SDM for the northern pika and assess its accuracy in predicting species distributions over time.

1.5 Study subject and area: the northern pika in Hokkaido

Pikas are small lagomorphs known to be highly adapted to cold environments (Wang et al., 2020; Yang et al., 2008). At present, there are 30 extant pika species found in Eurasia (28 species) and North America (2 species) (Fig. 1-3). Among them, climate change impacts have been studied in detail for the American pika (*Ochotona princeps*). Early studies on the physiology of the species demonstrated that the American pika is extremely weak to heat stress as they maintain high body temperatures of 40.1 °C on average and die from hyperthermia when exposed to ambient temperatures higher than 28 °C (MacArthur & Wang, 1973), or even 25 °C (Smith, 1974b). Reflecting these physiological constraints, higher temperatures have been linked with local extinctions and range contractions (Beever et al., 2011; Beever, Perrine, et al., 2016; Billman et al., 2021; J. A. E. Stewart et al., 2015, 2017), as well as restricting their distribution (Beever et al., 2010; Hall et al., 2016; Rodhouse et al., 2017) and abundance (Moyer-Horner et al., 2016; Yandow et al., 2015). Other climatic factors, such as decreasing rainfall and snowfall, have also been linked with local extirpations and population declines (Erb et al., 2011; Stewart et al., 2017). Future projections show dramatic reductions of the current distribution range of the American pika (Calkins et al., 2012; Schwalm et al., 2016; Stewart et al., 2015), although the high regional variability in the projected responses also suggest the complexity of generalizing future responses (Schwalm et al., 2016). Considering that related pika species could be equally threatened by climate change, studies assessing the vulnerability of other pika species are urgently needed.

Some pika species utilize various rocky landforms comprising of piled-up large rocks, such as talus slopes, lava flows, and moraines (Millar & Westfall, 2010; Rodhouse et al., 2010). These species, often referred to as the rock-dwelling pikas, use the interstice space between or underneath the rocks as their main microhabitat, and the ground surface for other purposes such as foraging, vocalizing, and haying (collecting plants for overwinter diet) (Gliwicz et al., 2005). Interestingly, these rocky landforms exhibit cooler and more stable thermal conditions than the local ambient air (Millar et al., 2016; Sakiyama et al., 2021; Varner & Dearing, 2014). This creates a complex spatial distribution of the cool thermal conditions across the entire pikas' distributional range, from the higher elevations to the lower elevations where warm ambient conditions prevail but patches of these rocky landforms are likely to provide key microclimates. Indeed, rocky landforms with cool microclimates buffer physiological stress and provide favorable conditions for pikas (Wilkening et al., 2015). Moreover, such landforms enable behavioral thermoregulation by allowing the pika to retreat into the rock interstices even under warm conditions, such as in low elevation habitats (Smith, 1974b; Smith et al., 2016), and are thus considered important feature for pikas to persist (Smith, 2020). Therefore, rock-dwelling pikas serve as an excellent study subject to assess the role of microclimates in maintaining species distributions under climate change.

The northern pika *Ochotona hyperborea* is one of the rock dwelling pika species (Gliwicz et al., 2005) (Fig. 1-4). It has the widest distribution among all pikas, occurring in northeastern Eursia from the Ural Mountains in the west to the Chukchi sea in the east, as well as island populations towards the south in Sakhalin and Hokkaido (Lissovsky et al., 2021) (Fig. 1-2). Recent work has described the cool and stable microclimate existing in rock interstices of northern pika habitats in Hokkaido (Sakiyama et al., 2021). However, the contribution of microclimate in driving the species distribution was not investigated as the thermal measurements were conducted only at occupied sites. Moreover, potential impacts of climate change on the distribution of northern pika remain largely unknown due to lack of studies. Hokkaido is located at the southern margin of the distribution of the species, suggesting populations on the island should be particularly vulnerable to climate change. Further, the northern pika in Hokkaido is classified by the Japanese Red List as a near-threatened species (Ministry of Environment, 2020), necessitating more studies for planning effective conservation.

1.6 The dissertation structure

In my doctoral dissertation, I explored the various aspects of the role of rock interstice microclimate in driving the distribution of the northern pika population in Hokkaido (Fig. 1-2).

In Chapter 2, I established the methodology to survey the occupancy of the northern pika by assessing the efficacy of aural detection approaches. The playback method was confirmed to be extremely efficient and served as the foundation of the field surveys for this dissertation.

In Chapter 3, I assessed whether the northern pika distribution is changing from the past by revisiting the previously occupied habitats along a wide elevational gradient (60–2,210 m). This chapter aimed to address the first question raised in section 1.4 (*Expanding the timeframe of microrefugia studies*). I then assessed the potential factors leading to the observed changes in species distribution.

In Chapter 4, I measured the thermal conditions in the northern pika habitat along a wide elevational gradient (350–2,200 m) and described the relationship between the ambient temperature and rock interstice microclimate. By conducting occupancy surveys, I further examined the various environmental factors driving the current distribution at the whole-distribution scale and at the trailing edge scale. I considered the effects of thermal conditions, topography, as well as human land-use on the distribution. This chapter aimed to answer the second question raised in section 1.4 (*Comparing the relative importance of microclimate with other environmental factors in the trailing edge populations*).

In Chapter 5, I developed a species distribution model that incorporated fine-scale climate to compare how predictions differ from the conventional, coarse-scale based models. I then predicted future distributions of the northern pika to assess how microclimate may maintain species distributions. Then, in Chapter 6, I tested whether the incorporation of fine-scale climates into SDMs in Chapter 5 actually led to obtaining more realistic predictions to answer the third question raised in section 1.4 (*Validating fine-scale species distribution models*). This was done by comparing the predicted distribution for the present with the occurrence data obtained in Chapters 3 and 4.

Finally, I discussed the role of microclimate in maintaining species distribution and its implications for species conservation in Chapter 7.

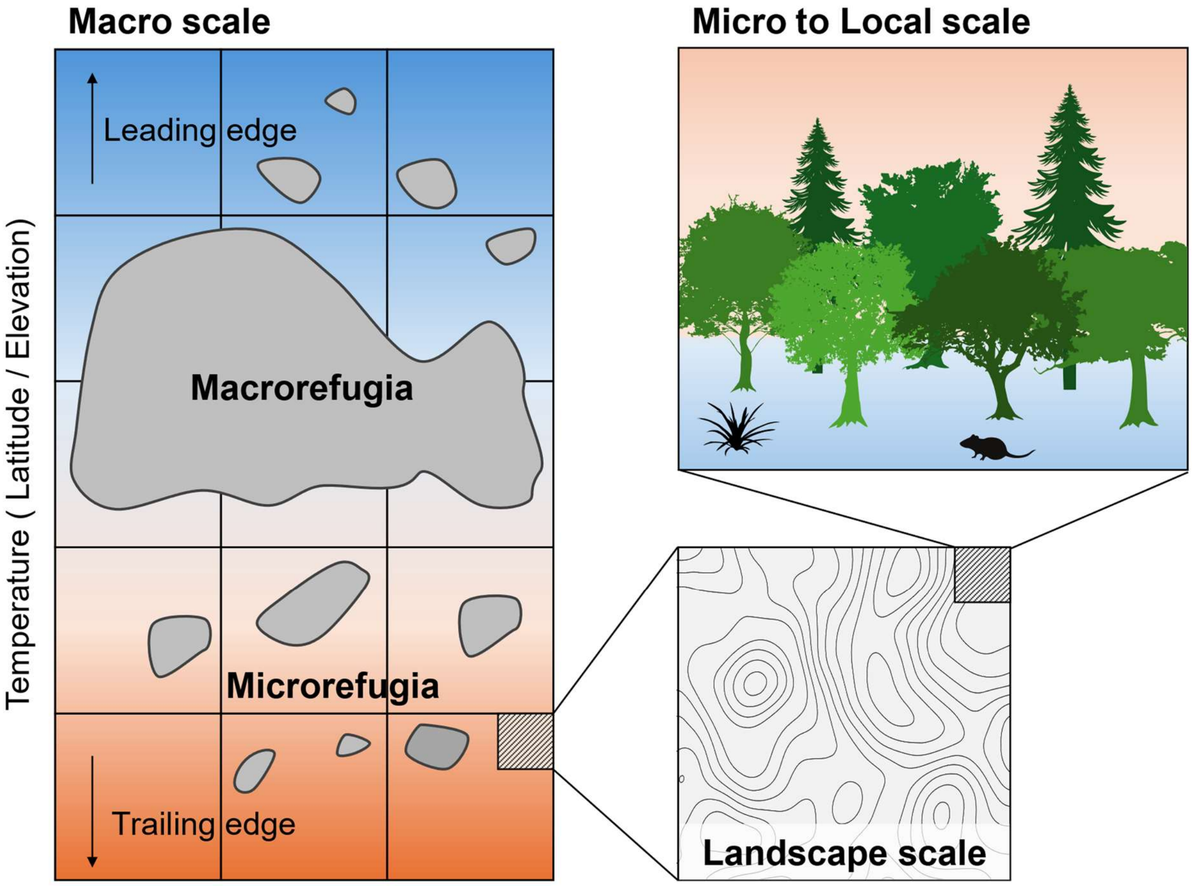


Fig. 1-1 Conceptual diagram of how environmental factors shape species distributions in a hierarchical structure. The background colors represent thermal conditions (blue = cooler, orange = warmer). The top-right diagram shows that cooler microclimates are created by tree canopies even in relatively warmer regions and both understory plants and animals experience such conditions. While species are generally responding to changes in climate at the macro scale, some local populations may persist at the trailing edge of the distribution in microrefugia if suitable climatic conditions are provided at the local-scale.

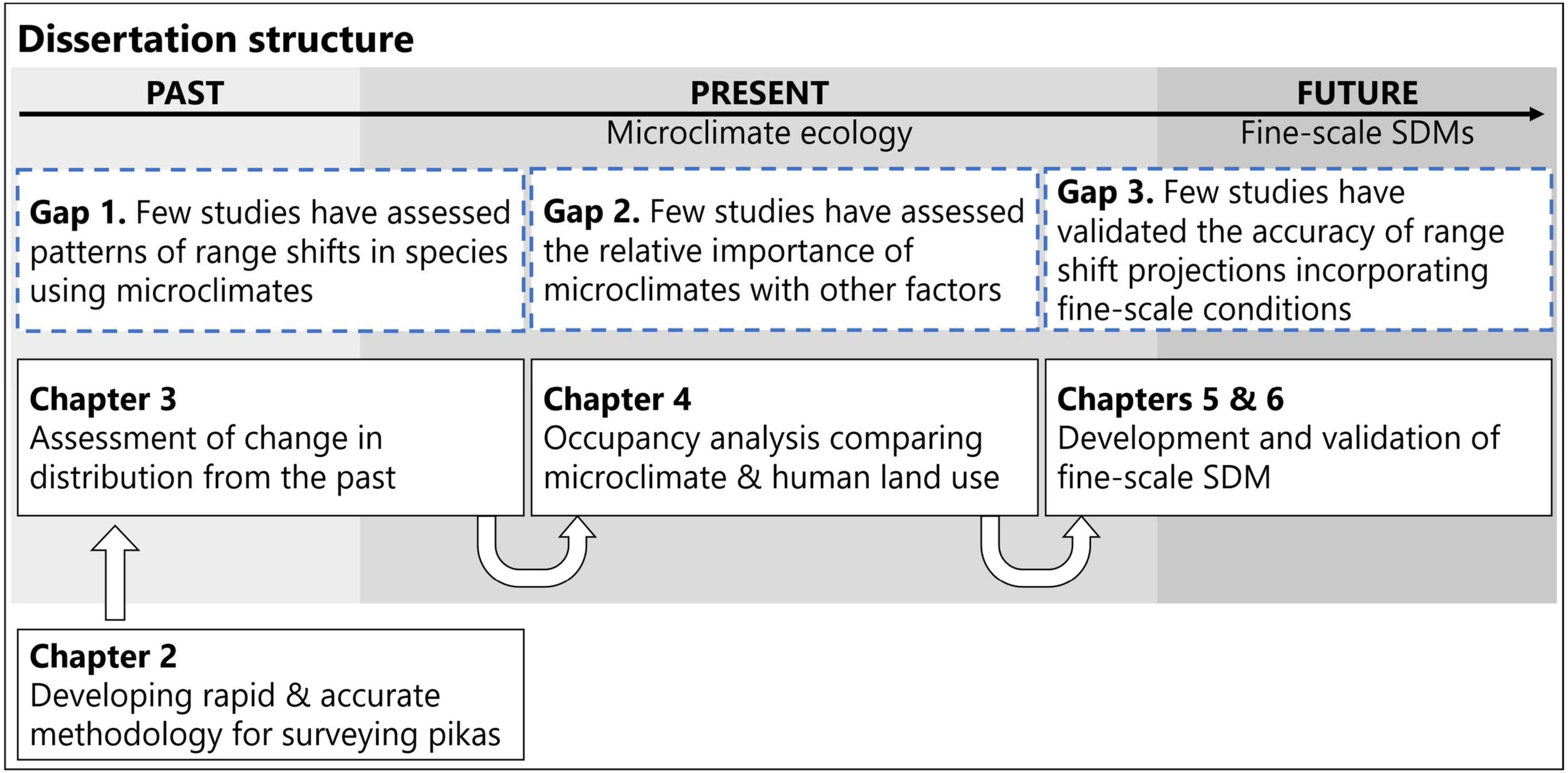


Fig. 1-2 A diagram showing the structure of this dissertation. Three knowledge gaps regarding the role of microclimates in maintaining species distribution under climate change were addressed throughout the dissertation. The main findings are discussed in Chapter 7 Comprehensive Discussion.

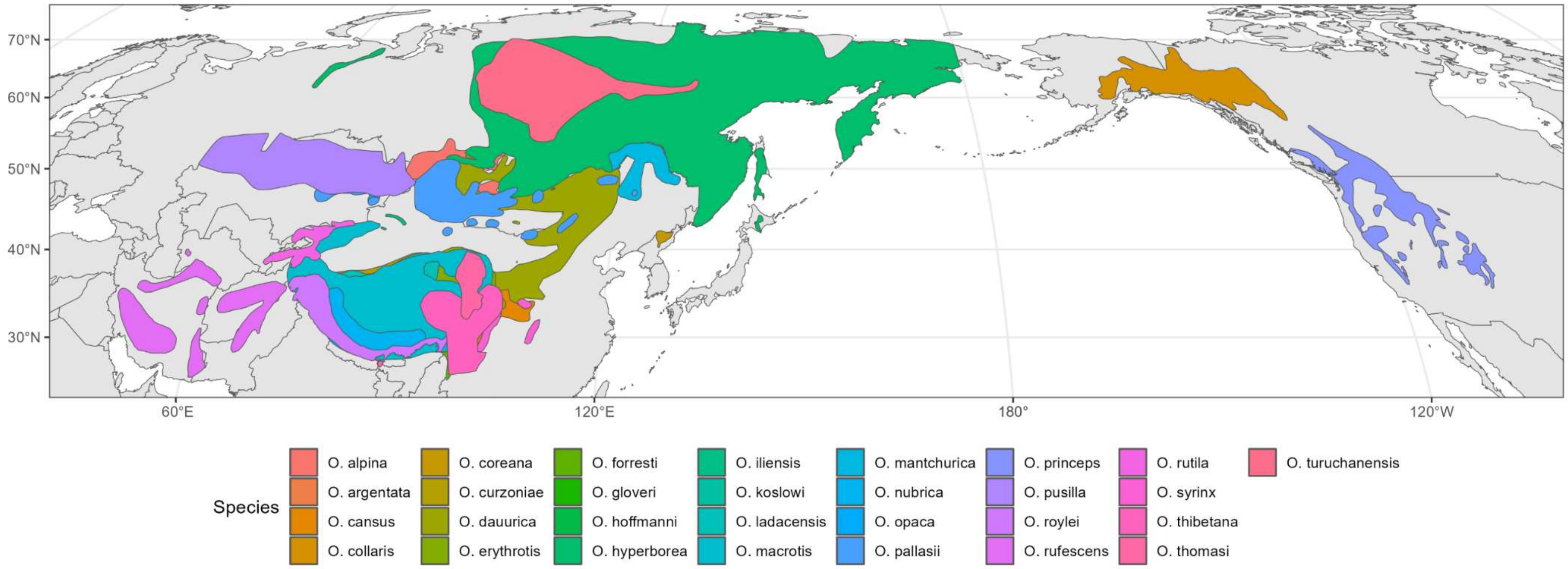


Fig. 1-3 The global distribution of pikas. Each species is shown in different colors. The distribution of the northern pika (*Ochotona hyperborea)* is indicated in green in Northeastern Eurasia. In this study, I focused on its southern margin population found in Hokkaido, Japan. Range boundary data from IUCN was used to make this map.

Fig. 1-4 Image of (a) the northern pika *Ochotona hyperborea* and its typical rocky habitat (e.g., talus slope) in (b) alpine and (c) forest ecosystems.

Chapter 2: Efficacy of aural detection methods for surveying the northern pika (*Ochotona hyperborea*) in rocky and densely vegetated habitats

Abstract

Wildlife monitoring plays a key role in species conservation, with growing importance under the threat of climate change. The northern pika (*Ochotona hyperborea*) is a cold-adapted species found in Hokkaido, Japan, presumably vulnerable to such threats. However, its high elusiveness hinders detailed population surveys, and visual detection methods—often used for other pika species—are not applicable to its densely vegetated habitats. In this study, I assessed the efficacy of aural detection methods to detect the northern pika through their distinct vocalizations. I conducted two types of point-count surveys—auditory observation and playback—during 2021 at 18 sites in and around Daisetsuzan National Park. I then assessed the efficacy of these methods in detecting presence and compared time until first detection of the animal. The northern pika was present at 11 of all surveyed sites, with a predominance at higher elevations. My results suggest that both auditory observation and playback are effective at detecting presence, but playback is more time efficient. I discuss the advantages and disadvantages of each method given these results. In conclusion, my results demonstrate that both survey methods are applicable for northern pika population surveys—even in densely vegetated habitats—representing valid and affordable survey methods that can help to improve current monitoring and conservation efforts and will be of increasing value given potentially negative effects of climate change on persistence of the species.

Introduction

Cumulative evidence suggests that wildlife populations are declining globally, and monitoring has been critical in detecting such changes (Collen et al., 2009; WWF, 2020). Understanding the drivers of these declines poses a significant challenge informing conservation policy and managing wildlife populations adaptively under global environmental changes (Di Fonzo et al., 2016; Yoccoz et al., 2001). However, some species are more elusive to detect than others (Thompson, 2004), making monitoring surveys of rare and elusive species prone to inaccurate detections and hindering our ability to obtain unbiased estimates of occupancy and abundance.

Pikas are small lagomorphs found at high latitudes or altitudes in Asia and North America. Because of their adaptation to cold environments (Wang et al., 2020; Yang et al., 2008), they are considered to be vulnerable to warming climates (Beever et al., 2011; Billman et al., 2021). Therefore, efforts to monitor the status of pika populations are needed to better understand how climate change affects population distribution and abundance. However, some pika species are highly elusive given their preference to live in rocky patches (Henry & Russello, 2011), and while research exists for the American pika (Ochotona princeps), it is lacking for many of other rock-dwelling species. This is true for the northern pika (*Ochotona hyperborea*), a species found in northeastern Eurasia that has the widest distribution among all pika species (Smith, 2018). Although a recent study in the eastern subspecies O. h. yesoensis in Hokkaido, Japan suggested its vulnerability to climate change due to thermal constraints (Sakiyama et al., 2021), the effects of climate change on local populations remain largely unknown. The absence of population studies on the northern pika in Hokkaido is not only due to its habitat preference for rocky patches, but also to the dense vegetation that covers their rocky habitats. Moreover, most habitats are located on steep slopes, making accessibility and site navigation extremely difficult and time-consuming. Therefore, establishing robust yet affordable methods to survey northern pika occurrence in Hokkaido and localities with similar habitat characteristics are needed.

Previous studies have surveyed rock-dwelling pikas either by detecting sign of animal presence visually or aurally, or indirectly through presence of feces and haypiles (Beever et al., 2010; Erb et al., 2011; Hall et al., 2016; Korolev, 2017; J. A. E. Stewart et al., 2015). Such an approach with multiple evidence likely aids in detecting the presence of this elusive animal, but the major assumption of the survey (although not mentioned) is that the visibility and navigability of the study sites allow for detection of these signs. This assumption, however, does not apply to the environments found in Hokkaido because of the aforementioned difficulties.

Here, I advocate instead for the use of survey methods based solely on aural detection as a reliable alternative and test their utility in the Hokkaido locality. Northern pikas are highly vocal, and their vocalizations are detectable from distant locations (up to 200 m; Kawamichi, 1969) even when the vocalizing individual is not visible (Kawamichi, 1970). Moreover, vocalizations are heard frequently during and after the reproductive season (Kawamichi, 1971), permitting population surveys in the snow-free season (i.e., summer) even though their habitats—typically located in remote settings such as deep forests and alpines—are inaccessible at other times of the year. Previous efforts have been made to survey a northern pika population based on their vocalizations (Korolev, 2017), but that survey was conducted only at sites of known presence since the study focused on abundance estimation. Occurrence surveys, in contrast, aim to establish whether the northern pika is present or absent at a given site.

I conducted field experiments to evaluate the efficacy of two aural detection methods—auditory observation and playback—for surveying northern pikas in Hokkaido. Auditory observation refers to a passive survey that involves listening to naturally occurring vocalizations and is the most commonly used aural detection method for pikas (Billman et al., 2021). Playback uses acoustic cues to trigger vocalizations from the target animal, enabling detection of their presence. The playback method has been often used in avian studies (Conway & Gibbs, 2005; Kawamura et al., 2016); however, recent studies have applied it to survey mammals including ungulates (Enari et al., 2017) and primates (Dacier et al., 2011; Gestich et al., 2017). Several studies have used playback with pikas (Conner, 1983, 1985, 1985; Somers, 1973; Trefry & Hik, 2009), but for purposes related to the communicative nature of vocalizations rather than for conducting population surveys. Studies applying the playback method to survey pika populations are scarce, with only two small-scale studies using it to assess the northern pika occupancy in Hokkaido (Ieiri & Yanagawa, 2009; Sato et al., 2009), although they did not detail their description of method and efficacy, and did not objectively contrast results with the auditory observation approach.

To fill this research gap, I (1) compare the efficacy of auditory observation and playback to detect northern pikas; and (2) further investigate how acoustic cues in playback promote species detection.

Materials and Methods

Study area

I conducted this study in Daisetsuzan National Park and the surrounding forests in the Tokachi region of Hokkaido, the northernmost island of Japan. I selected 18 rocky patches on talus slopes as study sites in June 2021 because rock interstices found within this landform are the primary microhabitats for northern pikas (Fig. 2-1). The study sites (elevation range 350–2200 m) were selected to cover to the greatest possible extent the known elevational distribution, ranging from 50 m (Kawabe, 1990) to 2200 m (Onoyama & Miyazaki, 1991). Vegetation changes across this wide elevational gradient, ranging from primarily forest vegetation at lower elevations to alpine vegetation at higher elevations. Based on differences in the structure and amount of vegetation types, I classified the study sites into higher (n = 9) and lower (n = 9) elevation sites (Fig. 2-1; Sakiyama et al., 2021).

All procedures in this study were conducted with the permission of the Hokkaido Regional Forest Office and Daisetsuzan National Park (Permit numbers 2106071 and 2106072) and followed the American Society of Mammalogists guidelines (Sikes & the Animal Care and Use Committee of the American Society of Mammalogists, 2016).

Occurrence survey

Surveys were conducted at each site every month between July and September 2021 because northern pikas in Hokkaido emit vocalizations frequently during these months and the sites are not covered with snow. Surveys were conducted on both clear and cloudy days, in the morning between 05:00 and 10:30 when pika activity is reportedly highest (Kawamichi, 1971). To determine the presence or absence of northern pikas at each site, I conducted two point-count aural detection surveys using both auditory observation and playback approaches. Auditory observation consisted of listening to the natural vocalizations of the northern pika without intervention. By contrast, playback involved the broadcast of a prerecorded pika vocalization as a cue to elicit responding vocalizations. Upon arrival at each site, I remained silent and inactive for 10 min to reduce the possibility of human arrival stimulating pikas to vocalize. After this initial waiting period, I conducted auditory observation first, followed by playback. Nonetheless, pika vocalizations detected prior to the survey upon arrival at the site were also recorded as a baseline to assess the efficacy of auditory observation and playback. For both methods, I listened to vocalizations in a fixed facing direction (upslope or downslope) and recorded the following information for each detected vocalization activity: (i) time from start of the survey (time after the broadcast ended in the playback); (ii) vocalization type (see next section); and (iii) direction at 10-degree intervals (all surveys were conducted by T. Sakiyama). The survey timeframes were 50 min for auditory observation and 5 min for playback. Auditory observation was longer because lack of intervention could delay the first detection, whereas I expected a much quicker detection for playback. After the survey, the site occurrence status was marked as present if any type of northern pika vocalization was detected and absent if not.

For playback, I broadcast an audio file from a monophonic audio speaker (JBL CHARGE4, JBL, California, USA; frequency response 60–20,000 Hz) as a cue to provoke vocalizations from individuals. The audio file consisted of three repetitions of a northern pika 'song' (also known as 'long call'; Kawamichi, 1981), each played with the speaker facing in three directions perpendicularly (leftward, forward, and rightward relative to the facing direction) to cover the entire study site. While the vocalization type used for playback was not mentioned in previous studies (Ieiri & Yanagawa, 2009; Sato et al., 2009), I used the song as a cue because I successfully heard responding vocalizations in a preliminary trial when using this type of call (T. Sakiyama, personal observation). I conducted surveys at a monthly interval to prevent pika individuals from habituating to recorded vocalizations (Trefry & Hik, 2009). The song was prerecorded using a stereophonic audio recorder (Olympus LS-P4 Linear PCM Recorder) located 5 m from a northern pika individual. After successfully recording the song, I reduced external noise in the audio, modified the song length from six elements (as defined in Kojima et al., 2006) to ten elements to enable longer broadcast, and created an audio file comprising of three repeats of the song with an approximate total duration of 30 s long. Both modification and creation procedures were conducted using Audacity v. 3.0.0 (Audacity Team, 2021) (Fig. S2-1).

In both auditory observation and playback, the auditory capability of a surveyor may bias detection. Therefore, each surveyor underwent preliminary training to locate pika vocalizations by ear, and I evaluated the auditory capability of the surveyor in locating the sound source (distance and direction) in a test experiment in order to confirm that a surveyor was efficient in detecting the northern pika vocalizations at different directions and distances (see Fig. S2-2). Moreover, northern pikas could have been more detectable from the front than from the back during the actual surveys because the surveyor faced one fixed direction in the talus patch during the surveys. To assess if such directional bias was introduced, I created histograms of the direction from which vocalization activity was detected for both auditory observation playback surveys. I counted the number of surveys that detected vocalization activities for each direction over the three sessions across sites and used it as the frequency.

Vocalization type classification

The northern pika is known to emit various types of vocalizations (Kawamichi, 1981; Lissovsky, 2005), and therefore, I distinguished the vocalization types by ear in the surveys. However, there has been high ambiguity in the terminology of each vocalization type in previous literature. For example, Kojima et al. (2006) followed terminologies in Kawamichi (1981), but Lissovsky et al. (2021) followed a different terminological system (Lissovsky, 2005; described in Russian). To minimize potential ambiguities, I consider literature descriptions of qualitative and quantitative characteristics of vocalization types as follows: the 'long call' described in Kawamichi (1981) matches the 'song' described in Lissovsky (2005); the 'short call' in the former matches the 'alarm call' in the latter; the 'trill' in the former equals the 'chirring' in the latter. Although I could not obtain detailed information on function and spectrogram for the 'submission call' in Kawamichi (1981) and the 'trill' in Lissovsky (2005), I did not detect these types in my surveys. Therefore, I only considered the three aforementioned vocalization types in this study, all being detectable by human ear (further detail in Extended Methods S2, Fig. S2-3, 2-4).

The detectable range of vocalization activities varied depending on the type of vocalization: both 'long call/song' and 'short call/alarm call' were detectable from a distance of 100 m, whereas 'trill/chirring' was only detectable from 25 m or closer. The detection range is more conservative than that of Kawamichi (1969; i.e., 200 m) because those ranges probably were attained under optimal ambient noise conditions. Given that these surveys were occasionally conducted in windy conditions (≤ 6.0 m/s) and cicada singing background noise (< 60 dB), I elected to use a conservative detection range of 100 m from the site center in these surveys.

Statistical analysis

To compare the efficacy of aural detection methods, I analyzed the accuracy of each method with respect to time spent on the survey by creating confusion matrices and computing the true positive rate and accuracy. True positive rate (also referred to as sensitivity) indicates the probability of a method detecting presence at sites that are truly occupied by the pika. Accuracy indicates the probability of a method determining the true occurrence status (i.e., present or absent) at each site. The true occurrence status at each site was based on the overall combined results from all surveys over the season. Here, I assumed that the overall surveys could detect the true occurrence status at each site and that it did not change during survey season (i.e., closed population setting). However, this assumption might not hold true because, according to one study, the northern pika disperses from late July through August (Kawamichi, 1971), which overlaps with the survey season. Therefore, I also examined how the number of sites detected changed over time. Since the timeframe differed between auditory observation and playback (50 and 5 min, respectively), I divided each auditory observation survey record into 10 survey periods of 5 min each and computed true positive rate and accuracy of detection for each.

I compared the time until first detection between auditory observation and playback methods to understand how intervention of the playback broadcast promoted their response. I used the detection result from the first survey period for auditory observation to match the timeframe of the playback survey and used only those cases where both methods succeeded in detecting the animal. I compared time until first detection using a generalized linear mixed model with a negative binomial distribution. I selected this distribution because the data included zero values (i.e., 0 s when detected) and because overdispersion was detected when data were first analyzed using the Poisson distribution. I fitted time of first detection as the response variable and methods (i.e., auditory observation and playback) as categorical explanatory variables. The intercept in the linear predictor was omitted from the model and site was included as a random intercept. I interpreted the difference between methods as significant if the 95% confidence interval of the prediction did not overlap. To examine the goodness-of-fit, I computed the marginal R^2 (variance explained by the fixed effects) and conditional R^2 (variance explained by both the fixed and random effects) values (Nakagawa & Schielzeth, 2013).

All statistical analyses were conducted using R 4.1.2 (R Core Team, 2021). Confusion matrix analysis was conducted using the caret package (Kuhn 2008) and mixed model analyses were conducted using the lme4 package (D. Bates et al., 2015).

Results

I detected northern pika at 11 of the 18 sites from the occurrence surveys, with eight sites corresponding to higher-elevation and three to lower-elevation sites (Fig. 2-1). The highest elevation among the present sites was 2,220 m at Mt. Hakuun, which corresponds with previous reports (Onoyama & Miyazaki, 1991). On the other hand, the lowest was 470 m along the Horoka-Piribetsu river, which to my knowledge has previously not been reported as northern pika habitat. The occurrence of northern pikas indicated a positive spatial autocorrelation pattern, where present and absent sites were found relatively close to other present and absent sites. I often detected presence upon arrival at the site in higher elevations in early summer. In contrast, such cases were uncommon at lower elevations, with lower-elevation sites necessitating the use of auditory observation or playback surveys to detect presence most of the season (Table S2-1). Among the different vocalization types, 'long call/song' and 'short call/alarm call' were more frequently heard than 'trill/chirring' for all months at both higher and lower elevations (Fig. S2-5).

Confusion matrix indices revealed that detection accuracy changed according to survey duration for the auditory observation method. When duration increased from the shortest (5 min) to the longest (50 min) setting, the true positive rate increased from 0.606 to 0.909 and accuracy increased from 0.759 to 0.944 (Fig. 2-2). Both indices initially changed drastically over shorter survey durations, reaching a plateau around the sixth survey period, approximately 30 min after the survey was started. For playback, which was conducted for only 5 min, the true positive rate and accuracy were 0.879 and 0.926, respectively. I found that values from playback are comparable to those of the longest duration setting of the auditory observation method (Fig. 2-2).

The time at first detection of northern pika vocalizations was statistically significantly shorter for playback than auditory observation (Table 2-1, Fig. 2-3). First vocalizations—recorded using playback—were detected 23.8 s after the audio was played on average, whereas they were detected after 127.6 s with auditory observation. The marginal and conditional R^2 values were 0.451 and 0.479.

During auditory observation surveys, northern pika vocalizations were detected more frequently from the front side than the back side for 'short calls/alarm calls'. However, in other cases, detections were oriented sideward (i.e., left and right sides), which differed from the initial expectations. Detection of 'trill/chirring' was rare during the surveys (Fig. 2-4, S2-5).

Discussion

In this study, I compared the performance of two aural methods for detecting presence of the northern pika by listening for their vocalizations. My results showed that both auditory observation and playback are highly and comparably effective in detecting presence. And while presence was more frequently represented at higher-elevation than lower-elevation sites (Fig. 2-1), this agrees with previous reports describing their distribution in Hokkaido (Kawabe, 2008; Onoyama & Miyazaki, 1991), and modelled distribution of the species that reflects their adaptation to cold environments (Sakiyama et al., 2021). These results indicate that vocalization-based surveys have high potential for monitoring the northern pika in its natural habitat and contributing to understanding the effects of environmental change on their populations.

Occurrence survey

The effectiveness of auditory observation increased significantly as survey duration increased. This result is intuitive because a longer duration increases the chance of recording vocalization activities. Pikas often vocalize for alarm and territorial purposes (Kawamichi, 1981; Lissovsky, 2005; Somers, 1973; Trefry & Hik, 2009), as well as for positioning and localizing other individuals (Conner, 1982). Since these natural events are likely to occur randomly over time, shorter survey durations are likely to include more false-negative detections. The initial expectation was that detection of northern pikas would require survey durations longer than 5 min, a timeframe used in bird surveys (Ralph et al., 1995), because of their low conspicuity. Nonetheless, my results revealed that detection efficacy reached a plateau when auditory observation was conducted for more than 30 min. This suggests that continuing the survey after 30 min does not provide significant gains in information relative to the effort invested—this saturation effect was also reported previously in a study that used a similar point-count method (Hutschenreiter et al., 2021).

Notably, the five-minute playback survey reached a similar level of efficacy as the longest auditory observation survey in detecting the presence of northern pikas. Moreover, the playback method detected, on average, their presence approximately four times earlier than the auditory observation method. Therefore, cues broadcast by the audio speaker are highly effective in eliciting vocal responses. Although this phenomenon has been observed and effectively used in previous studies to understand the behavioral nature of vocalization (Conner, 1982; Somers, 1973; Trefry & Hik, 2009), my results suggest that it can also be used as a highly effective, fast, and affordable method for surveying the presence in this species.

Another significant advantage of the aural detection survey was that it enabled detection of presence of northern pikas at lower elevations, including areas previously unreported as pika habitat (i.e., along the Horoka-Piribetsu river). These landscapes are characterized by denser vegetation structure and fewer rock interstices than higher elevations (Sakiyama et al., 2021), hampering traditional visual approaches for detection. Moreover, vocalization activities were not easily detected upon arrival at their habitats at lower elevations, in contrast to higher elevations (Table S2-1), making aural detection method the only effective approach. Lower-elevation populations inhabit marginal regions of their distribution, whereas core populations are located at higher elevations (Sakiyama et al., 2021). Therefore, aural detection provides a promising tool for efficient monitoring of northern pikas that might be more vulnerable to climate change and human land uses at lower elevations.

I found that the number of sites at which presence was detected increased gradually during the summer (Fig. S2-5), suggesting that occurrence could be surveyed by vocalization during and after the reproductive season, as expected from previous studies (Kawamichi, 1971). This trend was more apparent at lower elevations, and it could be a result of false-negative observations, even though they did inhabit the site from early in the season. This finding emphasizes the importance of repeating the survey throughout the summer to improve chances of detecting presence. However, northern pikas have been reported to disperse from late July to August at lower elevations (Kawamichi, 1971), whereas American Pikas disperse from mid-May to mid-August at high altitude (2,000 m) habitats (Smith, 1974b). Therefore, the increase in the number of sites at which they are present over the summer could instead be a result of dispersal events from adjacent sites. If this was the case, then the assumption of a closed population for the survey would not have been met. Although I primarily considered the timing of snowmelt to determine the survey season, a more precise definition may be needed to better accommodate the population setting in future studies. Fixing survey season prior to or after dispersal, for example, could enhance accuracy. To this end, further studies into the dispersal ecology of northern pika are urgently needed.

Advantages and disadvantages of aural detection methods

My results suggest that both auditory observation and playback are effective in surveying the presence of the northern pika, but each has advantages and disadvantages.

A common advantage of using point-count aural detection is that the surveyor need not venture into densely vegetated and potentially dangerous habitats. Talus slopes consist of piles of large, loose rocks with interspersed vegetation of various types and structures including lichens, bryophytes, herbaceous plants, shrubs, and trees (Sakiyama et al., 2021). Hence, walking steadily within the site requires care, and the simultaneous search for signs of pikas is laborious and time-consuming. Alternatively, when the surveyor does not move, vocalization is less influenced by these factors, although the observational environment (e.g., strong wind) needs to be considered in terms of its effect on auditory detection. The use of the point-count survey is also advantageous because it avoids trampling on and damaging vegetation, which is the main dietary resource of northern pikas. Additionally, while feces can represent incomplete signs of recent activity (Nichols, 2011), vocalization-based surveys only detect active signs of presence. Furthermore, the detections are plausibly not biased towards either sex given that both "long call/song" and "short call/alarm call" were frequently heard during the survey.

Nevertheless, the use of vocalization-based methods has several disadvantages. First, it is difficult to define the area where pika vocalizations can be detected by the human ear. I conservatively assumed that the aurally detectable range of the northern pika is 100 m, although complex topography could alter this range. My results show that detection of the vocalization activities was more prevalent in frontward and sideward directions (Fig. 2-4), suggesting that choice of surveying point and facing direction will influence results. Moreover, if the study area is larger than the range of detection by ear (approx. 100–200 m; Kawamichi, 1969), it will be important to conduct the survey at multiple points. Second, aural detection methods require training of the surveyor to differentiate northern pika vocalizations from other animals. While no other small mammals cooccurring in rocky patches make vocalizations identical to the northern pika, the Eurasian Woodcock (*Scolopax rusticola*) makes a vocalization similar to the 'short call/alarm call' during their nocturnal flights (T. Sakiyama personal observation). Therefore, I ensured no potential confusion by planning these surveys during the morning, and likewise avoiding the active time of other animals are likely to reduce false detections. Third, although I was cautious to minimize these factors, I did not assess if and how the presence of the surveyor could affect results. For example, although I stayed silent before and during the survey, animals could still have detected my presence through olfaction. If this was the case and their vocalizing behavior was reduced as a result, the estimation of presence would likely have been underestimated. Fourth, it remains unclear how behavioral differences at different life stages will affect aural detection results. For example, younger individuals might vocalize at lower volume and less frequently than older individuals, which could also lead to a reduction in detection probability.

The methodological differences between auditory observation and playback included duration of the survey (survey durations were up to 50 min for auditory observation method and 5 min for playback) and for the latter, broadcast of a prerecorded call to stimulate pika vocalizations. However, detection results between playback and auditory observation were comparable. Thus, playback has an advantage over auditory observation because it reduces survey duration and, therefore, effort and cost. Resource allocation is key in planning field surveys. With limited resources, researchers frequently face the challenging task of balancing the number of sites and survey effort within each site. A reduction in survey time enables an increase in the number of sites, which increases robustness of research results.

Playback was conducted by broadcasting prerecorded vocalizations to elicit responding calls from inhabiting individuals. The implementation of playback requires important considerations that are not required for auditory observation. First, pikas could become habituated to playback audio if it were played frequently (Trefry & Hik, 2009). Habituation of target species should be avoided because it may increase false-negative observations and preclude consistent surveys. This problem can be avoided by designing surveys such that they are sufficiently spaced over time (i.e., once a month in this study)—broadcasting audios recorded from different individuals could also reduce habituation. Second, the effect of the prerecording source on response remains unclear. If the response behavior differs depending on the spatial source of the broadcast (i.e., place of prerecording), as was reported for the American pika (Conner, 1983), the efficacy of playback will likely be spatially biased. However, this effect was likely minimal in the study because only a single acoustic dialect is found in northern pika populations in Hokkaido (Lissovsky, 2005; Lissovsky et al., 2021). Conversely, the choice of prerecording source will require in-depth consideration in situations where playback is conducted at a broader spatial extent, increasing the likelihood of including multiple dialects—in these kinds of surveys, the simplicity and passivity of auditory observation could be advantageous. Furthermore, using a single audio file for the playback could be considered a limitation of this study for the purpose of efficacy evaluation because the responses to the broadcast file could have varied among individuals. Nevertheless, I believe that the audio file used could be used for occurrence survey purposes in Hokkaido given that it worked well for all sites in this study.

In conclusion, aural detections could be a promising approach for surveying the northern pika occurrence to monitor the population trends under environmental change. I note that this approach has the potential to estimate the population density of the northern pika, for instance by conducting a line-transect survey, which could further improve our understanding of population trends. In these endeavors, it will be important to overcome the uncertainties of identifying individuals heard at far distances.

Table 2-1. Parameters and performance of generalized linear mixed models to assess the difference of time until first detection of the northern pika between auditory observation and playback.

Method	β	SE	*z*	*P*
Auditory observation	4.849	0.267	18.142	< 0.001
Playback	3.171	0.343	9.246	< 0.001

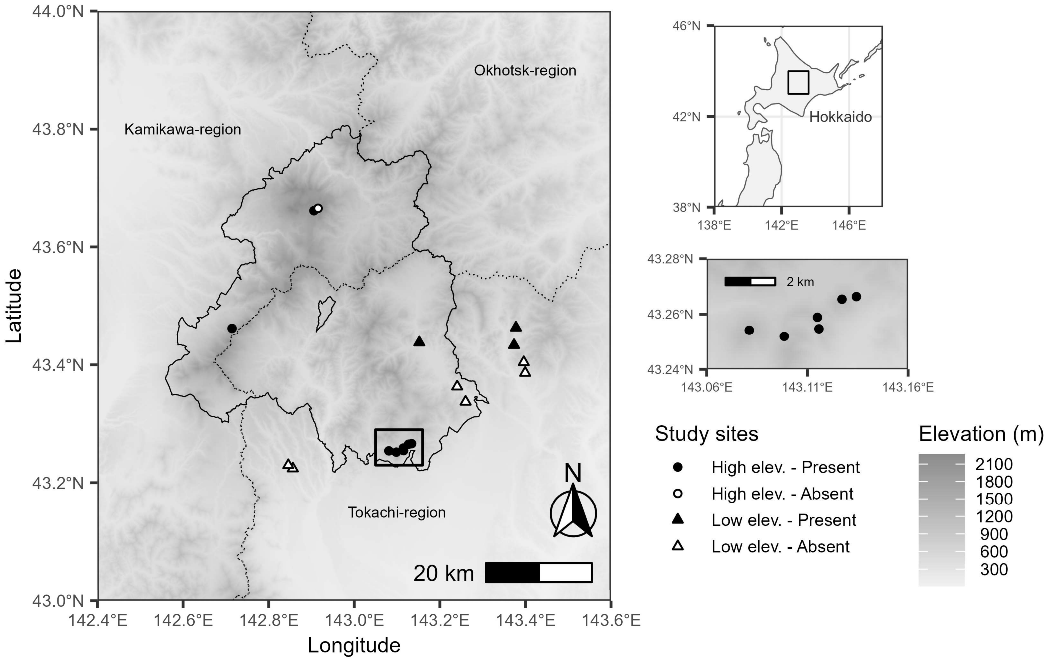


Fig. 2-1. Map of the study area in Hokkaido, Japan (top-right panel) and the study sites within to survey the occurrence of the northern pika (left panel), differentiated by occurrence status and elevation class (black indicates presence, white indicates absence, circle indicates higher elevations, and triangle indicates lower elevations). Aggregated sites are shown in higher resolution (mid-right panel). Regional boundary is indicated in dotted lines and the area of Daisetsuzan National Park is shown as a solid line.

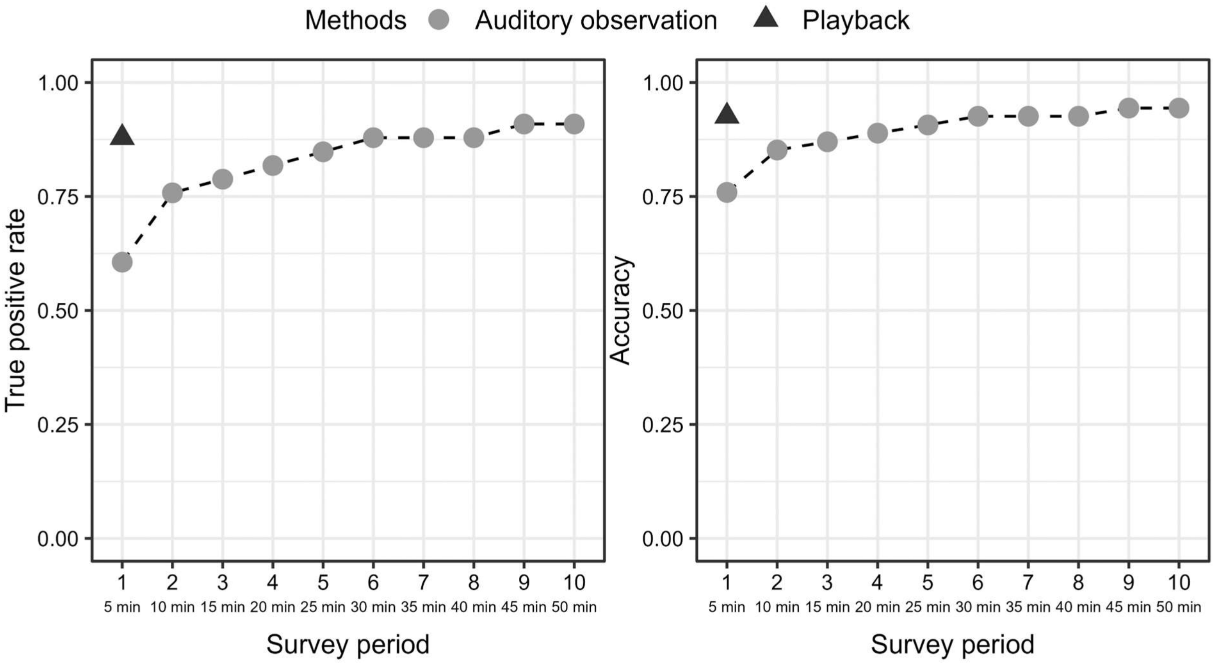


Fig. 2-2. Relationship between confusion matrix indices and duration of the survey to detect presence of northern pikas. Note that auditory observation (circle) was conducted for ten survey periods (five minutes × ten periods), whereas playback (triangle) was conducted only for one survey period (five minutes).

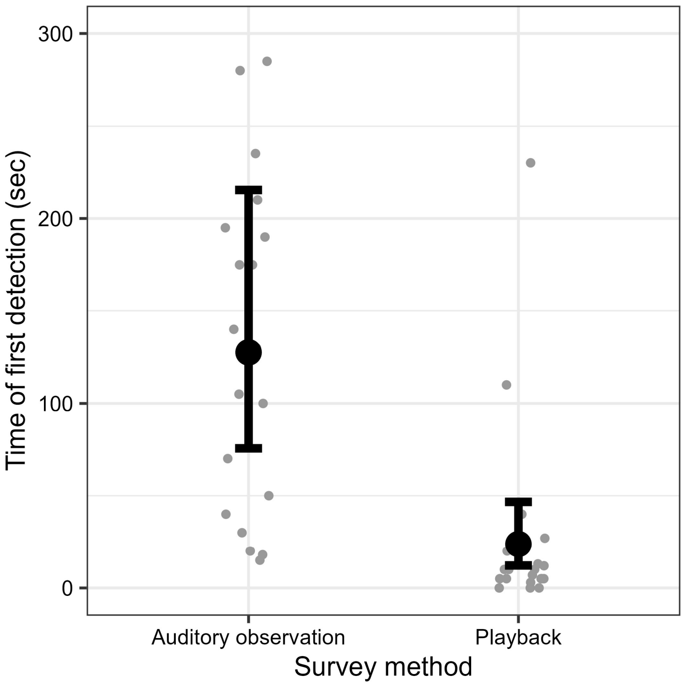


Fig. 2-3. Difference between time of first detection of the animal using auditory observation and playback method. Error bars indicate the 95% confidence interval around the mean.

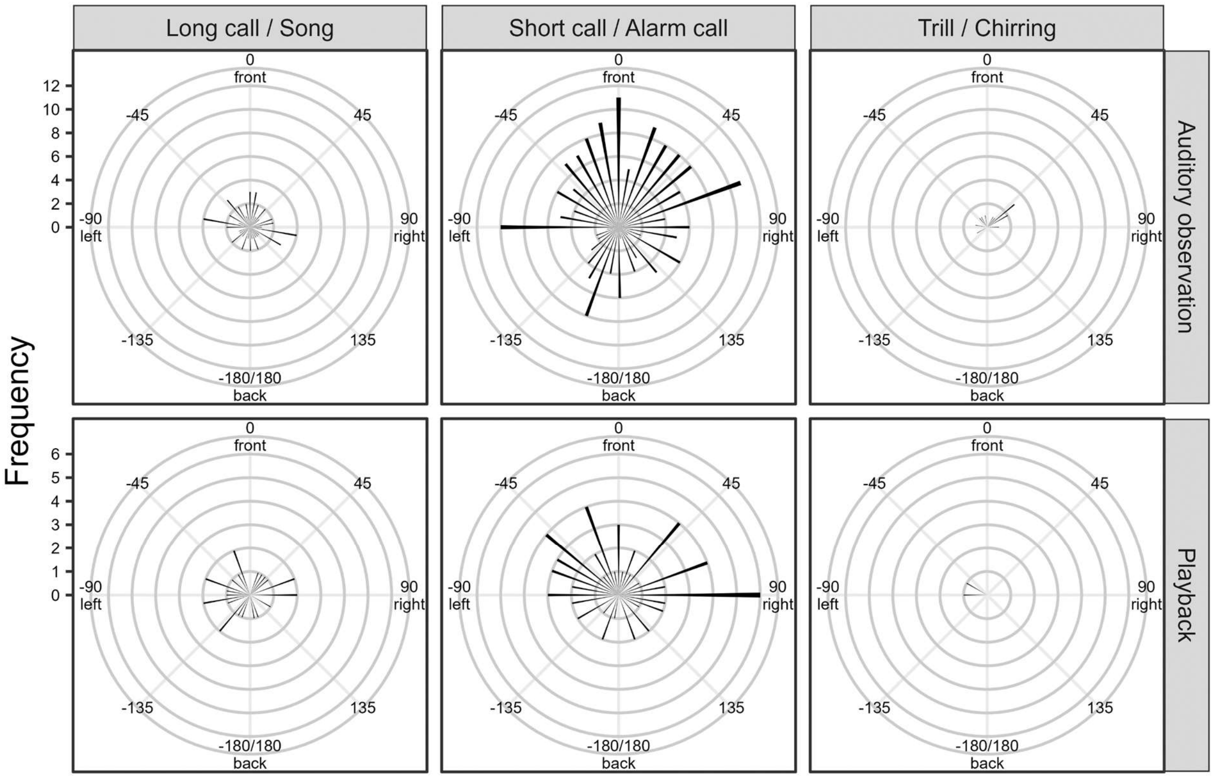


Fig. 2-4. Circular histograms showing frequency of the directions from which the vocalization activities were detected, plotted separately for the survey method and detected vocalization type.

Chapter 3: Resurveys reveal changes in the northern pika distribution: habitat size, temperature, and protection status affect persistence

Abstract

Local populations of many species are threatened by climate change. While species are generally shifting their distributions in response, a large variability exists around this trend. Complex topography is widely recognized as a key factor that may facilitate population persistence and thus delay range shifts by buffering regional-scale temperatures at the local-scale. However, there is still limited evidence supporting this relationship. Here, I assessed the distributional change of the northern pika, a small, climate-sensitive lagomorph occurring in rocky landforms that buffer ambient air conditions, in Hokkaido, Japan, along the elevational gradient. In 2021-2023, I conducted resurveys by visiting 61 sites in 5 regions (elevational range: 60–2,210 m) reported as occupied sites in the past (1961-2010) and evaluated the persistence of each local population. I detected population turnovers, changing from historical presence to current absence, at 20 sites (32.8%) and in one whole region. These absent sites were found from a wide elevational range of 60–1,550 m and thus largely overlapped with that of persisting sites. As habitat size was the most important factor positively affecting occupancy, local-scale habitat heterogeneity found in complex topography likely contributed to the persistence of local populations. Moreover, since mean summer temperature and protection status were found to be important factors, my results suggest that the northern pika population in Hokkaido is strongly influenced by the warming climate and conservation status. Considering the observed shifts in the northern pika distribution, monitoring programs are needed to keep track of the population statuses accurately.

Introduction

Climate change is one of the main threats to global biodiversity. Observations indicate that many species are changing their distributions in response, with potential knock-on effects on other species, ecosystem services and functions (Bellard et al., 2012; Pecl et al., 2017). With future climate projected to change continuously, understanding the drivers leading to current changes in species distributions will be imperative for conservation and management (Bonebrake et al., 2018; Dawson et al., 2011).

In mountain ecosystems, species are responding to climate change by shifting their distributions upslope (Moritz et al., 2008; Pauli et al., 2012; Rumpf et al., 2018). However, the observed magnitude and direction of these shifts are highly variable among species and difficult to generalize (Chen et al., 2011; Rapacciuolo et al., 2014; Rowe et al., 2015; Rubenstein et al., 2023; Tingley et al., 2012), challenging implementation of effective conservation and management. For instance, many species are found shifting their distribution but at slower rates than isothermal shifts, thus lagging behind climate change (Chen et al., 2011), while others are found staying in situ and indicating no shifts (Lin et al., 2023). Unexpected cases of range shifts towards downslope have also been reported (Rapacciuolo et al., 2014; Tingley et al., 2012). Complex topography is widely recognized as a key factor that contributes to lagged responses and population persistence (Moritz & Agudo, 2013). This is because topographical features generate thermal conditions that are distinct from regional-scale conditions at local scales, and species are expected to effectively reduce their physiological stress by utilizing optimum conditions existing locally while hostile conditions prevail at larger scales (Feldmeier et al., 2020; Keppel et al., 2012, 2015; Morelli et al., 2016). However, empirical evidence of complex topography maintaining species distributions over time and thus exhibiting refugial effects remains scarce in the literature (but see Maclean et al., 2015; Suggitt et al., 2018). Although previous studies have suggested that topographical features contribute to local population viability (Lawson et al., 2014; Shi et al., 2015), more studies are essential to explore its importance in range shift patterns.

Changes in species distribution are often evaluated through habitat resurveys (McCain & King, 2014; Moritz et al., 2008). In this framework, places where species occurrences were surveyed in the past are revisited to detect whether there have been changes in occupancy. By conducting the resurvey along environmental gradients of interest, factors underlying the observed patterns in species distribution changes can be assessed (Tingley & Beissinger, 2009; Verheyen et al., 2017). Many studies have incorporated thermal gradients into the resurvey to assess how heterogeneity in prevailing thermal conditions are linked with species persistence (Erb et al., 2011; Freeman et al., 2018; Soroye et al., 2020). On the contrary, non-climatic factors have received less attention in resurvey studies despite their general importance on population persistence (Cheng et al., 2019; Hagenberg et al., 2022). Fundamental properties of a species habitat, such as habitat size, could alter local population viability and affect distribution patterns since larger habitats generally have higher environmental heterogeneity and larger population sizes (Griffen & Drake, 2008), with support from empirical studies investigating range shifts (Beever et al., 2011; J. A. E. Stewart et al., 2015). Moreover, conservation efforts such as protected area designation may reduce negative impacts from human activities and contribute to persistence as higher habitat quality is available (Gillingham et al., 2015). Although the effectiveness of protected areas in mitigating climate change impacts is an open debate, some studies have shown that negative influences are smaller inside protected areas (Gaget et al., 2021).

Pikas are small lagomorphs occurring in mountain ecosystems perceived vulnerable to climate change due to their adaptations to cold environments (Wang et al., 2020; Yang et al., 2008). Some pika species are known for occurring specifically in rocky landforms, such as talus slopes and lava flows (Gliwicz et al., 2005; Rodhouse et al., 2010; Smith, 2018). Interestingly, the rock interstices within these landforms, which are the main microhabitat used by the rock-dwelling pikas, are known to buffer ambient air thermal conditions by generating cool and stable thermal conditions (Millar et al., 2016; Sakiyama et al., 2021; Varner & Dearing, 2014). Despite this feature, habitat resurveys on pikas have indicated substantial changes in the distribution as lower-elevation populations become extirpated due to warming (Beever et al., 2003, 2011), while other studies have suggested the importance of habitat size for persistence (J. A. E. Stewart et al., 2015). However, these resurveys have been so far only conducted for the American pika (*Ochotona princeps*), while it remains unclear how other rock-dwelling pika species are responding to climate change. This is particularly the case of the northern pika (*Ochotona hyperborea*), a species occurring in Northeastern Eurasia, for which no studies have yet assessed the pattern of range shift from the past.

The southern marginal populations of the northern pika are found in Hokkaido, Japan, where the entire regional population is designated as near threatened in the Japanese Red List due to limited amount of habitats (Ministry of Environment, 2014, 2020). These populations are presumably the most vulnerable to climate change given its southern locality and because temperature is a strong determinant of their distribution (Sakiyama et al., 2021; Sakiyama & García Molinos, 2024). Moreover, a recent study revealed the negative influence of human land use on its distribution (Sakiyama & García Molinos, 2024), which in turn suggests that conservation efforts, such as protected area designation, could be important for persistence. The geographical range of the northern pika in Hokkaido is highly heterogenous in thermal environments as it is influenced by the wide elevational range. In addition, its distribution has been reported both inside and outside protected areas, which allows for investigating the contribution of ongoing conservation efforts.

Here, I analyze how the northern pika distribution has changed under recent climate change in Hokkaido. I sought to explain the pattern of persistence by considering the effects of temperature, protection status, and habitat size. This study also aims to update the distribution information of the Hokkaido population. To the best of my knowledge, this study represents the first investigation of habitat resurveys on the northern pika.

Materials and Methods

Study area

Within Hokkaido, the northernmost island of Japan, the northern pika occurs in various mountain ranges in the central region, indicating a scattered spatial distribution (Onoyama & Miyazaki, 1991). To compare the historical and contemporary distribution, I selected the study sites based on previous studies reporting the presence of the northern pika, thus allowing inference for extirpations at those sites (Tingley & Beissinger, 2009), according to the following criteria: 1) the previous survey period was between 1960 and 2010, 2) the site location was indicated by a map and/or a detailed description (e.g., 1,738 m point on the Mt. Tomuraushi trail), 3) the survey methods were described clearly, and 4) multiple sites were surveyed in the same region. Although a total of 305 sites satisfied these criteria, I reduced the final number of survey sites due to time and logistic constraints. Accordingly, the final set of sites was selected to cover as best as possible the reported historical distribution of the species across the thermal gradient, different protection status of the sites, and in different geographical regions within the species' range. This resulted in a total of 61 sites selected from five regions for this study (Fig. 3-1). The five regions were namely, Daisetsuzan, Yubari, Tokachi, North Hidaka, and Erimo-Horoman, and were distinguished by considering their geographical locations and climatic differences. The elevational range of these sites was 60–2,210 m based on the 10 m-resolution digital elevation model provided by the Geospatial

Information Authority of Japan (2023). This included all known elevational range of the northern pika in Hokkaido (Kawabe, 1990; Onoyama & Kato, 1991).

Distribution survey

I surveyed the current distribution of northern pika in the summers of 2021 to 2023 by assessing the occurrence (i.e., presence or absence) at the selected sites. I used the modified version of the playback method described in Sakiyama and Garcia Molinos (2023), consisting of playing a pre-recorded northern pika vocalization from a loudspeaker and listening for responding vocalizations to determine the presence (response vocalization) or absence (no response vocalization) of the pika at each site. In a single survey, Playback was implemented multiple times during the approach to, the stay at, and the leave from each site until a response was heard (in cases of presence) or until the site and its periphery was fully surveyed (in cases of absence). The waiting time for vocalization responses after each playback was three minutes, which has been found to be long enough to detect most of the responding vocalizations from the northern pika (Sakiyama & García Molinos, 2023). Surveys were conducted at least twice at each site, except for those sites detected as present on the first survey, over the three years to reduce the possibility of false-negative detections to compare contemporary occurrence with the historical status.

In the resurvey, the exact location of some historical sites ($n = 8$) was difficult to determine since I could not detect rocky landforms with interstices in the field. In many of these sites, I was able to find rocks at the previously reported locations, but they were covered with dense vegetation and soil (Fig. S3-1). Thus, I recorded them as "low confidence" sites. However, I kept these sites also in the statistical analysis because I considered that these observations could also be reflecting the changes in the environmental conditions over time.

Environmental factors

To assess the environmental factors affecting the current northern pika distribution, I considered the effects of thermal condition, protection status, and habitat size of each site. For thermal condition, I considered the mean temperature of summer (July-August) using the climate data provided by the Japan Meteorological Agency (2022), which is an interpolated climate data based on weather station observations during 1991-2020. While the original data had a spatial resolution of 1 km, I downscaled it to 3 arcsec (68.1 meters horizontally) resolution via kriging analysis using the krigR R package (Davy & Kusch, 2021; Kusch & Davy, 2022). For the kriging analysis, I used the elevation data from the 3 arcsec MERIT digital elevation model (Yamazaki, Ikeshima, Neal, et al., 2017).

For protection status, I considered whether the site was located within a protected area or not. 45 sites (73.8%) are placed inside one of the three protected areas existing in the study area, namely the Daisetsuzan National Park, the Hidakasanmyaku-Erimo Quasi-National Park, and the Furano-Ashibetsu Prefectural Natural Park (Fig. 3-1). Given that lands outside protected areas do not necessarily involve land alteration by human activities, I checked the actual effect of protection status over the lands surrounding each site by visually inspecting aerial images, which were taken extensively in the late 1940s, late 1970s, and late 2010s in the study area, to detect any signs of land conversion for human land use within a radius of 200 m from each site. By considering the years of the historical survey, the land conversion history of each site was categorized into: 1) no activities in any period, 2) initiation of land conversion after the survey, and 3) presence of land conversion from before the survey. I found that a vast majority of protected sites had not experienced land conversion for human activities (40/45 sites; 88.9%), whereas 10 of the 16 unprotected sites (62.5%) had experienced some level of land conversion for human activities either before (5 sites) or after (5 sites) the historical surveys were conducted. Therefore, these results support the use of protection status as a negative correlate to presence of human activities. Observed land conversion included land clearance for construction of dams and roads as well as forest plantations.

Habitat size was defined by calculating the area covered with rocks and interstices based on its width and length measured in the field. Considering that the area covered by the playback method to infer the northern pika occurrence was 10,000 m^2 (100 m x 100 m), I set this as the maximum habitat size. For sites with steep, complex terrains (n = 20), I quantified the habitat size using aerial images in QGIS (QGIS Development Team, 2023) due to limited navigability and visibility in the field. Nonetheless, habitat size could not be measured at three sites either in the field, due to strict protection for ground vegetation, nor from aerial image because of the forested vegetation. Therefore, these sites were not considered for the statistical analysis, resulting in a final sample size of 58 sites. Still, I was able to detect the presence of the northern pika at these sites from nearby trails using the playback method. Therefore, I included these sites for examining the overall number of persistent sites from the past (i.e., turnover rates). For the low-confident sites, the habitat size was recorded as zero since each site lacked rock interstices.

Statistical analysis

I used a single-season occupancy model to examine the effects of thermal condition, protection status, and habitat size on the persistence of northern pika (MacKenzie et al., 2002). This is a hierarchical modeling framework consisting of observation process and state process models. The observation process model is used to assess the detection probability or the probability of detecting species' presence at an occupied site during a survey. The state process model is used to assess the occupancy probability or the probability that a site is occupied by the focal species given the habitat environment. The advantage of this model is that it avoids underestimating occupancy probability by accounting for imperfect detection of species (Kery & Royle, 2015). Despite the study comprising multiple years for the resurvey, I used the single-season framework because I was interested in assessing the factors influencing the contemporary site occupancy (i.e., overall occurrence for the multiple years) rather than the year-by-year changes in site occupancy. The assumption here was that the occurrence of the northern pika was closed during the time-span of the resurveys (Kery & Royle, 2015; MacKenzie, 2018).

For the observation process model, I considered including the survey date (i.e., Julian date) since a previous study detected the northern pika more frequently later in the survey season (Sakiyama & García Molinos, 2023). However, since the predictive performance did not improve from the null model in the obtained data, I only included the intercept for the observation process model. For the state process model, I assessed the pairwise correlation among all predictor variables using the Pearson correlation coefficient and confirmed that no variable pairs were strongly correlated ($|r| > 0.7$) (Table S3-1) Thus, I fitted occupancy models with all possible variable combinations and included the survey region as the random effect in all models (Table 3-1). All covariates were centered and scaled before analysis. I used the "ubms" R package for fitting the models in a Bayesian framework using the *stan_occu* function (Kellner et al., 2022). All models used default priors (Logistic [0,1] prior) and were performed with five independent runs of 40,000 Markov chain Monte Carlo iterations each, discarding the first 20,000 iterations as burn-in. Model selection was performed by ranking the fitted models using the expected predicted log density (ELPD) via leave-one-out (PSIS-LOO) cross validation and selecting models with difference in ELPD from the top-ranked model (ΔELPD) lower than the standard error of the ΔELPD (Vehtari et al., 2017). As Pareto $\hat{k}$ diagnostic was used to assess the reliability of each leave-one-out case, I detected one observation with $\hat{k} > 0.7$, which indicates high influence and inaccurate approximation, in multiple models. Thus, I report the model selection results after removing this observation, where I detected the only presence of northern pika out of the 11 sites surveyed in the North Hidaka region. Model convergence was examined by visually inspecting the trace plots and assessing whether the $\hat{R}$ statistic was close to 1 (Gelman et al., 2013). I considered the effect of the predictors as statistically significant when the 95% credible interval did not overlap zero.

Separating the effects of temperature and protection status

Although mean summer temperature and protection status were not strongly correlated (*r* = -0.59; Table S3-1), my sampling design was imbalanced as all sites in cooler regions occurred in protected areas. This reflects the existing elevational bias in conservation planning where higher elevations tend to be protected. Consequently, given I was not able to sample the occurrence for sites characterized by low temperatures and lack of protection, the sampling design precluded separating the individual effects of temperature and protection status on occupancy. Therefore, I assessed how mean summer temperature and protection status influenced the occupancy of northern pika at lower-elevation sites only, where both protected (*n* = 8) and unprotected (*n* = 16) sites were available. I did this by classifying these sites into a contingency table considering if the sites are in warmer (16.0-17.0 °C) or cooler (17.0-18.4 °C) areas based on mean summer temperature as well as if they are protected or not. Then I computed the proportion of present and absent sites for each class and compared the proportions across classes.

Results

I detected presence of the northern pika at 41 sites in 4 regions out of the 61 sites in 5 regions surveyed (67.2%). At the region level, I documented a large variation in site persistence. Where all 22 sites remained present in the Daisetsuzan region from the past, observed turnovers (i.e., sites where historical presence turned into current absence) were recorded in the other four regions with present site proportions of 75.0 % (6/8 sites), 69.2 % (9/13), 9.1 (1/11), and 0% (0/4) in the Erimo-Horoman, Tokachi, North Hidaka, and Yubari regions, respectively. Overall, this indicates that the local populations of northern pika have experienced turnover at 20 sites and in one whole region. These patterns were consistent after removal of the low-confident sites, which were all absent sites, with presence detected at 41 sites in 4 regions out of 53 sites in 5 regions (77.4%). This still indicates that turnover happened at 12 sites and in one whole region.

Population turnovers were found from low- to mid-elevations, spanning a large elevational range (60–1,550 m). The highest absent site in elevation was from Mt. Yubari.

However, present sites were also detected within this elevational range. As a result, present sites are currently distributed more sparsely along the elevational gradient towards the lower elevations relative to their historical distribution (Fig. 3-2). Correspondingly, I detected an upshift in the lower elevation limit of the study sites from 60 m to 110 m, while the higher elevation limit remained the same from the past at 2,210 m. Across all sites, the elevation of the occupied sites rose from 1,180 ± 640 m to 1,350 ± 670 m (mean ± standard deviation), although this upslope shift was not statistically significant (one sided *t*-test, $t = -1.33$, df = 100, $p = 0.09$).

Three models were selected as competing parsimonious models (ΔELPD < SE ΔELPD) in the occupancy analysis, which included habitat size, mean summer temperature, and protection status as the predictors (Table 3-1). Habitat size was included in the top two models with a consistent positive effect on occupancy probability. Mean summer temperature was included in all models and exhibited a significant negative effect in the second-best model. Protection status, included in the first and third models, showed a positive trend, though the effect was not statistically significant (Table S3-2).

Occupancy evaluation across low-elevation sites based on mean temperature conditions (cooler vs. warmer) and protection status (protected vs. unprotected) indicated that all warmer sites lacking protection ($n = 5$) were unoccupied (Fig. 3-3). Moreover, while absent sites composed 33% of the warmer, protected sites ($n = 3$), the proportion was higher for the cooler, unprotected sites ($n = 11$) with 82 %. The proportion of absent sites was the smallest in the group of sites characterized by cooler conditions and protection ($n = 5$) with 20%. Based on the relationship with land conversion history, my results show that some sites are experiencing turnovers without evident human intervention.

Discussion

Complex topography is expected to mitigate impacts of climate change on species' range shifts by providing thermal conditions that are locally buffered and distinct from conditions prevailing at larger scales, although empirical evidence supporting this refugial effect remains scarce. As I surveyed the current distribution of the northern pika along a wide elevational gradient (60–2,210 m) in Hokkaido since cooler conditions are found in their rocky habitats (Sakiyama & García Molinos, 2024), I observed turnovers from historical presence across a large part of the elevational range towards low- to mid-elevations (60–1,550 m). As I revisited the survey sites in multiple occasions and used the playback, a strong detection method for this species (Sakiyama & García Molinos, 2023), I consider that this trend is not a result of misidentifying the true occupancy status nor an artifact of detecting absence in the short-term (i.e., single-visit). This suggests that local populations in warmer regions are experiencing extinction, and that the overall distribution is changing from the past. Importantly, however, many local populations were also observed persisting in the elevational range where turnovers were detected. Considering that cooler conditions are provided locally in the rocky landform habitats, this study provides evidence of local population persistence at the trailing edge in a species using microclimates.

Habitat size was an important factor affecting persistence by exhibiting a positive effect, suggesting that larger habitats have a higher probability of maintaining populations over time. This is likely because larger habitats generally accommodate larger populations and have lower extinction risks resulting from demographic stochasticity (Griffen & Drake, 2008). Indeed, a positive relationship has been reported between patch size and population size in a related pika species (Franken & Hik, 2004). In the case of northern pika, larger rocky landforms may have had higher thermal heterogeneity that enabled reducing heat stress. Habitat size has also been reported to be important for persistence of the American pika (Beever et al., 2003; Smith, 1980; J. A. E. Stewart et al., 2015; J. A. E. Stewart & Wright, 2012), although the temporal and spatial scales of those studies are not directly comparable with this study. Smith (1980) assessed persistence at a shorter time interval than this study of just five years, while Beever et al. (2003), Stewart et al. (2015), and Stewart & Wright (2012) considered the effect of habitat size at a relatively large spatial scales by using aerial imagery (i.e., habitable area within a 1-km radius; 3.14 km^2). However, Smith (1980) showed also the stability of populations in larger habitats at spatial scales matching well with this study. Similarly, in Beever et al. (2003) , Stewart et al. (2015), and Stewart & Wright (2012), habitat size was the strongest factor positively affecting pika persistence for temporal scales of the habitat resurvey that match this study (i.e., multi-decadal interval). Collectively, habitat size appears to be a strong factor driving persistence of pikas across various temporal and spatial scales as well as species.

Measurement of habitat size was difficult for the low-confidence sites (n = 8) because the rocks were mostly buried in soil or covered by dense vegetation lacking interstice space (Fig. S3-1). This lack of interstice space render these sites as unfunctional habitats because rock interstices are the main microhabitat of the northern pika (Gliwicz et al., 2005). I think it is unlikely that these sites were devoid of rock interstices when the historical surveys were conducted because these reports clearly mentioned that "rocks were exposed" in the surveyed area (Haga et al., 1979) or that there were “large rocks” and “rock interstices” (Kojima & Kawamichi, 2001). These descriptions are in stark contrast with the current situation observed in the field (Fig. S3-1). Therefore, the most plausible explanation for the loss of interstice habitat seems to be ground formation and vegetation growth, which in turn would have driven the observed turnover at these previously occupied sites. To the best of my knowledge, such an instance has not been reported for other pika species.

Northern pika persistence was negatively affected by mean summer temperature, suggesting that heat stress is linked with the observed turnover. This result agrees with the observed lack of present sites from lower elevations and with previous studies assessing the distribution of northern pika in Hokkaido (Sakiyama et al., 2021; Sakiyama & García Molinos, 2024), and the American pika (Beever et al., 2011; Billman et al., 2021; Rodhouse et al., 2010, 2018; J. A. E. Stewart et al., 2015). Pikas are generally perceived vulnerable to heat because of their limited ability to dissipate heat (MacArthur & Wang, 1973). Thus, physiological stress from heat is reduced by using cooler areas available within their habitats (i.e., behavioral thermoregulation; MacArthur & Wang, 1974). This type of response is crucial in warm environments as experimental studies have shown that restricting such activities causes death from hyperthermia (MacArthur & Wang, 1973; Smith, 1974b). Moreover, pikas have been observed to be active during the cooler times of the day, such as in the morning and evening, presumably to avoid heat stress (Onoyama, 1991; Smith, 1974b; Smith et al., 2016). However, the recent rise in thermal conditions could have lowered the efficacy of these behavioral responses and affected the local population viability. While change in biotic interactions due to rising temperatures could be the hidden, but responsible keys for the observed distribution change (Cahill et al., 2013), this relationship requires investigation in future studies as interactions between the northern pika and its predators (e.g., carnivores), prey (e.g., plants), and competitors (e.g., small herbivores) remain poorly studied.

Protected area designation positively affected the northern pika persistence. This implies that protected areas helped maintaining the persistence of local populations over time, suggesting their effectiveness as a conservation strategy (Gillingham et al., 2015). Conversely, this result indicates that human activities negatively influence the northern pika, which agrees with a recent study that found reduced northern pika occupancy due to human land-use (Sakiyama & García Molinos, 2024). Nonetheless, it is important to note that not all sites in protected areas functioned as safe habitats over time since I could not detect presence at all sites in the Furano-Ashibetsu Prefectural Natural Park ($n = 4$; Yubari region) and a few sites in the Hidakasanmyaku-Erimo Quasi-National Park ($n = 2$; Erimo-Horoman region).

These sites were commonly characterized as small-sized habitats (median = 375 m^2) in comparison to sites where presence was confirmed (median = 6,405 m^2) within protected areas. Although I did not include an interaction term in the model due to limited sample size, it will be interesting to test the synergistic effect of protection status and habitat size on persistence by increasing sample size in future studies.

Nevertheless, the interpretation of these results requires care since all sites in cooler areas were from protected areas, confounding the effect of temperature and protection on persistence. Nonetheless, the comparative assessment of the potential pathways leading to the observed pattern in persistence on low-elevation sites (where both protected and non-protected sites are available for both warming and cooling areas) support that both climate and protection status contributed to persistence independently, although I could not conduct statistical tests due to limited number of samples. This analysis suggests that the effect of protection status may be stronger than that of temperature, as only 40% of the protected, warmer sites were absent, in contrast to 83% for unprotected, cooler sites (Fig. 3-3). However, this trend is possibly affected by external factors such as habitat size and initiation of human activities, although controlling the interrelationships among habitat size, mean summer temperature, and protection status was difficult since my study sites were defined from previous studies and due to the elevational bias in conservation planning.

The level of confidence finding the exact location of the previously reported sites was a methodological issue with the habitat resurvey. Such uncertainty is not uncommon in resurvey studies. For example, Stewart et al. (2015) had a maximum uncertainty of 1 km for historical site identification, which is a scale impractical in my study area due to dense forested vegetation and steep terrains. Since unknown errors in location of sites could potentially affect research outcomes (Miller et al., 2007), accurate recording of the geographical locations using GPS is imperative for habitat resurveys. Recording photographic evidence of vegetation conditions at the time of the survey will also be beneficial as it allows direct comparisons. Another possible approach to detect distribution changes is to conduct surveys along the same elevational gradient as the previous reports through random sampling, which does not essentially require conducting the resurveys at the exact locations (Moritz et al., 2008). This approach may be advantageous to avoid issues with the confidence of site search and location.

Despite these limitations, my findings have important implications for the conservation of the northern pika in Hokkaido. According to the results, habitats that are large in size or located in protected areas or cooler areas should be prioritized for conservation. With turnovers detected in low elevations, it is also important to monitor populations continuously for early detection of changes in the distribution. However, there are currently no practices intended for such purposes for the northern pika. This is possibly the case for many of the species designated as near threatened in the Japanese Red List, like the northern pika, which are species currently regarded to have low extinction risk but that could transition to an endangered status depending on changes in their populations. The potential dilemma here is that the likelihood for a timely identification of such population changes in population status is relatively low due to the lack of monitoring programs. Therefore, populations may undergo drastic decreases to a level that meets the endangered species criterion without being detected (Lavery et al., 2021). I think that sufficient resources should be invested to regularly monitor population trends for the northern pika in Hokkaido, for which the results from this study may be a useful contribution. Although long-term monitoring programs are costly, it is the most effective assessment for understanding the impacts from environmental and climate changes, which typically operate at long temporal scales. For example, a recent study has shown that the American pika recolonized previously extirpated sites after more than 10 years (Millar & Smith, 2022). Playback was a very useful method in this study because it facilitated detecting presence of the northern pika from distant locations in a short time. While searching for feces and haypiles provide additional information of the site use history (Nichols, 2011; J. A. E. Stewart & Wright, 2012), playback is a promising tool for balancing resource (e.g., funding, time) and number of sites for conducting monitoring surveys (Sakiyama & García Molinos, 2023).

Regarding regional differences in occupancy trends, I did not find any evidence of northern pika presence in the Yubari region, while at least one local population was found persisting in other regions. This was an unexpected result considering that local populations in Yubari were situated at higher elevations (1,350-1,550 m). Geographically, these Yubari local populations are considered a subset of the larger Yubari-Ashibetsu regional population (Kojima & Kawamichi, 2001). This regional population was designated as an endangered population until 2012, while no other of the regional populations were regarded as a concern for endangerment at that time. However, this categorization was later modified to include the whole Hokkaido northern pika population as near threatened (Ministry of Environment, 2014), thus lowering the endangerment rank particularly for the Yubari-Ashibetsu regional population. Nonetheless, my results indicate that this regional population may be more vulnerable than other populations, possibly due to the limited amount of habitat at both the patch and regional scale as well as its isolated locality within the species distribution.

Previous studies on the American pika have shown that population responses to the environment vary across regions (Beever, Perrine, et al., 2016; Schwalm et al., 2016). Therefore, it is urgent that thorough investigations into the vulnerability of this regional population are conducted. Considering the vulnerability, it will be important to conduct such investigations also for other regional populations with low occupancy (i.e., North Hidaka).

In conclusion, this study represents the first attempt to explore the contemporary distributional change of the northern pika in Hokkaido. Extirpations were detected at the lower portions of the distribution, with both climatic and non-climatic factors deemed responsible for the observed changes. Future studies should increase resurvey sites and regions to better interpret the mechanisms underlying these changes. This study also calls for initiating practical conservation measures such as continuous monitoring programs to further detect changes in the overall distribution as well as to monitor the viability of each regional population under climate change.

Table 3-1. Model selection results for the occupancy analysis ranked based on the expected log predictive density (ELPD). Each model contains the state process (Ψ) and observation process (p) models. Model rank, formula, number of parameters (*K*), ELPD, difference in ELPD with the top-rank model (ΔELPD), standard error of ΔELPD, model weight, and selection results are provided. Abbreviations correspond to Mean_temp = mean summer temperature, Protection = protection status, and Size = habitat size.

Rank	Model	K	ELPD	Δ ELPD	SE of Δ ELPD	Weight	Selection
1	Ψ(Mean_temp + Protection + Size + (1|Region))p(.)	5.285	-73.25	0	0	0.507	1
2	Ψ(Mean_temp + Size + (1|Region))p(.)	5.063	-73.485	0.236	0.833	0.149	1
3	Ψ(Mean_temp + Protection + (1|Region))p(.)	5.215	-73.647	0.398	1.730	0.344	1
4	Ψ(Protection + Size + (1|Region))p(.)	5.400	-74.177	0.927	0.720	0	0
5	Ψ(Mean_temp + (1|Region))p(.)	4.861	-74.256	1.006	1.939	0	0
6	Ψ(Protection + (1|Region))p(.)	5.146	-74.879	1.630	2.096	0	0
7	Ψ(Size + (1|Region))p(.)	5.347	-75.093	1.843	1.306	0	0
8	Ψ((1|Area))p(.)	4.985	-78.625	5.375	3.086	0	0

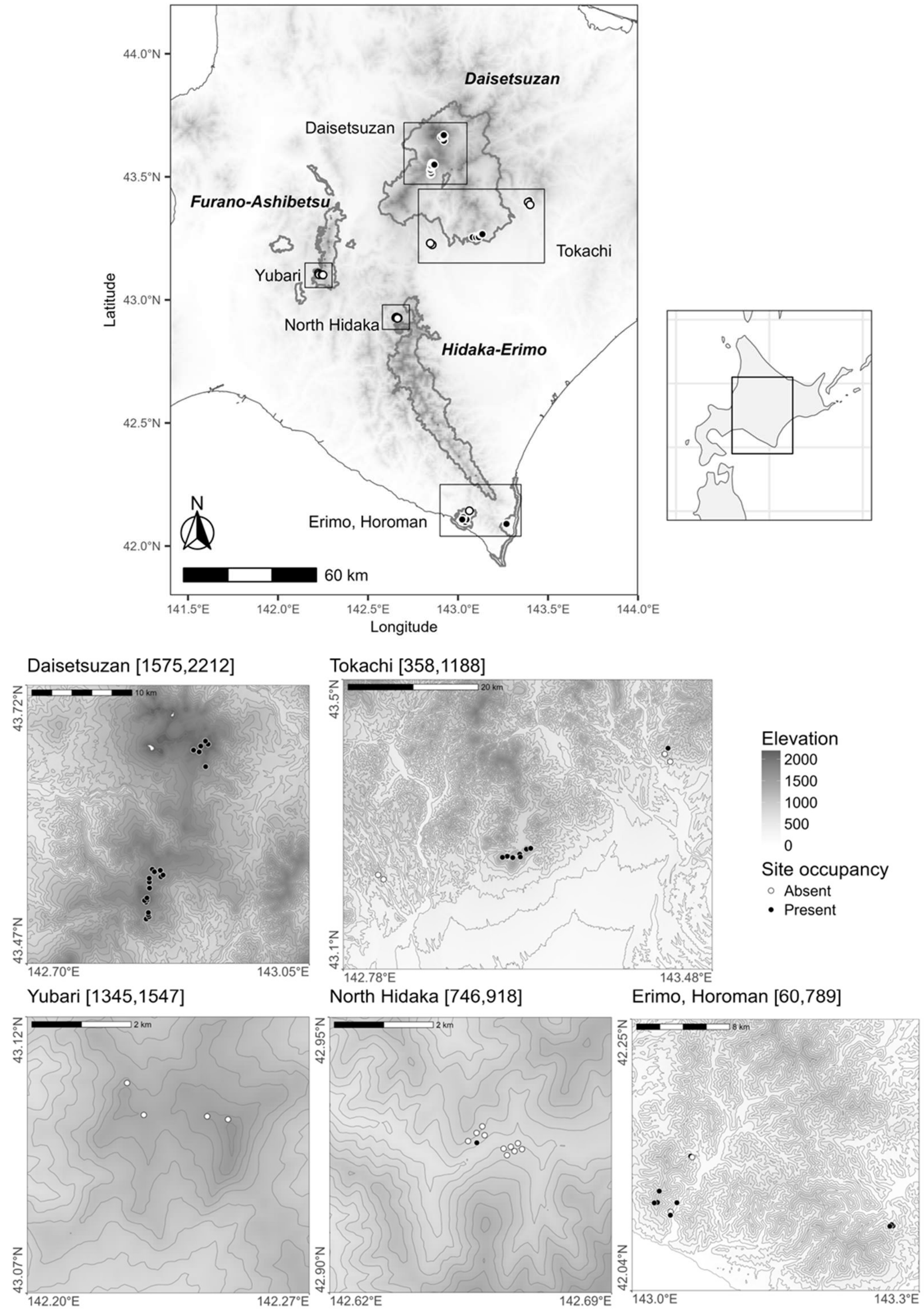


Fig. 3-1. Study area maps indicating the five resurvey regions and the border line of the protected areas (top) and observed site occupancy statuses of the northern pika for each region (bottom). Point colors represent absence (white) or presence (black) at each site. Background colors indicate the elevational gradient.

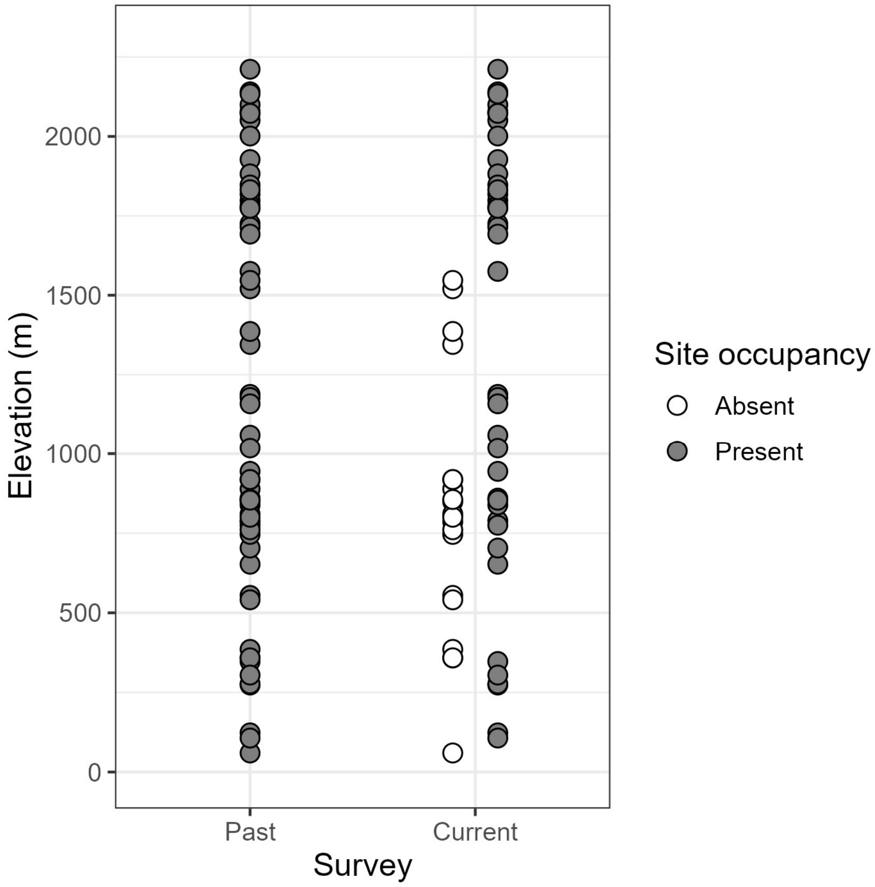


Fig. 3-2. Elevational distribution of the absent and present sites of the northern pika based on historical records (past) and this study (current).

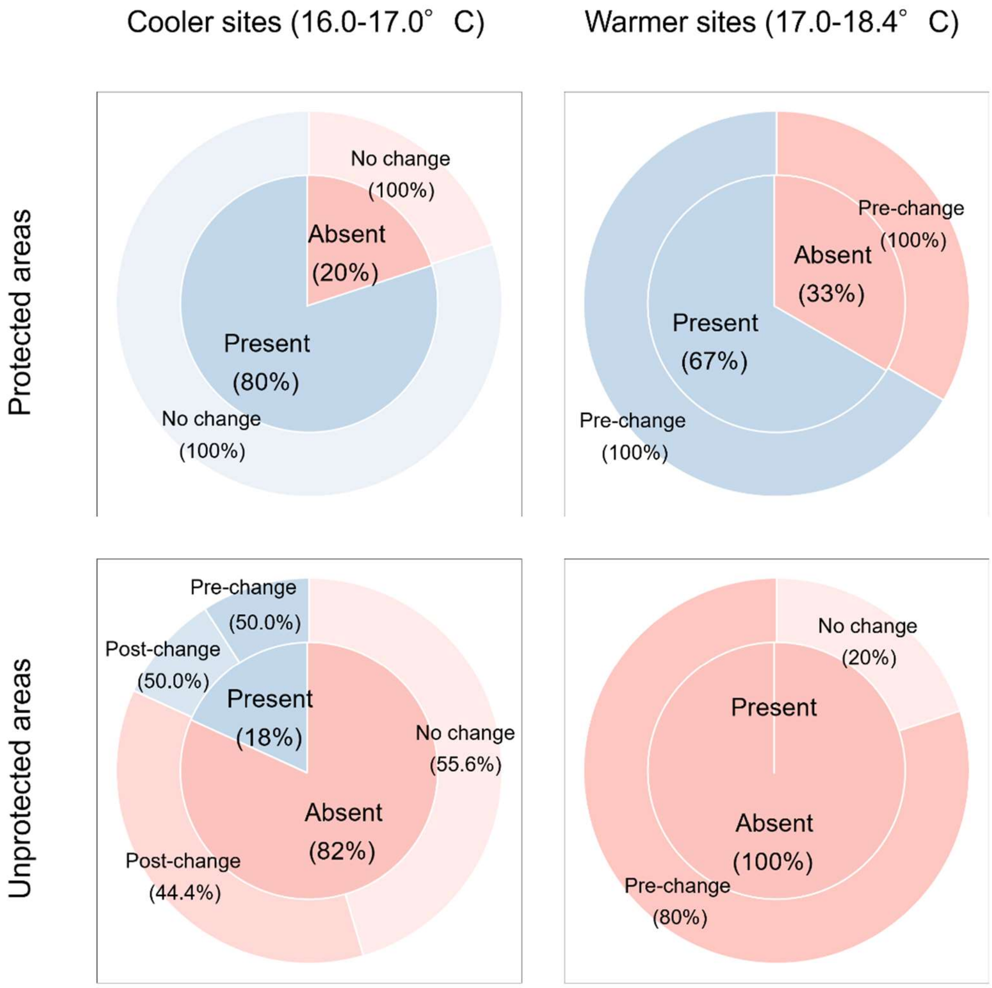


Fig. 3-3. Pie charts indicating the site occupancy at lower elevations separated into a two-way table considering the contrasts of protected vs. unprotected sites and cooler vs. warmer sites. Pie colors for the inner circle represent absence (pink) and presence (blue). The outer circle further represents the proportion of the human activity history around the sites, categorized as follows: "No change" indicates no activities in any period, "Post-change" indicates initiation of land conversion after the survey, and "Pre-change" indicates presence of land conversion from before the survey.

Chapter 4: Northern pikas experience reduced occupancy due to surrounding human land use despite the occurrence of suitable microclimates

Abstract

Despite warming temperatures, some species are found persisting at the trailing edge of their distribution. Microclimates provided by complex topography are considered a key factor in these cases of range stationarity, buffering stress from exposure to warming and enabling persistence. However, for species with trailing-edges located in human-modified landscapes, refugial conditions provided by microclimates could be disrupted by human activities. Here, I aimed to understand the determinants of trailing-edge occupancy for a small lagomorph found in rocky patches harboring cool microclimates. I surveyed the occupancy of northern pikas (*Ochotona hyperborea*) across a wide elevational gradient (350–2,200 m) in Hokkaido, Japan, for two consecutive summers. Ambient air and microhabitat (i.e., rock interstices) thermal conditions were measured to assess their relationship. I then analyzed their effects on occupancy at two nested spatial scales: (1) whole-distribution, and (2) at identified trailing-edge sites where I explored the effects of microclimates and surrounding human activities (i.e., distance to nearest road and area of human land use such as plantation forests or agricultural fields). Overall, rock interstices exhibited cooler conditions than ambient air with temperature differences of 1–2 ºC. The overall distribution of northern pikas was affected by both mean ambient temperature and microhabitat availability, with warmer (lower elevation) sites with less microhabitats corresponding to the trailing edge of its distribution. Interestingly, trailing edge occupancy patterns were best explained by the negative effect of surrounding human land despite the existence of suitable microclimates in the rocky patches. These findings suggest that the local refugial conditions supported by cool microclimates are likely to be disrupted by the effects of human land at the larger landscape scale. This result highlights the importance of considering the effects of human activities and landscape alteration for effective microrefugia conservation.

Introduction

Understanding the factors driving spatial patterns of species distributions is essential for biodiversity conservation (Whittaker et al., 2005). Mounting evidence suggests that species distributions are shifting poleward and upward on a global scale in response to climate change (Chen et al., 2011; IPBES, 2019). Yet, response variability around this intuitive general pattern of range shift is still high, with many species experiencing little or no change in their distribution or even shifting against expectations (Chen et al., 2011; Gibson-Reinemer & Rahel, 2015). Such variability in range shift responses to climate change needs careful consideration for effective conservation planning and thereby requires further understanding (Rubenstein et al., 2023).

Stationarity of the trailing edge of the distribution, preventing ranges from contracting, is a common phenomenon frequently associated with the local effect of complex topographical features. Such features provide suitable climatic conditions at finer spatial scales (i.e., microclimate), effectively buffering local populations from the unsuitable climate driven by broad-scale factors (Moritz & Agudo, 2013). Often referred to as microrefugia (Rull, 2009; J. R. Stewart et al., 2010), they are considered a key habitat for some species to persist under the rapidly changing climate (Ashcroft, 2010; Hampe & Petit, 2005). This view is also supported by paleoecological insights demonstrating that species persistence under past periods of rapid climatic change was often facilitated by the access to climatic refugia locally available within their distribution range (McLachlan et al., 2005; Provan & Bennett, 2008). However, while the importance of incorporating identification and management of climatic refugia into the biodiversity conservation toolbox is becoming increasingly recognized (Morelli et al., 2020), empirical evidence showcasing the importance of microclimates in maintaining species distribution is scarce (Suggitt et al., 2011). Therefore, a wide knowledge gap exists between theory and observation on range shifts to accomplish incorporation of microrefugia into conservation planning (Oldfather et al., 2020). The recent development of low-cost and high-quality instruments to measure microclimates makes it now possible to address this gap (Bramer et al., 2018).

The importance of microclimates in shaping species distributions has still not gained sufficient recognition because mainstream analyses, such as ecological niche modeling (Elith & Leathwick, 2009), typically use macroclimate grids, which lack consideration of climate-forcing factors operating at finer spatial scales (Austin & Van Niel, 2011; Lembrechts et al., 2019). Moreover, the spatial resolution of these climate data is often much larger than the home ranges of the focal species (Potter et al., 2013). While these models are undoubtedly useful and have helped to advance our understanding of macroecological patterns, such as prediction of areas where species can persist in the future, they primarily consider the effect of climatic macrorefugia on species ranges (Ashcroft, 2010), and therefore can result in overestimation of potential range shifts (Maclean & Early, 2023). Thus, considering spatial variability of climate at fine scale has the potential to innovate conservation by highlighting areas that are currently underrepresented but will likely support species persistence under climate change (Zellweger et al., 2019). Integrating microrefugia populations into conservation is also important for maintaining genetic diversity of the species, since range edge populations can be genetically distinct (Mosblech et al., 2011).

An important but overlooked aspect regarding microrefugia formation at the trailing edge of a species distribution is whether the use of available microrefugia is influenced by human alterations of the landscape (Morelli et al., 2016). As lands are modified by human activities, suitable habitats for the species become smaller and more isolated (Fahrig, 2003; Fischer & Lindenmayer, 2007). Habitat loss and fragmentation can lead to reduced population sizes and compromise the long-term viability of local populations in the remnant habitats, ultimately pushing them into extirpation (Lefoe et al., 2022; Newbold et al., 2015). Moreover, as animal movements within the landscape are reduced by habitat isolation (Tucker et al., 2018), habitat patches surrounded by human land use are less likely to be recolonized after becoming vacant (Semper-Pascual et al., 2023), which affects occupancy negatively. Thus, even if suitable microclimates are available in remnant habitats, such locations may not function as refugia in the presence of exacerbating human impacts. Therefore, when assessing the capacity of microrefugia to facilitate species persistence, focusing solely on the beneficial effect of local conditions without consideration of the landscape-scale impacts from human activities risks misunderstandings and could be problematic for further implications (Morelli et al., 2016). However, the relative importance of both factors in shaping occupancy at trailing edges of a distribution has not been assessed in previous studies.

Pikas are small lagomorphs adapted to cold environments considered to be vulnerable to climate change (Beever et al., 2011; Wilkening et al., 2015). Multiple pika species are known for inhabiting rocky patches on mountain slopes (such as talus slopes), using the interstice space between or beneath the rocks as their main microhabitat. While these rocky patches are found discretely in mountainous regions across a wide elevational gradient, they exhibit cooler and more stable microclimates in rock interstices than the ambient air (Millar et al., 2016; Varner & Dearing, 2014). Thus, cooler conditions, predominant at higher elevations, are also found patchily as microclimates towards the lower elevations where warm ambient conditions prevail, which are known to shape complex spatial distributions of American pikas, *Ochotona princeps* (Billman et al., 2021; Hall et al., 2016; Rodhouse et al., 2017). However, such relationship remains understudied for the northern pika, *O. hyperborea*, which occurs in Northeastern Eurasia (Lissovsky et al., 2021). Recent work has described the thermal conditions of northern pika microhabitats (Sakiyama et al., 2021), but their contribution towards occupancy was not investigated since thermal measurements were conducted only at occupied sites. Moreover, while human activities and resulting alterations of the landscape are likely to be higher at lower elevations, the relationship between human impacts and microclimates and their effect on the species distribution is unclear. Here, I aimed to understand the relationship between ambient and microhabitat thermal conditions in northern pika habitats and the relative importance of these thermal conditions on their whole distribution. I then focused on the trailing edge of its distribution to examine the relative importance of microclimate and human impacts in shaping occupancy at the range edge.

Materials and Methods

Study area

I conducted this study in the Daisetsuzan and Tokachidake mountain ranges and their peripheral areas in the Kamikawa, Tokachi, and Okhtosk regions in Hokkaido, the northernmost island of Japan (Fig. 4-1). This area encompasses a wide elevational gradient (200–2,290 m) with corresponding changes in vegetation structure from cool-mixed forests at lower elevations to alpine vegetation at higher elevations. A large proportion of the study area is designated as the Daisetsuzan National Park, where higher elevations receive strict protection for its unique volcanic landscape. Lower elevations within the national park and its peripheries are moderately protected or unprotected and therefore are exposed to intermittent human activities (e.g., forest management, agriculture, etc.).

Within this study area, I established 19 study sites in 2021 and added 18 more sites in 2022, resulting in 37 study sites for the occupancy survey (Fig. 4-1). Each study site was chosen by searching for large rocky patches (> 50 m x 50 m) along hiking trails and forest roads. Some sites were based on previous reports on pika distribution (Kawabe, 1989, 2008; Kawabe et al., 2004; Onoyama & Miyazaki, 1991; Sato et al., 2009; T. Yamada, personal communication). I ensured that all sites were at least 400 m from their nearest neighbor to prevent sampling similar environmental conditions considering the home range size of northern pikas (i.e., 20–40 m in diameter; Haga, 1960). The elevational range of the study sites was 350–2,200 m, which widely covered the known species elevational range (i.e., 50–2,230 m; Onoyama & Miyazaki, 1991). I conducted the surveys between June and October considering the phenology of the northern pika so that the site occupancy status does not change within that period, which is the baseline assumption of the analytical framework (i.e., closed-population setting).

Occupancy survey

I used playback as the main detection method, consisting of playing a prerecorded vocalization of the northern pika through an audio speaker (JBL CHARGE4, JBL, California, USA; frequency response 60–20,000 Hz) to provoke vocalizations from the individuals inhabiting the site as a response (Sakiyama & García Molinos, 2023). This survey method enabled me to accurately determine the presence or absence of northern pikas even in the densely vegetated habitats of Hokkaido. I recorded a site as present when I detected any vocalization activity as I remained silent for five minutes after the broadcast (see Sakiyama & García Molinos, 2023 for details on the sampling method). Other than the playback, vocalization activity occasionally detected upon arrival at or departure from a site, or during environmental surveys, and visual signs of recent pika activity, such as fresh feces and food cache with green hues of chlorophyll, were used as proof for northern pika presence to complement playback results (Hall et al., 2016; J. A. E. Stewart et al., 2015). To account for the bias of imperfect detections in the statistical analysis, I repeated the playback survey at each site in at least three different months within the same year (see Table S4-1 for details).

Characterization of habitat environments

Thermal conditions

I used thermal loggers (HOBO UA-001-08, MX2201, or MX2202, Onset Computer Corporation, Massachusetts, USA) to measure the local thermal conditions in the survey sites. At each site, one logger was deployed at a constant height of 1.2 m to measure the near-surface, ambient thermal conditions. These conditions can be affected by both broad-scale (e.g., elevation) and local-scale factors (e.g., forest canopy) (Shi et al., 2016), since the study sites cover a wide elevational gradient including sites under forest canopy and those without it (i.e., above treeline). A second logger was placed to measure the thermal conditions existing inside rock interstices, the main microhabitat of northern pikas, at a depth of 0.5 to 1.0 m, which was expected to be buffered from the ambient temperature. Both loggers were housed in white perforated PVC pipes to avoid direct sunlight. While both loggers can be considered to be deployed locally, for the purpose of this study I refer to the thermal conditions in rock interstices as microclimates and those outside of interstices as ambient conditions. Since interstice temperatures can show local variation (Sawada et al., 2003), I located an interstice with approximate average thermal conditions for deployment at each site using an infrared thermal camera (FLIR ONE Gen3, FLIR Systems, Inc., Oregon, USA) (Fig. S4-1). Ambient and interstice temperatures in each site were measured at one hour interval during the surveys.

I used thermal data from July 1st to August 31st to analyze the effects of ambient and microhabitat thermal conditions on occupancy because summer conditions are known to limit pika activities (Beever et al., 2010). Hourly ambient and interstice temperatures were summarized into mean daily temperatures and thermal ranges (T_{max} - T_{min}), which were then averaged over July and August. Mean temperature and thermal range are indicators of thermal magnitude and stability, respectively, both known to be related to biophysical stress and occupancy of pikas (Rodhouse et al., 2017; Wilkening et al., 2011, 2015).

Site topography

In addition to the thermal environment, I assessed the topographical characteristics of each site. I made two parallel 50 m transects spaced 50 m apart and placed 1 m^2 quadrats at each meter mark (a total of one hundred 1-m^2 quadrats). In each quadrat, I recorded whether large rocks (> 30 cm) or interstices (> 5 cm in diameter) were found to represent the rock-interstice availability of the site, which was quantified as the percentage of quadrats including both features. This index was considered to reflect the microhabitat availability of each site.

Human impacts

To evaluate the impacts from human related activities on northern pika occupancy, I considered the effects of two types of indicators of human pressure at each surveyed site. First, because proximity to roads has been documented to have a negative effect on the occurrence of the American pika (Ray et al., 2012), I computed the Euclidean distance between each site and the closest road using the road vector data available from OpenStreetMap (2023). I only considered roads potentially used by vehicles for the analysis by excluding minor pathways assigned as “track” in the road category, which in my study area corresponded mainly with hiking trails. Second, I estimated the total area of human land use, understood as landscapes modified or intervened by humans, within a 3-km circular buffer taken from each site. In the study locations, these include plantation forests, agricultural fields, and residential areas. I used a buffer radius of 3 km because this represents the maximum dispersal distance described for the northern pikas in Hokkaido (Kawabe & Nakaoka, 2000). Although the effect of human land use on pika occupancy remains understudied, previous studies have reported the negative influence of livestock grazing (Hafner & Sullivan, 1995; Millar, 2011; but see Beever et al., 2003, 2011). While the study area includes other types of human land use, I expect that such landscape-scale modification would affect occupancy negatively through habitat loss, fragmentation, and limiting or impeding animal movements (Lefoe et al., 2022; Prugh et al., 2008) since northern pikas are obligate rock-dwelling species (Gliwicz et al., 2005).

Statistical analyses

I examined how environmental factors are related to the occupancy of northern pikas at two nested spatial scales to understand the relative contribution of ambient and microhabitat thermal conditions. First, I considered the effects at the scale of whole distribution of the species by including all study sites. Second, I focused on the study sites found at the trailing edge of the distribution range to understand the effects of the environmental factors. These two scales were considered because I intended to define the trailing edge as objectively as possible based on whole-distribution scale data to investigate the importance of microclimate.

For the whole-distribution analysis, I used a single-season site-occupancy model (MacKenzie et al., 2002). In this model, species detection results are considered to arise from the combination of the underlying state process (i.e., whether a site is occupied given its environmental conditions), and the observation process (i.e., whether the animal is detected given its presence). This enables me to account for cases of imperfect detection in the data to prevent underestimation of species-environment relationships (Kery & Royle, 2015). The structure of a site occupancy model can be written as

$$z_i \sim Bernoulli(\psi)$$
$$y_{ij}|z_i \sim Bernoulli(z_i p)$$

where z_i denotes the true state of occupancy (present or absent) at site i being drawn from a Bernoulli distribution with the success parameter given by the occupancy probability ψ, and y_{ij} denotes the detected occupancy (present or absent) at site i during survey j being drawn from a Bernoulli distribution with the success parameter given by the product of the occupancy state z_i and the detection probability p. Both ψ and p are modeled with a logit link function to assess their relationships with site and observation covariates, respectively. Our survey period of June to October was selected for each year considering that the occupancy state z_i does not change during this period (closed-population setting).

For the state process, I included the following variables: mean ambient temperature, mean interstice temperature, mean ambient thermal range, mean interstice thermal range, and rock-interstice availability. I excluded effects of human impacts (i.e., distance to road and area of human land use) because they were highly correlated with mean ambient temperature (i.e., $|r| > 0.7$; Fig. S4-2), reflecting prevalence of human activities at lower elevations. For the observation process, I included the effect of survey date (i.e., Julian date) because a previous study showed that detection of northern pikas was more frequent later in the survey season (Sakiyama & García Molinos, 2023). Based on these variables, I constructed a set of candidate models ($n = 22$; Table S4-2), and included site as a random effect (i.e., random intercept) in all of them to avoid pseudo-replication across years. I preferred using this "stacked-design" over dynamic occupancy model with the multiple-year data because I was interested more in factors associated with occupancy, not state transitions (see Kery & Royle, 2021). Observation and state covariates were scaled before analysis. Models were implemented in a Bayesian framework using the stan_occu function in 'ubms' package in R (Kellner et al., 2022). All models used default priors (Logistic (0,1) prior) and were performed with five independent runs of 20,000 Markov chain Monte Carlo iterations each, discarding the first 10,000 iterations as burn-in. After fitting all models, I ranked the predictive accuracy of each model by computing their expected predicted log density (ELPD) via leave-one-out cross validation (Kellner et al., 2022). Model selection was then performed by retaining all models with differences in ELPD (ΔELPD) from the top-ranked model (i.e., highest ELPD) lower than the standard error of the ΔELPD across all candidate models (Vehtari et al., 2017). I then assessed model convergence for the resulting set of competing models by visually inspecting the traceplots and examining whether the Gelman-Rubin Statistic (i.e., $\hat{R}$) was close to 1 (Gelman et al., 2014). I conducted a MacKenzie-Bailey chi-squared test to evaluate the goodness-of-fit of the occupancy models by considering p values near 0.5 as an indication of good model fit (Broms et al., 2016; MacKenzie & Bailey, 2004). Effects of each covariate were considered significant if the 95% credible intervals generated from the posterior distribution did not overlap zero.

For the second stage of the analysis, I selected sites located at the trailing edge of the distribution based on the occupancy-environment relationship elucidated from the whole-distribution analysis. Sites with low occupancy probability predictions from the whole-distribution model were considered as trailing edge sites. To do so, I conducted a sensitivity analysis by applying different probability thresholds to the predictions ($p = 0.9, 0.8, 0.7, 0.6$) to evaluate whether factors related to trailing edge occupancy differed depending on the selection of threshold (i.e., subdivision scale). In contrast to whole-distribution analysis, the small number of trailing-edge sites and the very limited sample size per site precluded implementation of site-occupancy models and inclusion of mixed effects in the model (Theall et al., 2011). As an alternative, to avoid issues with pseudo-replication given the existence of sites that were surveyed in both years, I built generalized linear models using data for the second year only (i.e., the year with higher number of sites surveyed) with a Bernoulli distribution and a logit link function. Model predictors included the effects of human impacts (distance to road and area of human land use) and microclimates (mean interstice temperature and thermal range). Since mean interstice temperature indicated a convex relationship with the observed occurrences, I used a quadratic model as a candidate model. Model performance was compared based on the Akaike Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson, 2002).

Results

Occupancy survey

Overall, northern pikas were found at least once during the multiple surveys at 13 out of 19 sites in 2021 (68.4%) and 23 out of 37 sites in 2022 (62.2%). Considering the combination of site and year, there were 36 present yearly sites out of 56 yearly sites (64.3 %). Present sites were located in both Daisetsuzan and Tokachidake mountain ranges as well as lower elevation forests in all regions of the study area (i.e., Kamikawa, Tokachi, and Okhotsk). While no absences were detected in sites located in the two mountain ranges, lower elevation sites comprised both present and absent sites (Fig. 4-1). Consequently, the mean elevation of present sites was 700 m higher than absent sites (one sided t-test, $p < 0.001$). Within the 36 present yearly sites, I detected pika presence during the playback survey at 34 yearly sites (94.4%) and failed to do so at two yearly sites, where the presence was instead confirmed by natural vocalization activities detected at departure from one site in 2021 and during the habitat environmental survey of another site in 2022 (Table S4-1). Although I found haypiles at a site where I did not hear any vocalizations, I regarded this site as currently absent because the haypiles were old.

Relationship between the ambient and interstice temperature

Mean summer thermal conditions were cooler in rock interstices than ambient air at most sites (54 yearly sites; 96.4 %) (Fig. 4-2). Thermal differences between ambient and interstice temperatures varied among sites, but a large proportion of sites (76.8 %) harbored microclimates up to 4 °C lower than corresponding ambient temperatures; 1–2 °C difference being the most frequent (Fig. 4-2; S4-3). This relationship was reflected by the strong correlation between mean ambient and interstice temperatures (Fig. S4-4), which indicates that microclimate is also correlated with site elevation (Fig. 4-2).

The rest of the sites indicated interstice temperatures largely deviating towards cooler conditions from the ambient temperature or what would be expected from the elevational gradient (Fig. 4-2). Thermal differences between ambient and interstice temperatures were highly variable among these sites, with the coolest site harboring a mean interstice temperature of 2.2 °C, which was 15.2 °C lower than its ambient temperature (Fig. 4-2; S4-3). This deviation component of microclimates was found at sites with relatively warmer ambient conditions located at lower elevations within the species distribution, harboring mean interstice temperature as cool as or cooler than high elevation sites (Fig. 4-2). The distribution of present sites within this bivariate thermal relationship was complex, although overall corresponded to sites with both lower ambient and interstice temperatures. Still, northern pikas were absent in the three sites harboring the coolest microclimates measured (Fig. 4-2).

Whole-distribution analysis

Model selection showed two competing models with mean ambient temperature and rock-interstice availability included in the state process model component (Table 4-1). Posterior distribution of coefficient estimates revealed a significant negative effect of mean ambient temperature on occupancy probability while rock-interstice availability had a significant positive effect (Table S4-3). This result suggests that rocky patches with cooler ambient temperatures and more microhabitats are suitable for northern pikas (Fig. 4-3). The change in occupancy probability along both variables was relatively gradual, accurately reflecting the observed occurrences transitioning from the predominance of present sites to absent sites. Nonetheless, the chi-square test indicated a marginal model fit ($\chi^2 = 156.7$, $p = 0.13$). Although I incorporated the effects of mean ambient thermal range, mean interstice thermal range, and mean interstice temperature on the state process, I found no support for any of these variables. In these two top-ranking models, Julian date of the survey was included in the observation process of the best model, with the posterior distribution ranging toward positive values. However, its effect was considered insignificant since the 95 % credible interval of the posterior distribution overlapped zero (Table S4-3). The competing model did not include Julian date in the observation process (Table 4-1), suggesting that the survey date is not an important factor affecting observation outcomes.

Trailing-edge analysis

As I applied multiple thresholds to define sites located at the trailing edge, slightly different subsets of study sites were retained with varying proportions of absent and present sites. However, the best supported model across all resulting subsets consistently included the sole negative effect of area of human land use (Table 4-2), reflecting that a site is likely to be absent if the surrounding landscape is modified for human activities (Fig. 4-4). Nonetheless, this effect was found to be significant only when the trailing edge was defined using higher thresholds (0.9 and 0.8). For the 0.7 threshold, the null model was found as one of the competing models (ΔAICc < 2), suggesting that the inclusion of predictors did not increase the parsimony of the model. The fact that the null model ranked relatively close to the best model in other trailing edge settings further suggests caution when interpreting the results. Models including primary term of mean interstice temperature, interstice thermal range, and distance to road had higher AICc than the null model indicating lack of statistical support (Table 4-2).

Discussion

Microclimates are recognized as the fundamental component in establishing microrefugia at the trailing edge of a species distribution (Ashcroft, 2010; Hampe & Petit, 2005). Despite their importance for biodiversity conservation under climate change (Morelli et al., 2020), our understanding of how cooccurring human impacts may disrupt such refugial conditions and affect species inhabitance remains unassessed. This study provides novel evidence that distinct cool microclimates can be found at the trailing edge of the northern pika distribution even in human modified landscapes. However, my results also indicate that the negative impact of human land use drives occupancy dynamics of the species at the trailing edge of its distribution. This result implies that microrefugia establishment requires not only the availability of suitable microclimates at trailing edges, but also low levels of human disturbance at the landscape-scale.

Microclimates in northern pika habitats

My measurements of thermal conditions across all sites, spanning ~1850 m in elevation, revealed that rock interstices in northern pika habitats provide thermal conditions cooler than the ambient air. This thermal buffering effect by rock interstices is supported by previous pika studies (Sakiyama et al., 2021; Varner & Dearing, 2014), and is considered an important characteristic of talus slopes to provide pikas with refugial conditions under climate change

(Millar et al., 2016). However, I found two distinct components in this relationship: while most sites showed small thermal differences following a strong linear trend, a minority of sites harbored strikingly cool microclimates that deviated strongly from this general trend (Fig. 4-2).

The first component suggests that average thermal conditions in rock interstices can be effectively estimated from the ambient temperature using a simple linear regression. This contrasts with a previous study in which microclimate estimation from ambient conditions was found to be difficult (Millar et al., 2016). This contradiction is likely caused by the temperature variability associated to the temporal scale of the analysis. Whereas the previous study focused on estimation at the hourly scale, I instead focused on average conditions across the summer. This result suggests that summarized statistics of rock interstice temperatures across coarse temporal resolutions (e.g., monthly to annual) can show good correlation with ambient temperatures across the pika habitat. This has important implications to improve coarse-scale analyses, such as species distribution modeling, by enabling the estimation of average microclimate conditions from extensively available climate data (Gril et al., 2023). Given this association, the present trend of rising temperatures may also be reflected in microclimates, necessitating an assessment of how it would degrade future refugial conditions.

The second component indicated that interstice temperatures could deviate strongly from ambient thermal dynamics and show idiosyncratic conditions. These unexpected cool microclimates were found from lower elevations, which is supported by previous geological studies in the study area demonstrating its association with sporadic distribution of permafrost in talus slopes (Shiboi, 1974; Shimizu, 2004). Particularly, talus slopes are known to harbor a complex air circulation system, called “wind holes” in Japan (Sasaki, 1986), where cold air blows out from the interstices to the exterior in summer as the interstice air is cooled by the existing permafrost (Sawada et al., 2003). Therefore, the occurrence of permafrost is likely linked with the observed strong thermal buffering of the northern pika microhabitats (Millar & Westfall, 2010), which likely contributes to the reduction of physiological stress at lower elevations (Whipple et al., 2022).

However, I did not observe extremely cool microclimates in some of the sites despite the existence of permafrost in the area. For instance, permafrost is known to exist around Mt. Hakuundake and Mt. Nishi-Nupukaushinupuri (Ishikawa & Hirakawa, 2000; Sawada et al., 2003), but interstice microclimates in these mountains followed the general trend based on elevation (i.e., the first component). This result suggests that the cooling effect of permafrost on interstice microclimate could be variable among sites, presumably because absolute depths of rock interstices differed among sites, which could have altered the distance between thermal loggers and extant permafrost. Moreover, other conditions of the local topography, such as the size of rocks, the size, depth, and quantity of interstices, and vegetation cover (Varner & Dearing, 2014), could also have an effect. On the other hand, the relative location of the logger deployment within the talus slope could also have caused such variations (Sawada et al., 2003). The obtained single measurement of interstice temperatures per site, selected to represent average thermal conditions at each site, can result in a poor descriptor of the existing thermal conditions in northern pika habitats if interstice thermal variability is high. Deploying multiple loggers at multiple sites should enable disentangling the effects of physical features on interstice temperature and provide deeper understanding of the relative importance of these various features for northern pika populations. Furthermore, since rock surfaces could exhibit different thermal conditions from the ambient air (Varner & Dearing, 2014), it will be important to measure consider its effect on the distribution in future studies. The reliability of thermal measurement also needs to be addressed by considering the effect of the instruments and how they are deployed to interpret the measurement results with high accuracy (Maclean et al., 2021). Finally, permafrost has been predicted to be melting in the mountain ranges of Hokkaido (Yokohata et al., 2021, 2022), which could have potential effects on the extent and availability of interstice microclimates in northern pika habitats.

Occupancy at the whole-distribution scale

Northern pikas were found to be present more frequently at higher than lower elevations (Fig. 4-1); a pattern that was indicated by the state process modeling in the whole-distribution scale analysis with a strong negative effect of mean ambient temperature on occupancy (Table 4-1; Fig. 4-3; Table S4-3). This result was supported by previous studies showing that distribution of pikas is dominantly affected by summer thermal conditions (Billman et al., 2021; Sakiyama et al., 2021; J. A. E. Stewart et al., 2015), and reflects the adaptation of pikas to cold environments since they have evolved in high elevations (Wang et al., 2020). In the case of northern pikas in Hokkaido, southern localities within the species distribution likely required high-elevation environments for their persistence.

Among the topographical variables considered, occupancy was positively related to rock-interstice availability (Table 4-1; Fig. 4-3; Table S4-3). In line with previous findings showing the positive effect of habitat size on occupancy (Billman et al., 2021), this result suggests that physical structure of the habitat is also important for northern pika occupancy and that they prefer rocky patches with higher microhabitat availability. Pikas are known to show strong territoriality (Gliwicz et al., 2005; Kawamichi, 1976). Therefore, larger habitats generally support larger populations and have lower extinction risks (Franken & Hik, 2004). Moreover, higher availability of microhabitats could be beneficial for pika populations by providing diverse environmental conditions at the local scale (Badgley, 2010), and by facilitating avoidance of predators (Humphries et al., 2011; Norbury & Van Overmeire, 2019). This result suggests that rock-interstice availability could potentially be used as a reliable proxy for the habitat space for pikas.

I expected microclimates to be important in driving occupancy at the whole-distribution scale since northern pikas use rock interstices as their main microhabitat. However, both the magnitude and the range of microclimates were not included in the top ranked models. Conversely, mean ambient temperature was found to have a significant effect (Table 4-1; Table S4-3), suggesting that occupancy at the whole-distribution scale is more affected by ambient conditions than interstice microclimates. Pikas experience ambient thermal conditions for above-ground activities, such as grazing, haying, vocalizing, and surveilling (Varner et al., 2016). These activities contribute to energy acquisition and predator avoidance and comprise fundamental components for survival. Therefore, an increase in ambient temperature at lower elevations could have influenced populations adversely by reducing above-ground activities. Although above-ground space is the secondary microhabitat for northern pikas (Kawamichi, 1969), my result demonstrates that thermal ambient conditions are nonetheless important for maintaining their distribution. Alternatively, the overriding effect of ambient temperatures over microclimate could partly be related to the analytical scale. While I focused on a spatial scale that covers the elevational gradient occupied by northern pikas in Hokkaido, inclusion of such wide environmental gradients in the analysis could have increased the relative weight of broad-scale factors over local- or microscale factors as drivers of the species' distribution (Pearson & Dawson, 2003; Willis & Whittaker, 2002).

Occupancy at the trailing-edge scale

I defined the trailing edge of the pika distribution range in the study area as locations with lower occupancy probability at the whole-distribution scale by applying multiple thresholds to the occupancy-environment relationships. Since mean ambient temperature and rock-interstice availability were included in this relationship, this subset procedure narrowed the environmental variation among sites, selecting sites at lower elevations and with less microhabitats. My results showed that occupancy at the trailing-edge scale was negatively affected by the area of human land use surrounding the study sites (Table 4-2; Fig. 4-4), suggesting that northern pikas occupy rocky patches with less human impacts at the range edge. These results point towards the occurrence of plantation forests and agricultural fields, the two land uses accounting for a larger proportion of human land use (Fig. S4-5), in the surrounding landscape as particularly detrimental to northern pikas. This is intuitive because these practices in my study area frequently involved removal of rocks for land levelling (Fig. S4-6), which effectively reduced potential pika habitats at the landscape-scale. This may lead to the extirpation of local pika populations in the long-term due to reduced habitat size, increased population isolation and restricted dispersal and metapopulation connectivity of the species (Castillo et al., 2014). Consequently, northern pikas at the trailing edge of the distribution are affected by lower chances of patch colonization and persistence due to habitat fragmentation (Prugh et al., 2008), and thereby experience reduced occupancy.

Few publications are available in the literature that discuss the effect of human activities on pikas, but livestock grazing has been reported to be a potential factor affecting American pikas (Hafner & Sullivan, 1995). In the presence of grazing effects, pikas have been reported to have access to a lower diversity of plants and store haypiles at less favorable locations on the talus, which could impair their physical condition (Millar, 2011). Moreover, livestock grazing has been reported to occur at sites experiencing local pika extirpations, although with uncertainty (Beever et al., 2003, 2011). This study involves different human impacts operating at different scales, i.e., landscape scale whereas grazing in the case of American pika studies was more localized at the patch scale. Nonetheless, my results also need to be interpreted with care as they contain uncertainty calling for more exhaustive analyses in the future.

Importantly, my results suggest that microclimate was not contributing significantly to the occupancy of northern pikas at the trailing edge of the distribution, despite cool microclimates being provided in rock interstices (Table 4-2; Fig. 4-2). The fact that human land use consistently overwhelmed the positive effect provided by microclimates across all edge thresholds tested suggests that availability of suitable cool microclimates may not be sufficient to maintain viable populations in the long-term if the surrounding landscape is significantly altered by human activities. This result likely reflects the fact that patch occupancy is influenced not by patch quality, but by the quality of the habitat matrix surrounding the patch (Prevedello & Vieira, 2010; Ricketts, 2001). While patch quality is generally more important for population viability than matrix quality (Hodgson et al., 2011), this relationship is known to differ among species depending on whether it can use the matrix as a secondary habitat (Bender & Fahrig, 2005; Eycott et al., 2012). Given that northern pikas are habitat specialists requiring rocky patches, their ability to use highly modified landscapes as secondary habitat is presumably low and could have affected the occupancy. Conversely, the presence of northern pikas found at lower elevation sites with less human impacts was possibly facilitated by the use of available microclimates existing at both the patch and landscape scale.

Implications for conservation

The results from the whole-distribution analysis suggest that protecting areas with low ambient temperature and high rock-interstice availability should be prioritized for northern pika conservation. Low ambient temperature is available at high elevations, but most of these areas within the species distribution range in Hokkaido are already designated as national parks with strict protection schemes. In contrast, a factor largely absent from the current protection schemes is the topographical complexity, such as the rock-interstice availability that provides animals with microhabitats. A huge challenge here is the exploration of rocky patches, which are often unrecorded in spatial environmental data and are therefore difficult to inventory from a management perspective. While I searched for rocky patches visually in the field, this approach will become unpractical at the scale needed for conservation and management plans. Aerial imagery could be effective for the identification of rocky patches in the mostly open alpine areas (Pu et al., 2021), but is ineffective at the trailing edge due to forest canopy. Here, the development of predictive models to classify topographical characteristics at a finer scale may provide a solution worth exploring in future studies.

The situation regarding the conservation of northern pikas in low elevations in Hokkaido is nonetheless problematic given their weaker or no protection status, where extensive landscape modification for human land use is reducing potential for microrefugia formation. Therefore, I believe that extant rocky patches providing cool microclimates in less modified landscapes should be first prioritized for conservation by considering protection at the landscape-scale. To assess the thermal conditions of extant rocky patches, thermal measurement procedures used in this study and other novel techniques using UAV thermal imagery should be of assistance (Hoffrén & García, 2023). In highly modified landscapes, I believe that restoring landscape permeability should also be a conservation priority (Prevedello & Vieira, 2010). Nonetheless, defining the proper approach for such restoration will require deeper understanding of how landscape configuration and connectivity influence the metapopulation dynamics of northern pikas.

Table 4-1. Model selection results for northern pika occupancy at the whole-distribution scale. The table lists models selected based on comparisons of the differences in expected log predictive density (ELPD) relative to the top-ranking model (ΔELPD) with the standard error of ΔELPD across all models, and the null model. Model rank, model formula, number of parameters (K), and model weight are provided. Abbreviations correspond to Ambient_mean = mean ambient temperature; Rock_interstice = rock-interstice availability; and Date = Julian date of the survey. The mean and 95% credible intervals of the posterior distribution for each parameter are provided in Table S4-3.

Rank	Model	K	ELPD	ΔELPD	SE of ΔELPD	Weight
1	ψ(Ambient_mean + Rock_interstice) p(Date)	7.21	-78.6	0.00	0.00	0.18
2	ψ(Ambient_mean + Rock_interstice) p(.)	6.40	-79.29	-0.69	1.64	0.35
Null	ψ(.) p(.)	15.62	-88.32	-9.72	3.17	0.00

Table 4-2. Model selection results for northern pika occupancy at the trailing-edge scale. The table lists all models analyzed for each trailing edge threshold, with indication of the number of absent and present sites within the range edge (n_{absent}, $n_{present}$), model rank, formula, AICc, ΔAICc, and parameter coefficient estimates with respective standard error for each variable on the standardized scale. Abbreviations correspond to Area_landuse: area of human land use within 3-km radius; Distance_road: distance to the closest road; Interstice_mean: mean interstice temperature; Interstice_range: mean interstice thermal range; 1: Null model. Models with two coefficient estimates correspond to the primary and quadratic term, respectively. Significant effects ($p < 0.05$) are indicated with asterisks (*).

Threshold	Rank	Formula	AICc	ΔAICc	Intercept	Coefficient estimate
0.9	1	Area_landuse	27.87	0	-0.51 (0.54)	-1.32 (0.62)*
$n_{absent} = 19$	2	Interstice_mean + I(Interstice_mean^2)	30.73	2.86	0.88 (0.74)	-1.13 (0.98), -1.96 (1.49)
$n_{present} = 12$	3	1	31.97	4.1	-0.37 (0.43)	
	4	Distance_road	32.34	4.47	-0.32 (0.46)	0.73 (0.55)
	5	Interstice_range	34.38	6.51	-0.37 (0.43)	0.06 (0.48)
	6	Interstice_mean	34.39	6.52	-0.37 (0.44)	0.03 (0.47)
0.8	1	Area_landuse	27.1	0	-0.61 (0.54)	-1.23 (0.62)*
$n_{absent} = 19$	2	Interstice_mean + I(Interstice_mean^2)	29.42	2.32	0.73 (0.74)	-1.17 (0.97), -1.84 (1.35)
$n_{present} = 11$	3	1	30.12	3.02	-0.49 (0.45)	
	4	Distance_road	31.32	4.22	-0.45 (0.47)	0.57 (0.54)
	5	Interstice_range	32.57	5.47	-0.49 (0.45)	0.03 (0.5)
	6	Interstice_mean	32.58	5.48	-0.48 (0.45)	-0.01 (0.48)
0.7		Area_landuse	24.1	0	-0.94 (0.61)	-1.21 (0.69)
$n_{absent} = 19$		Interstice_mean + I(Interstice_mean^2)	25.5	1.4	0.45 (0.76)	-1.47 (1.05), -1.85 (1.28)
$n_{present} = 9$		1	25.93	1.83	-0.77 (0.49)	
		Distance_road	27.64	3.54	-0.74 (0.51)	0.49 (0.55)
		Interstice_range	28.34	4.24	-0.78 (0.5)	0.17 (0.54)
		Interstice_mean	28.37	4.27	-0.76 (0.5)	-0.14 (0.5)
0.6	1	Area_landuse	17.16	0	-2.3 (1.45)	-2.48 (1.67)
$n_{absent} = 18$	2	1	20.82	3.66	-1.18 (0.57)	
$n_{present} = 7$	3	Interstice_mean + I(Interstice_mean^2)	20.89	3.73	0.19 (0.86)	-1.93 (1.36), -2.27 (1.68)
	4	Interstice_range	22.26	5.1	-1.24 (0.62)	-0.63 (0.64)
	5	Interstice_mean	23.22	6.06	-1.16 (0.58)	-0.25 (0.56)
	6	Distance_road	23.34	6.18	-1.2 (0.58)	-0.16 (0.64)

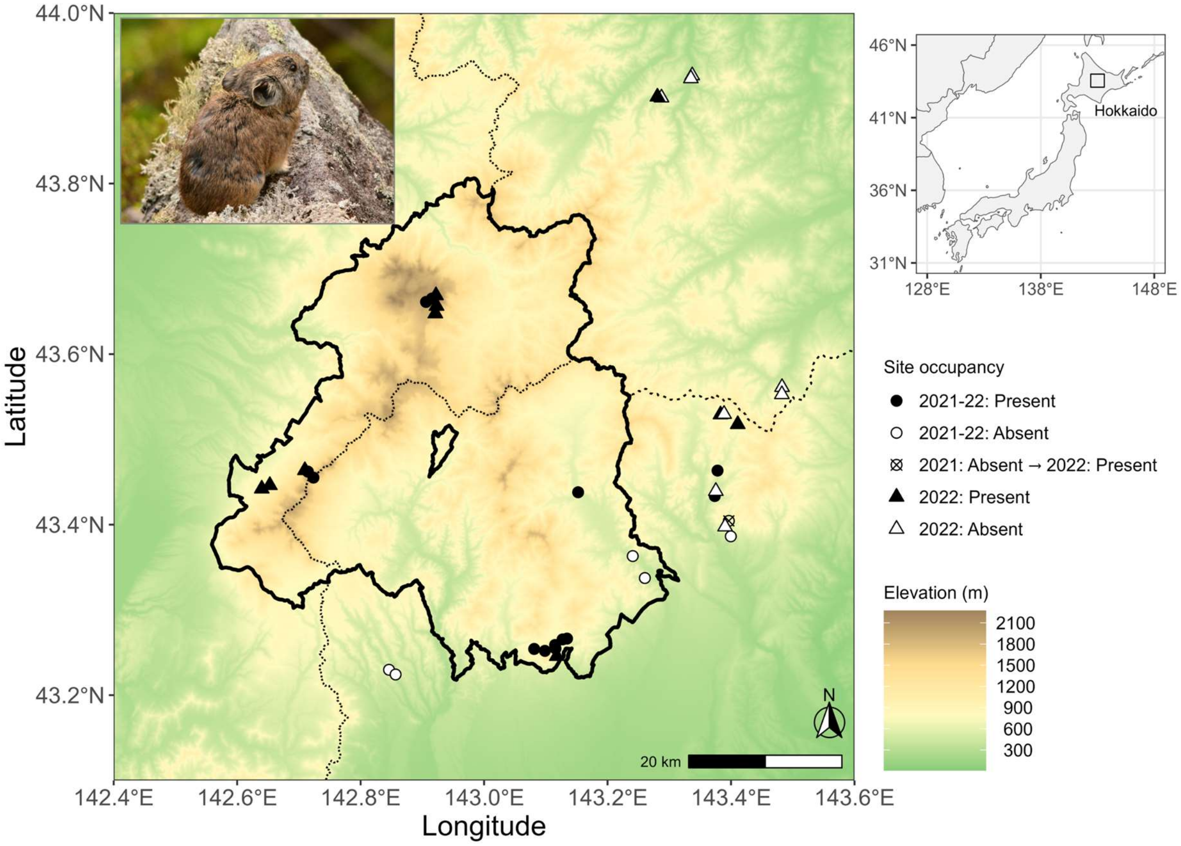


Fig. 4-1. Map of the study area with observed site occupancy statuses of the northern pika (*Ochotona hyperborea*) in Hokkaido, Japan. Symbols depict absent (white) and present (black) locations for sites surveyed in both 2021 and 2022 (circle), and in 2022 only (triangle). One site showed population turnover (circle with x sign) changing from absent in 2021 to present in 2022. Background color indicates the elevational gradient, the black solid line indicates the area of Daisetsuzan National Park, and the black dotted line indicates administrative borders between Tokachi, Kamikawa, and Okhotsk regions.

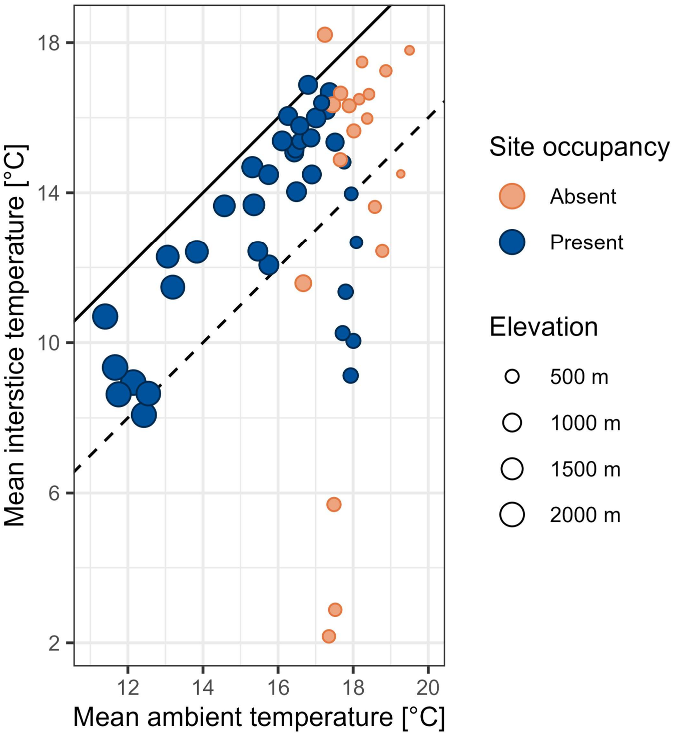


Fig. 4-2. Relationship between mean interstice temperature and mean ambient temperature at northern pika habitats in Hokkaido, Japan. Site temperatures were measured from July 1st to August 31st in the years 2021 and 2022, with each point representing average conditions for a year-site combination. Information on observed site occupancy status is provided for absence (red) and presence (blue) sites. Site elevation is given by the size of the circle. The solid line indicates a 1:1 relationship between the interstice and ambient temperatures and the dashed lines indicates a relationship where interstices are 4 °C cooler than the ambient as a reference.

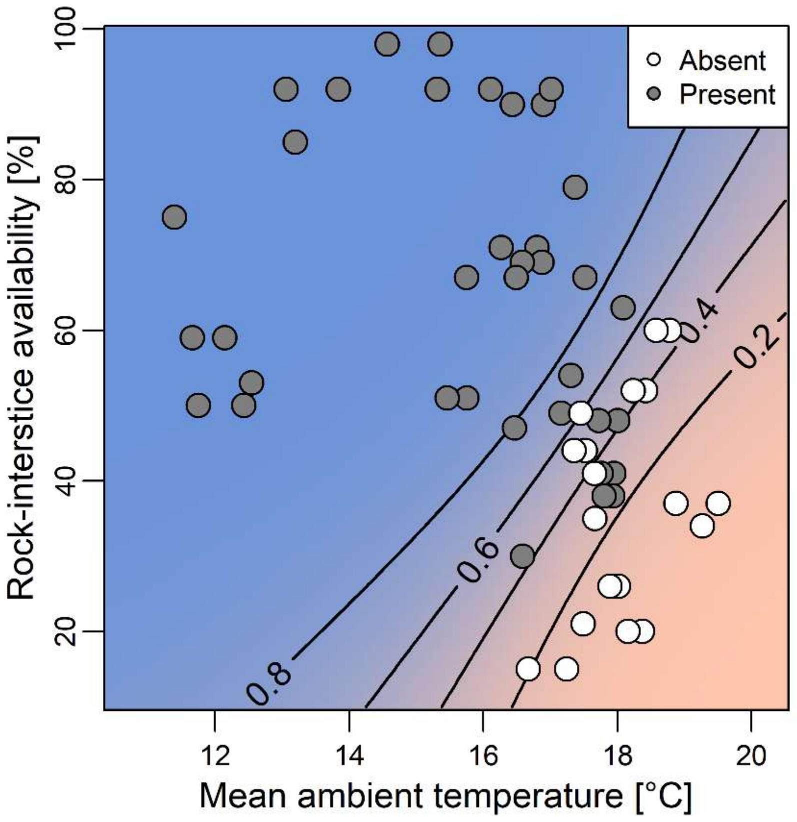


Fig. 4-3. Contour plot showing occupancy probability estimates of northern pikas in Hokkaido, Japan. Occupancy probability is predicted as a function of mean daily ambient temperature and rock-interstice availability using results from the best model in the whole-distribution analysis.

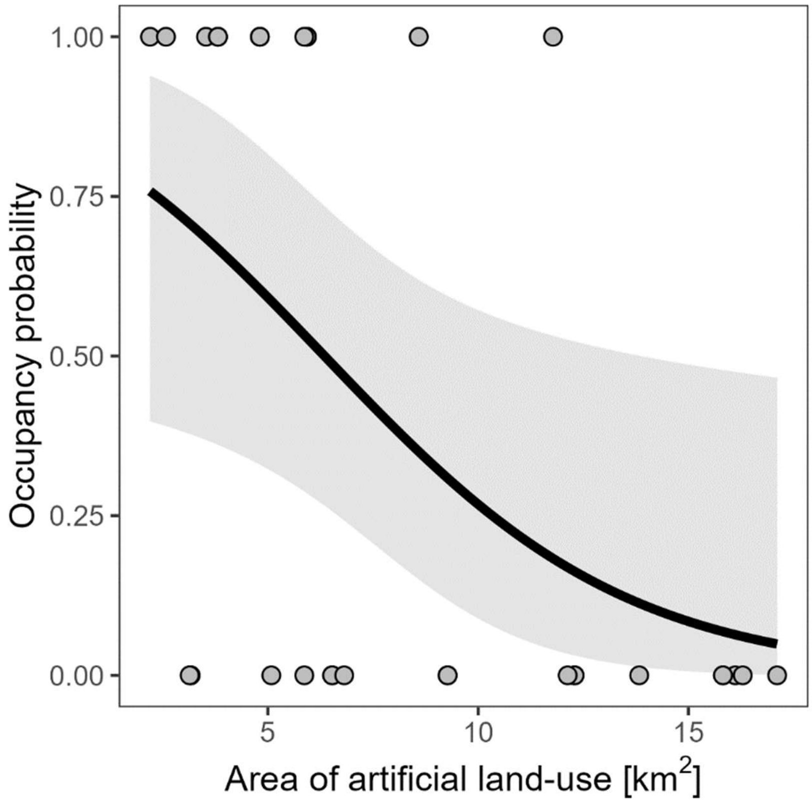


Fig. 4-4. Occupancy probability estimates of northern pikas at the trailing edge of the distribution for a trailing edge threshold of 0.9 (see Methods for details). Occupancy probability and its associated 95% confidence interval (gray envelop) are predicted from the best model. Similar responses were predicted for other trailing edge thresholds (0.8, 0.7, and 0.6).

Chapter 5: Mapping fine-scale distribution of the northern pika (*Ochotona hyperborea*) considering duality in microhabitat thermal conditions

Abstract

Species distributions are frequently modeled using predictors that exceed the spatial scale experienced by the focal species. Incorporating fine-scale environmental conditions is therefore expected to lead to more realistic model predictions. However, the importance of the variety in the existing fine-scale conditions on species distribution remains poorly assessed although species can effectively utilize multiple microhabitats for behavioral adaptation to withstand climate change impacts. Here, I developed a fine-scale species distribution model based on ambient air conditions for the northern pika (*Ochotona hyperborea*), a small lagomorph found in rocky landforms, to first understand the improvement in the model performance from the conventional coarse-scale model. I then assessed how model predictions alter by incorporating the rock-interstice microclimates that are found in their habitats for the baseline (1981–2010) and future periods (2041–2100). The fine-scale model performed better and overall predicted lower habitat suitability across the study area than the coarse-scale model. Incorporation of rock-interstice microclimate increased the habitat suitability markedly relative to predictions based on ambient conditions, which resulted in predicting more suitable areas in lower elevations and more areas remaining suitable into the future. This result suggests that the northern pika may withstand the negative impacts from rising ambient temperatures by effectively utilizing rock interstices via behavioral adaptation. My findings highlight the importance of analyzing species distribution at fine scales and considering local environmental heterogeneity, which helps species mitigate the adverse impacts of climate change, for conservation under climate change.

Introduction

Climate change is having a profound influence on species distribution worldwide. Evidence from historical resurveys shows that species distribution limits are generally expanding at the leading edge and contracting at the trailing edge towards higher elevations and latitudes (Lenoir et al., 2020; Moritz et al., 2008). These range shifts are predicted not only to affect species extinction risks, but also ecosystem functions and services (Pecl et al., 2017). It is therefore important in contemporary biogeography to assess accurately how species will change their spatial distribution in the future and identify conservation priority areas to mitigate those impacts. Species distribution models (SDMs) have become extremely useful in this role by relating species occurrence with environmental data and enabling forecasts of how suitable habitats and associated distribution ranges will change over time (Elith & Leathwick, 2009). Yet, SDMs have been criticized for analyzing species occurrence and environment relationships at spatial resolutions that are often too coarse relative to the actual scales at which species utilize those habitats (Potter et al., 2013). Therefore, endeavors to develop SDMs that incorporate environmental conditions at biologically relevant scales are warranted (Lembrechts et al., 2019).

The spatial resolution of SDMs is of concern particularly in rugged terrains where coarse-scale climate data cannot capture appropriately the fine-scale environmental conditions created by complex topographies (Austin & Van Niel, 2011). A growing body of literature has explored the effect of resolution and spatial scale on SDMs (Franklin et al., 2013; Gillingham et al., 2012; Guisan et al., 2007; Maclean & Early, 2023; Patiño et al., 2023). Recent studies are further attempting to improve the performance and prediction accuracy of fine-scale models by shifting from simply using downscaled climate data to incorporating microclimates that are predicted based on *in-situ* thermal sensor measurements (Haesen et al., 2023; Stark & Fridley, 2022) and remote sensing techniques (Stickley & Fraterrigo, 2023). These studies show that incorporation of fine-scale conditions can improve model performance and alter predictions of suitable areas, thus affecting the trajectory of potential range shifts over time (e.g., Maclean & Early, 2023). Therefore, relying solely on coarse-scale models is problematic for conservation practice under climate change because it can lead to poor decisions that overlook suitable areas when designing protected areas and allocating resources for management. Further research is therefore required in this field because a wide variety of environmental features create distinct climates at various spatial scales (Morelli et al., 2017), and how species utilize and interact with them is system-specific (Shi et al., 2016).

One of the perspectives still unexplored in this field, particularly for animals, is that a given species can experience various fine-scale thermal conditions even within a single grid cell as vertical structures also generate heterogenous conditions (e.g., Scheffers et al., 2014). Most previous studies have only considered the condition of a single vertical position, overlooking the fine-grain heterogeneity in environmental conditions that likely influences overall habitat suitability of a given location that an individual occupies. This is particularly important in the context of species adaptation to climate change since species may mitigate the negative impacts by altering their behavior effectively to exploit local heterogeneity in climatic conditions (Beever, O'Leary, et al., 2016), which may cascade to have broader implications for patterns in the overall distribution (Marske et al., 2023). Therefore, predicting habitat suitability considering the variety of fine-scale conditions should improve the assessment of climate-induced species range shifts.

Pikas are small lagomorphs adapted to cold environments in montane ecosystems. Various aspects of temperature, such as magnitude and variation, often act as strong drivers of their distribution (Beever et al., 2010; Rodhouse et al., 2017) and abundance (Moyer-Horner et al., 2016). Mounting evidence also suggest their vulnerability to recent climate change, with field observations reporting local extinctions (Erb et al., 2011; J. A. E. Stewart et al., 2015) and range contractions (Beever, Perrine, et al., 2016; Billman et al., 2021). Other studies have predicted future range contractions (Bhattacharyya et al., 2019; Schwalm et al., 2016). However, despite occurring in complex terrain, previous studies modeling pika distribution have only used coarse-scale climate data, possibly introducing bias into the habitat suitability predictions and associated range shift estimates.

Some pika species belonging to the *Pika* subgenus dwell in rocky landforms such as talus slopes, lava flows, and moraines. At the fine-scale, these rock-dwelling pikas experience duality in thermal conditions as they utilize both the above-ground and sub-ground microhabitats. The above-ground space is used for moving, vocalizing, foraging and collecting winter diet (i.e., haypile), and pikas experience the local ambient air conditions during these activities. In contrast, the sub-ground space in the rock interstices is used as the shelter (Gliwicz et al., 2005), which provide pikas with cool and stable microclimates buffered from the ambient air temperatures (Sakiyama et al., 2021; Varner & Dearing, 2014). While both microhabitats are essential for pikas, observations show that pikas respond flexibly to avoid the heat stress from the local ambient air by utilizing rock interstices (Smith et al., 2016). Therefore, rock interstices are considered a key feature for their distribution by allowing the species to occur in counterintuitive, low-elevation areas and for them to persist under climate change (Smith, 2020). Predicting the habitat suitability at fine-scales for both the above- and sub-ground space should thus facilitate a more accurate assessment of their vulnerability to climate change while also taking their adaptive capacity into account.

Here, I incorporate fine-scale thermal conditions in rocky landforms into SDMs to predict the distribution of the northern pika (*Ochotona hyperborea*) in Hokkaido, Japan. I evaluate how this incorporation changes model performance, suitable area prediction, and range shift forecast from the conventional coarse-scale approach. In particular, I use macroclimate data (30 arcsecs) and downscaled macroclimate data (3 arcsecs) to build the coarse-scale model (hereafter macroclimate model) and the fine-scale model (local-climate model), respectively, and compare their performances and habitat suitability predictions across the whole distribution. While the local-climate model considers the effects of fine-scale, above-ground temperature, I further assessed the habitat suitability for the sub-ground space by incorporating rock-interstice microclimates into the predictions, which I modeled based on local thermal measurements (Sakiyama & García Molinos, 2024). I then projected future range shifts for the species and compared the area of suitable habitat between local-climate and microclimate-based predictions. I hypothesized that (1) the local-climate model will have higher model performance than the macroclimate model; (2) the local-climate model will predict habitat suitability distinctively from the macroclimate model reflecting the complex topography; (3) the rock-interstice microclimate enhances the habitat suitability from the local-climate model prediction; and (4) the rock-interstices retain the suitable habitats in future predictions.

Materials and Methods

Study area and species distribution data

I modeled the distribution of northern pika populations in central Hokkaido, Japan, because this is the core distribution area of the species in Japan and detailed fine-scale habitat thermal measurements have been conducted in this area (Sakiyama et al., 2021; Sakiyama & García Molinos, 2024). The northern pika in Hokkaido is located at the southern margin of its distribution and therefore its population is likely among the most vulnerable of the species to climate warming. Although northerly neighboring populations are found across the Sea of Japan in Sakhalin and Primorsky, the Hokkaido population is essentially a disjunct population. As such, it is likely to respond to climate change by shifting upslope, but previous studies have not predicted future distributions.

To model the distribution of northern pikas, I compiled occurrence data in central Hokkaido from previous literature. Given almost all the compiled data comprised presence (but not absence) locations, I decided to apply a presence-only algorithm for distribution modeling (see *Model Development* section). I only used presence locations reported on high resolution maps (i.e., 1/25,000 and 1/50,000 scale) for analysis since I was interested in modeling at fine scales. Overall, a total of 305 presence points encompassing a wide elevational gradient (50–2,210 m) were obtained from the literature (Table S5-1; Fig. S5-1a). Survey years spanned between 1963 and 2009 (Fig. S5-1). Detection signs of northern pika presence were clearly mentioned for almost all points (298 points, 97.7%), with the vocalization representing the main method enabling detection of 241 points (79.0%). This suggests that the detection methods were relatively consistent among different literature consulted. Other detection methods reported were direct sightings (78 points, 25.6%), haypiles (47 points, 15.4%), feces (35 points, 11.5%), and eatmarks (9 points, 3.0%).

As calibration extent for this study, I considered the area corresponding to the known geographical range of the species comprising the continuous mountainous areas in central Hokkaido delimited by the flatlands (i.e., river valleys) as the extent borders. Specifically, I considered the Abira and Ishikari River systems as the western, the Teshio River system as the northwestern, the Shokotsu River system and the Sea of Okhotsk as the northeastern, the Abashiri and the Tokachi River systems as the eastern, and the Pacific Ocean as the southern borders of the extent (Fig. S5-1a). Next, I removed irrelevant land cover types from within the study extent area such as urban land, agricultural fields, and aquatic area (e.g., lakes) since northern pikas require pristine montane conditions for inhabitation. The resulting filtered study extent area covered approximately 21,000 km^2 in central Hokkaido (Fig. S5-1a).

Model settings

To understand how differences in spatial resolutions of climate data affect model performances and predictions of species distribution, I constructed macroclimate (coarse-scale) and local-climate (fine-scale) models (Fig. 5-1; Table S5-2). In the macroclimate model, I used environmental predictors at a resolution of 30 arcsecs, which converts to a grid cell of 691 m by 926 m (longitude x latitude) and size of 639,682 m^2. I consider this setting to be a coarse resolution for the northern pika because their home range is much smaller, typically within the range 1,822–11,530 m^2 (n = 4; Onoyama et al., 1991). I also note that, the mountainous terrains of my study area are significantly smoothed at this resolution, with median and maximum elevational differences within one 30-arcsec grid cell as large as 182 m and 770 m, respectively, when computed based on 10-times finer (3 arcsecs) elevation data (Fig. S5-2). Since species occurrence-environment relationships might be confounded by such a large degree of simplification, I developed the local climate model using environmental data at 3 arcsecs, which converts to a grid cell of 69.1 m by 92.6 m and size of 6,397 m^2. I consider this setting to reflect the local ambient air conditions within individual home ranges. Based on the local-climate model, I then generated two habitat suitability predictions to account for the variety of fine-scale thermal conditions. The first corresponds to the model raw predictions based on local-climate data and represents the above-ground habitat suitability. The second prediction incorporates information on rock-interstice microclimates to further predict sub-ground habitat suitability.

Topographical and geological variables

I used the terrain slope angle as topographical predictor in the SDMs because it has been shown to have a positive relationship with the northern pika distribution (Sakiyama et al., 2021). I computed the slope angle raster in QGIS 3.34 (QGIS Development Team, 2023) using the MERIT DEM (Yamazaki, Ikeshima, Tawatari, et al., 2017), a digital elevation model provided at a spatial resolution of 3 arcsecs. Slope angles for the macroclimate setting were calculated using a DEM aggregated to 30 arcsecs (Table S5-2). I also considered surface geology as a categorical binary predictor because 99 % of the known distribution of the northern pika lies on igneous and metamorphic rocks and moraines (Kawabe, 1992). To do so, I assigned whether any of these geological types occurred per grid cell within the study area based on the Seamless Digital Geological Map of Japan (1:200,000) V2 (Geological Survey of Japan, National Institute of Advanced Industrial Science and Technology, 2017) (Table S5-2).

Bioclimatic variables

To model and predict the distribution of northern pikas, I computed the mean daily temperature and mean diurnal range over July and August to account for the effects of thermal magnitude and variation during the summer. I focused on summer conditions (i.e., July and August) because the effects of climate change on cold-adapted species are likely to be particularly strong during this season. Briefly (see Extended Methods S5 for a detailed explanation), I first obtained climate data at 30 arcsecs using the *chelsa-cmip6* R package, which provides access to downscaled Global circulation model (GCM) projections (Karger et al., 2023). Four GCMs that are known to reproduce well the climatic conditions of my study area were selected (i.e., ACCESS-CM2, IPSL-CM6A-LR, MIROC6, and MRI-ESM2-0)

(Shiogama et al., 2021). I used climate data for 1981–2010 to model the baseline distribution. To create the bioclimatic variables, I adapted the computation formulas used in ANUCLIM, a software package used to build spatial climatic data (Xu & Hutchinson, 2011, 2013), to the summer season, and calculated mean summer temperature and mean summer diurnal range. The resulting variables were then used for the macroclimate setting (Table S5-2).

For the local-climate setting, I downscaled the climate data obtained at 30 arcsecs to 3 arcsecs as follows. Temperature data was downscaled using kriging with the *krigR* R package (Davy & Kusch, 2021; Kusch & Davy, 2022). This approach first models the relationship between temperature and elevation at the coarse scale (30 arcsecs), which is then used to interpolate the fine-scale temperature using elevation at the same target scale (3 arcsecs). I used the raw MERIT DEM (Yamazaki, Ikeshima, Tawatari, et al., 2017) dataset, provided at 3 arcsecs, as the elevation data for the fine-scale interpolation and the aggregated version at 30 arcsecs to model the coarse-scale relationship (Table S5-2).

Finally, for the rock-interstice microclimate, I considered that northern pikas can utilize sub-ground thermal conditions in rocky landforms, which are known to be buffered from the ambient air temperature (Sakiyama and García Molinos, 2024). However, given the absence of sufficient spatial distribution information regarding rocky landforms throughout my study extent, I selected three representative regions where I had sufficient data separated by elevational ranges: Biei (1,100–2,000 m), Shikaribetsu (600–1,250 m), and Oketo (400–800 m). For Biei, I was able to map the rocky landforms directly using aerial images. For Shikaribetsu and Oketo, I referred to the mapped occurrence of rocky landforms in previous literature (Kojima, 2004; Kurumada, 2010). For these regions, I then used an empirical relationship between ambient and interstice temperatures previously derived from northern pika taluses in my study area (Sakiyama and Garcia Molinos, 2024) to convert downscaled ambient temperature into interstice temperature for each of the 3 arc second grid cells containing rocky landforms (Fig. S5-3; Extended Methods S5). Here, my assumption is that northern pikas experience local ambient climatic conditions in cells devoid of rocks since these landforms are patchily distributed within each region. I validated my downscaling and microclimate incorporation approach by comparing the thermal conditions measured in northern pika habitats with the values of each bioclimatic variable in the grid cells where those observations had been made (see Extended Methods S5). Results confirmed that the local-climate data was moderately accurate in reflecting observed ambient temperature and that the microclimate data was highly accurate in reflecting observed rock interstice temperatures (Fig. S5-4, S5-5).

Model development

I performed the distribution modeling analysis of northern pikas in Hokkaido using maximum entropy (MaxEnt; Phillips et al., 2006). Models were developed separately for the macroclimate and the local-climate settings considering the years 1981–2010 as the baseline period, thus using the presence points during this period for model fitting. Prior to model fitting, I reduced the effect of spatial sampling bias by thinning the presence data using the spThin R package (Aiello-Lammens et al., 2015) at a distance of 500 m as presence locations could be viewed as independent at this distance considering the complex mountainous terrain and the limited mobility of the northern pika. Considering that the diagonal distance of macroclimate grid cells is larger than this thinning distance and duplicate sampling thus could occur, I randomly selected a single point for each cell after thinning. This pre-selection process resulted in a total of 80 presence points remaining. I generated 10,000 background points throughout the study area, which are used in MaxEnt for characterizing the extant environmental conditions within the study area. To avoid multicollinearity issues (Dormann et al., 2013), I computed the pairwise Pearson's correlation coefficients among the continuous predictors and confirmed that all pairs did not have a strong correlation ($|r| > 0.7$) (Fig. S5-6).

Since MaxEnt models with default settings can lead to overfitting (Anderson & Gonzalez, 2011), I initially tuned the model hyperparameters to control the complexity while fitting well to the data. To do this, I used various hyperparameter combinations of feature classes, which determines the shape of the response curves, and regularization multipliers, which controls the model complexity (Phillips et al., 2006; Phillips & Dudík, 2008), and selected the combination that resulted in the highest predicative accuracy. For the feature class, I considered linear (L), quadratic (Q), product (P), and/or hinge (H) characteristics, and for the regularization multipliers, I used values ranging from 0.2 to 2.0 with intervals of 0.2. The predictive accuracy was assessed for each model by separating the presence data into training (80%) and test (20%) data and computing the area under the receiver operating characteristic curve (AUC), which indicates the accuracy condition on a range of 0 to 1 (Fielding & Bell, 1997). All tuning processes were conducted using the *optimizeModel* function in the SDMtune R package (Vignali et al., 2020). After hyperparameter tuning, I evaluated the optimized model's predictive accuracy based on 5-fold cross validation using Continuous Boyce Index (Hirzel et al., 2006), and compared these values among the model settings.

Comparing baseline predictions

For both the macroclimate and the local-climate models, I predicted the habitat suitability for the baseline period across the study area and compared the predicted suitability by computing the difference. I also generated binarized maps of predicted species occurrence (i.e., presence or absence) based on the habitat suitability prediction across the whole study area. Since discriminant thresholds were likely to differ between the optimized models for the macroclimate and local-climate and could be problematic for comparison, I instead used a sensitivity analysis approach by applying a moving threshold from 0 to 1 at 0.01 increments to discriminate presence or absence. Binary predictions were then compared between the macroclimate and local-climate models by assessing the proportion of predicted presence areas in the study area, calculated as the total amount of presence cells divided by the number of all cells, for each moving threshold. I used proportion instead of simply calculating the total area of presence because the total study area was subtly different between the scales due to processing procedures of environmental data. I then predicted the habitat suitability for the sub-ground space for the three selected regions by replacing the local ambient temperatures by the modeled rock interstice temperatures for the prediction of habitat suitability using the local-climate model. I consider this prediction to reflect the habitat suitability of the rock-interstices within individual home ranges defined based on the relationship between occurrences and ambient air temperatures. The resultant prediction was compared with those based on the macroclimate and local-climate.

Hindcasting

I used a hindcasting approach to evaluate the transferability of the models to project distributions over time (see Nogués-Bravo, 2009) by projecting the distribution of the species to the past and comparing it to known past presence points from the same past period for validation (Hodel et al., 2022). Although this approach is still rarely used in SDM studies (Yates et al., 2018), it allowed us to assess how confident I can be using the models to predict distributions for a (past or future) time period different to that the model was calibrated for. I projected the distribution of northern pikas for the years 1961–1980, a period for which early presence records are available (Table S5-1; Fig S5-1). The same procedures as the baseline climate data were used for processing past data. I evaluated the model’s predicative accuracy via the Continuous Boyce Index (Hirzel et al., 2006).

Future projection

To project the future distribution of the northern pika, I obtained climate data for two future time periods, 2041–2070 and 2071–2100, considering two emission scenarios, SSP1-2.6 and

SSP5-8.5, representing a globally sustainable and a fossil-fuel based development scenario, respectively. I predicted the future distribution for the study extent based on the macroclimate and local-climate models using the future bioclimatic data, which were processed based on the same procedures for the baseline climate data (i.e., I assume that future topographical and geological variables will remain the same as present). I binarized the suitability predictions to presence or absence by applying the same approach used for the baseline period to calculate the proportion of presence areas.

Moreover, I also projected the future distribution of the northern pika for the three selected regions to assess how microclimate contributes to retaining suitable conditions in the future. When processing the future microclimate data, I assumed that the buffering effect of the rock interstices (i.e., the empirical relationship between local ambient and rock-interstice temperatures) will remain invariable over time. I believe that this assumption is robust because the field thermal measurements from which this relationship was derived contained a large elevational gradient of 350–2,200 m and the model residual was stable across the ambient temperature gradient (Sakiyama and Garcia Molinos, 2024), although I note that some extrapolation did occur for some lower elevation areas where future conditions exceeded the observed thermal gradient. I binarized the suitability predictions for both local-climate and microclimate using the maximum true skill statistic computed for the local-climate model. The consensus among the resulting binarized predictions from each of the four GCMs was then computed by considering a cell as present whenever that cell was predicted as present by two or more individual GCMs (i.e., ≥50% consensus). The consensus predictions in the selected regions were compared visually between the local-climate and microclimate-based predictions for each period and emission scenarios.

Results

Model performance and variable importance

Both the macroclimate and local-climate models converged to the same hyperparameter combinations for the best-fit model comprising an LQP feature class and a regularization parameter value of 2. Using these hyperparameters, the Continuous Boyce Index was 0.73 and 0.80 for the macroclimate and local-climate models, respectively (Table 5-1). This indicates that the continuous predictions reflected the species distribution well and that the local-climate model was more accurate than the macroclimate model.

Mean summer temperature was the most important predictor explaining the northern pika distribution in both models with a permutation importance of 74.5 % and 76.2 % for the macroclimate and local-climate models, respectively (Fig. S5-7). Mean summer temperature decreased occurrence probability in both models, indicating that the northern pika is more likely to be present in cooler areas. However, I detected a slightly steeper slope in the response curve of the local-climate model, which indicates that the local-climate model fitted towards cooler conditions than the macroclimate model (Fig. S5-8). In both models, surface geology was the second most important predictor with 20% and 18 % permutation importance, respectively (Fig. S5-7), and a positive relationship with occurrence probability (Fig. S5-8). The permutation contribution of daily thermal range and slope was less than 5% in both models (Fig. S5-7).

Habitat suitability for the baseline period

The negative effect of mean summer temperature was reflected in the habitat suitability predictions at the whole distribution scale in both models, with higher elevations predicted as highly suitable areas and the suitability lowering gradually towards downslope (Fig. 5-2a,b). Specifically, large mountain ranges such as the Daisetsuzan and Hidaka Mountain Ranges, which contain summits over 2,000 m, as well as mountains in the Eastern Daisetsu region (elevation of the main peaks 1,800–2,000 m) were recognized as the most suitable areas. Mid- to high-elevation mountain ranges, such as the Yubari-Ashibetsu (1,600–1,720 m), Teshio (1,400–1,600 m), Ashoro (1,200–1,300 m), and Shikaribetsu Mountains (1,100–1,250 m), were predicted as areas with moderate to high suitability. Finally, low-elevation mountains were predicted to be low in habitat suitability for northern pikas in almost all regions although some presence points were reported from such areas (e.g. central and northeastern regions). One exception was the Samani-Erimo region, which was predicted to have high suitability despite the region being predominated by low elevations (Fig. 5-2a,b).

As I compared the macroclimate-based and local-climate based predictions, the former was generally higher in habitat suitability than the latter across the study area (Fig. 5-2c). The difference in suitability was relatively large in the mountainous areas, particularly in the slopes rather than the summits, with suitability differences up to 0.5. However, habitat suitability from the local-climate based were also higher than the macroclimate-based predictions in some mountainous areas as well as the Samani-Erimo region. The habitat suitability difference was relatively small in low elevations.

The proportion of predicted presence areas for both models indicated similar curves along the moving binarization threshold (Fig. 5-3a). The curve inverse shape means that, while the whole study area is discriminated as present when the threshold is zero, a large proportion becomes absent at relatively low thresholds, although a small proportion of the study area remains present until the threshold becomes one. In other words, while most of the study area is predicted to have low suitability, some areas have distinctively high values. Comparing the curves between the models, the proportion of presence areas was higher in the macroclimate-based prediction than in the local-climate based prediction across the whole range of binarization threshold (Fig. 5-3a). This suggests that the macroclimate model predicted a larger area of suitable habitat than the local-climate model regardless of the binarization threshold.

In the three selected regions, the habitat suitability based on the macroclimate and local-climate showed a gradually changing pattern, likely reflecting the elevation difference. In contrast, accounting for the rock interstice microclimate in local-climate predictions boosted the habitat suitability distinctively within these regions (Fig. 5-4). For instance, while the habitat suitability in Biei was relatively high given its high elevation in both the macroclimate- and local-climate-based predictions, the rocky landforms further increased the suitability to mostly reaching a suitability of 1 (Fig. 5-4). This trend was more evident in Shikaribetsu, the mid-elevation region, where the predicted suitability reached as high as 0.99 in the microclimate-based predictions despite the surrounding landscape having suitability less than 0.5 (Fig. 5-4). In Oketo, the low-elevation region, the total area that increased in suitability was relatively small given the limited area of rocky landforms, but the predicted suitability within rocky landforms reached as high as 0.66 (Fig. 5-4). The maximum values of predicted suitability based on the macroclimate and local-climate models were 0.55 and 0.41 in Shikaribetsu and 0.24 and 0.25 in Oketo, respectively. In all these three regional-scale predictions, the habitat suitability was predicted in a more detailed and complex manner in the fine-scale (3 arc sec) predictions than that in the coarse-scale (30 arc sec) predictions as evidenced by the variation in habitat suitability of the local-climate and microclimate predictions within the coarse-scale grid cells (Fig. 5-4).

Hindcasting and future projection

In the hindcasting analysis, both macroclimate and local-climate models had Continuous Boyce Index values well above zero (Table 5-1), suggesting that the models were accurate in predicting past distributions. This result supports the transferability of these models to predict distributional change over time. Accordingly, I was able to predict future distributions for both model settings with confidence.

Both models indicated inverse curves in the proportion of presence areas in the future (Fig. 5-3b). Compared with the baseline proportions, future distribution was predicted to decrease by more than 60% in both time periods and emission scenarios considered (Fig S5-9). Between the two future time periods, the difference in the habitat decrease rate was relatively small under the SSP1-2.6 scenario, suggesting that presence areas will decrease until 2041–2070 but will then remain relatively stable until 2071–2100. However, the habitat decrease was apparent under the SSP5-8.5 scenario, suggesting that suitable habitats will continue to decrease until 2071–2100. (Fig. 5-3b; S5-9).

Patterns of predicted distributional change largely differed among the three selected regions between the local-climate and microclimate-based predictions. Based on the local-climate, predicted presences were found in Biei in both future time periods and scenarios and in Shikaribetsu under the SSP1-2.6 scenario, while none were found in Oketo under all future settings (Fig. 5-5). Conversely, predicted presences were found in almost all regions in all future settings when accounting for rock interstice microclimates, except in Oketo for the far future under the SSP5-8.5 scenario (Fig. 5-5). Discrepancies between local-climate and microclimate-based predictions were high towards the lower elevations and under the higher carbon emission scenario (SSP5-8.5).

Discussion

I developed distribution models for the northern pika that incorporated fine-scale temperatures experienced by the species to assess how model performances and predictions change from a conventional model based on coarse-scale conditions. My results show that predictive accuracy was higher for the fine-scale model. I also found that the predicted habitat suitability varied among regions and at smaller spatial scales in the fine-scale prediction. These results confirm that accounting for fine-scale environments can lead to distinct and more complex predictions than those obtained from a coarse-scale model and that solely depending on coarse-scale predictions can result in biased predictions that overlook potential suitable habitats.

There are two possible reasons that likely contributed to the higher predictive accuracy in the fine-scale model. First, model response curves showed some important differences in the modeled relationship between occurrence and the environmental predictors. While mean temperature had a dominant negative effect on the distribution in both models (Fig. S5-7; S5-8), a response also observed in a previous study (Sakiyama et al., 2021), the response curve was steeper in the local-climate model. This indicates that the model fitted towards cooler conditions, which may be reflecting the actual response of the northern pika more accurately than the macroclimate model. Interestingly, my input data for the distribution model indicated that many of the occurrence records in higher elevations were located in areas higher than its surroundings and thus had cooler temperatures at the fine-scale (Fig. S5-10). Although I referred to presence points recorded in previous literature, it remains unclear whether this trend is due to a potential sampling bias in convex topographies such as ridgelines and mountain tops. I believe that assessing species distribution at fine-scales could introduce its scale-dependent issues, which requires attention as more fine-scale SDMs are developed (Mitchell et al., 2017). Second, the quality of the predictors may have also had an effect on model accuracy. Even when coarse- and fine-scale models exhibit the same relationship between occurrence and environment, the validated accuracy is likely to decrease if predictors are generalized at the coarse-scale. Instead, fine-scale predictors are more likely to accurately represent true environmental conditions, which could have resulted in higher predictive accuracy by resolving better local complex topographies. Thus, the overall increase in accuracy of the local-climate model can be attributed to these small refinements in the modeled relationship and predictors. In general, my results are in agreement with recent studies finding higher performance in SDMs incorporating fine-scale climates (Haesen et al., 2023; Stark & Fridley, 2022).

My results showed that incorporating fine-scale environments into SDMs resulted in a decrease of suitable areas compared to the coarse-scale prediction. This is likely due to differences in the modeled response of mean summer temperature between the models. Such differences likely emerged from the local-climate model being fitted towards cooler temperatures relative to the coarser macroclimate model resulting in lower predicted occurrence probabilities at certain temperatures or elevations. Consequently, this leads to a greater area of predicted presence in the macroclimate model along the moving threshold when binarizing the habitat suitability predictions. In previous literature, fine-scale models have resulted in both greater (Stickley & Fraterrigo, 2023) and smaller suitable areas (Franklin et al., 2013; Haesen et al., 2023). Hence, the difference in the predicted habitat area resulting from incorporating fine-scale environments into SDMs may be specific to each study system and the scale-dependent relationship between the occurrence records and environmental predictors used in the model. Furthermore, in my study, both models projected drastic future declines in the northern pika distribution, with over half of the suitable habitats predicted to disappear by mid-century. This suggests that, similar to other pika species, northern pikas in Hokkaido are vulnerable to climate change (Beever et al., 2011; Bhattacharyya et al., 2019). Importantly, the predicted change in species distribution depended strongly on the future period and emission scenario. This result stresses the need to enforce effective policies for greenhouse gas emission mitigation and to guide effective conservation of the species by protecting areas that will account for the effect of climate change and maintain its distribution in the future.

At the regional scale, the incorporation of the rock-interstice microclimate provided distinct predictions for both the baseline and future. Overall, the cooler conditions provided by rock-interstices resulted in the microclimate predictions markedly enhancing habitat suitability compared to the local-climate based prediction in all three regions. This demonstrates that a single location (grid cell) can exhibit dual habitat suitability due to the existence of diverse thermal conditions in complex topographies. However, what are the implications for the northern pika distribution? In rocky landforms, the habitat suitability can simply be categorized into three combinations based on the local-climate and microclimate conditions: high-high, low-high, and low-low. The combination of high-low suitability was not observed because rock interstices were always cooler than local ambient conditions, hence more suitable. Northern pikas are expected to be present in areas with high-high suitability, and absent from areas with low-low suitability. However, whether areas with low-high suitability serve as functional habitats for northern pikas will likely depend on the extent to which the rock interstice condition mitigates the impact of poor thermal ambient conditions, which should be strongly linked to the capacity of northern pikas to adapt their thermoregulation behavior. Previous studies have indicated that northern pikas utilize above-ground space during the cooler times of the day (Onoyama, 1991), a behavior also observed in American pika studies (Smith et al., 2016). Additionally, research on the American pika suggests that it regulates body temperature by reducing above-ground activities and retreating into rock interstices (MacArthur & Wang, 1974). Thus, the northern pika may exhibit high behavioral flexibility to respond to unfavorable ambient conditions, enabling them to inhabit areas with low-high suitability. Consequently, the actual overall suitability of a given rocky landform should be influenced by a more complex combination of these two suitability conditions (above and below ground).

Despite its simplicity, my approach to predict microclimate-based habitat suitability is innovative because it enables detecting potential suitable habitats that are likely to be overlooked in predictions based solely on ambient conditions, especially in the lower elevations. Therefore, this approach can be used as a first-cut approach to identify potential priority areas for conservation. Assessing occupancy in areas with low-high suitability will be therefore important for resource allocation, although the large elevational range of observed presence of the northern pika, despite their cold adaptation, already suggests they are inhabiting such counterintuitive areas perhaps through behavioral adaptation. Moreover, this approach has implications for identifying climate change refugia for the northern pika as all three regions were predicted to contain areas supported by rock interstice microclimate in the future despite the deterioration of local-climate conditions. Areas with favorable microclimates that support species persistence under a changing climate (i.e., microrefugia) are often cryptic (Provan & Bennett, 2008), and therefore, extensive identification of such areas based on spatial data should facilitate effective protection of vulnerable populations. In my case, however, the current lack of an extensive dataset reporting presence of rocky landforms in my study area limits such endeavors. Therefore, further refinements in geospatial data are warranted for predicting potential microrefugia. Deeper understanding of the behavioral responses of the northern pika to ambient and rock interstice thermal conditions will also be important to assess the reliability of behavioral adaptation in driving species distribution patterns (Marske et al., 2023).

The importance of fine-scale SDMs are being increasingly recognized as they often provide distinct predictions from conventional scales and information in fine-scale predictions are essential for improving downstream objectives, such as designing effective conservation plans under climate change (Nadeau et al., 2022). In this study, the local-climate model prediction proved to be valuable for achieving such objectives as it provided distinct habitat suitability predictions. Additionally, an important implication of fine-scale SDMs is their role in filling the gap between predictions and observations of ongoing species range shifts (Chen et al., 2011). This is because conventional approaches have been criticized for overestimating range shifts due to the lack of consideration for the fine-scale climates that may facilitate species persistence in warmer regions (Pearson, 2006). Therefore, it is important to validate whether fine-scale models effectively reduced overestimation by conducting ground-truthing surveys. A study by Maclean and Early (2023) exemplifies this, demonstrating that fine-scale predictions reduced the number of species at extinction risk and were in agreement with the actual observed patterns, while coarse-scale predictions estimated several species to become extinct.

One of the limitations of my study is that, despite using the downscaled macroclimate data, I still rely on a simplified representation of time and space to develop the fine-scale models. Rocky landforms exhibit high heterogeneity, with ambient air and rock interstice temperatures varying depending on height and depth, respectively, and changing across seasons (Benedict et al., 2020; Millar et al., 2016; Smith, 2020). In this regard, my study may still be considered as a coarse-scale representation of reality in time and space. Like other SDM studies, my model relies on the correlative relationships between presences and climatic and topographical predictors. Studies have demonstrated that predicted distributions are altered by incorporating biotic interactions (Bateman et al., 2012), dispersal settings (Zurell et al., 2016), and lineage information (Zhang et al., 2021) into the models. Therefore, further research is needed to incorporate these aspects into the prediction of the distribution of the northern pika.

In conclusion, the incorporation of fine-scale climate data into SDMs yielded contrasting predictions to the coarse-scale prediction. Future distributions were predicted to decrease increasingly with both further away time horizons and higher emission scenarios considered, stressing the importance of enforcing effective mitigation measures to curb greenhouse gas emissions. Together, this information is essential for the conservation of northern pikas in Hokkaido, as previous studies have not assessed such impacts. Incorporation of rock-interstice microclimate data significantly increased the habitat suitability and predicted more suitable habitats for both the baseline and future. Behavioral adaptation is considered crucial for the inhabitance of the northern pikas at lower elevations, which is important for the conservation of the northern pika because its distribution is often considered to be restricted to the alpine zone. Based on these results, I advocate for the identification of rocky landforms and their integration into conservation planning to effectively leverage microclimates in conservation efforts.

Table 5-1. Optimized hyperparameters and Continuous Boyce Index values of the best macroclimate and local-climate models.

Model	Feature class	Regularization multiplier	Continuous Boyce index	Hindcast: Continuous Boyce index
Macroclimate	LQP	2.0	0.73	0.82
Local-climate	LQP	2.0	0.80	0.96

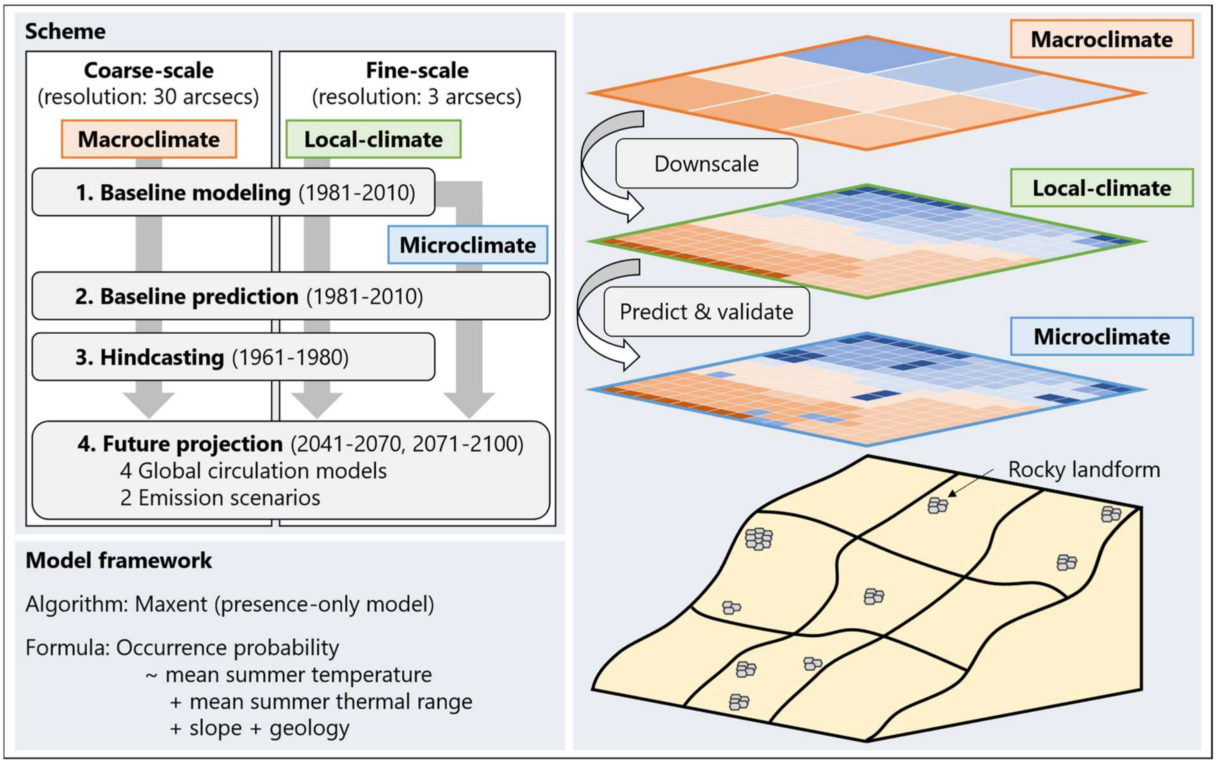
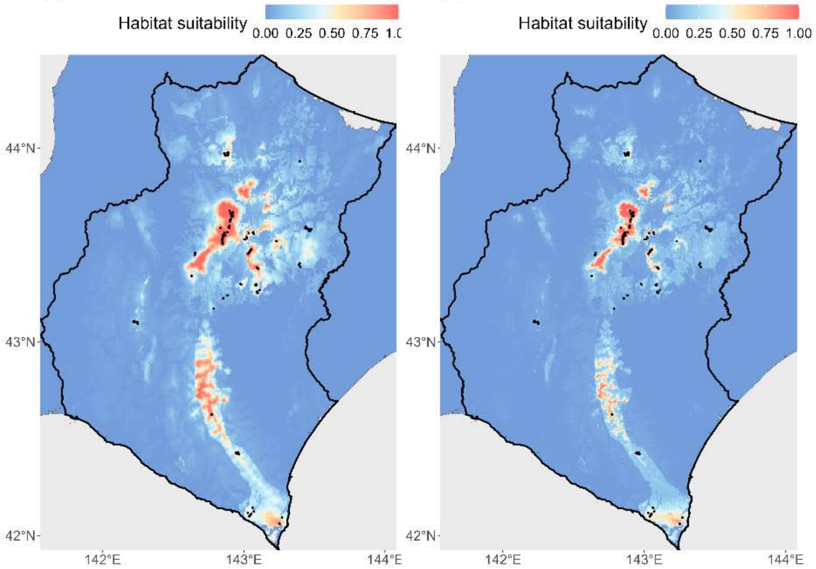
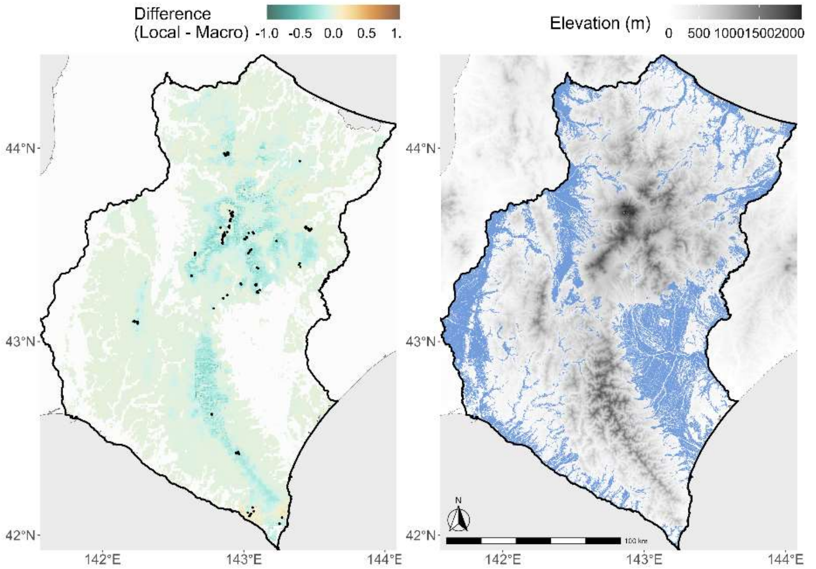


Fig. 5-1. Schematic diagram describing the different model and prediction settings of the study. First, distribution modeling was conducted at two spatial resolutions: coarse (30 arcsecs) and fine (3 arcsecs). I used the macroclimate data in the coarse-scale setting to reflect the conditions often used in traditional SDM studies. In the fine-scale setting, I used the downscaled macroclimate data or the local-climate data, which I considered to represent the local ambient conditions. Second, I predicted the baseline habitat suitability based on these models. At the fine-scale, I further predicted the habitat suitability using the rock-interstice microclimate data, which I predicted based on empirical thermal measurements. Third, I conducted a hindcasting analysis to evaluate the original models' capability of predicting species distribution over time. Fourth, I projected the future distribution based on macroclimate, local-climate, and microclimate, considering four Global circulation models and two emission scenarios.


(a) Macroclimate

(b) Local-climate


(c) Habitat suitability difference

(d) Elevation

Fig. 5-2. Predicted habitat suitability of the whole distribution of the northern pika in Hokkaido, Japan based on (a) macroclimate and (b) local-climate models. In (c), the habitat suitability difference between these two predictions (Local – Macro) is provided. Black points represent presence locations. In (d), the elevation of central Hokkaido is shown in the background. The black border line denotes the model's calibration extent with blue areas within representing areas that were excluded from the analysis (see Methods for details).

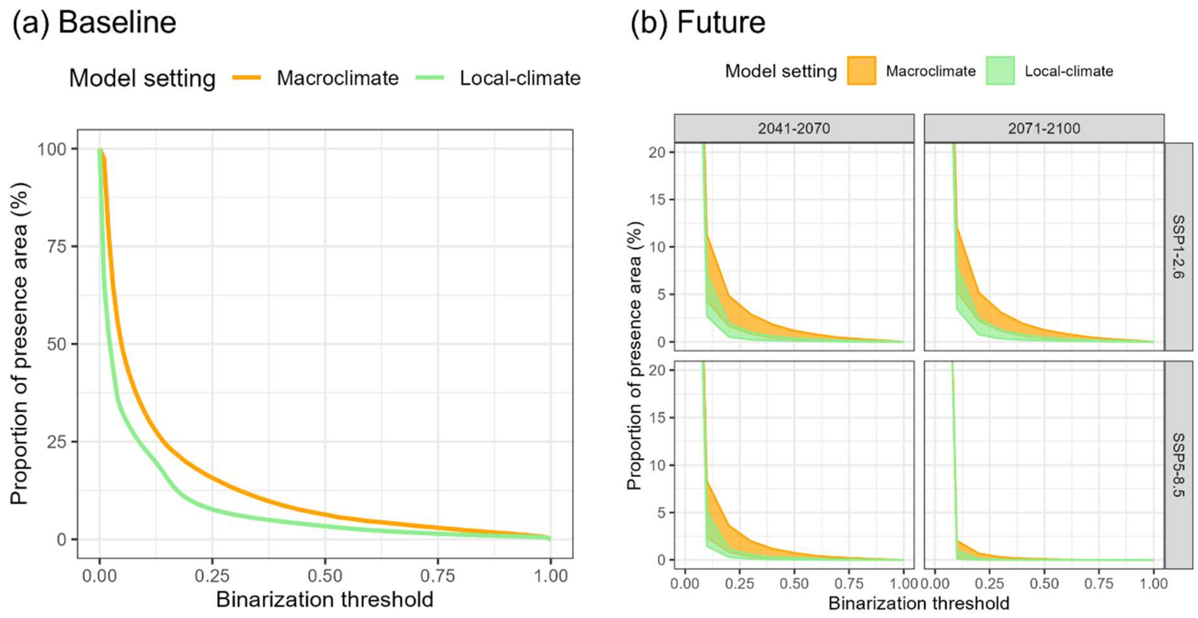


Fig. 5-3. Proportion of the study extent area predicted as present area along the binarization threshold applied as a moving window at 0.01 increments (see Methods for details) for the (a) baseline and (b) future periods. The lines and shade colors represent model settings (orange = macroclimate, green = local-climate). The future panels are divided by time period (2041–2070 and 2071–2100) and emission scenario (SSP1-2.6 and SSP5-8.5), while the filled envelopes represent the range of the future proportions of presence area predicted for the four Global circulation models.

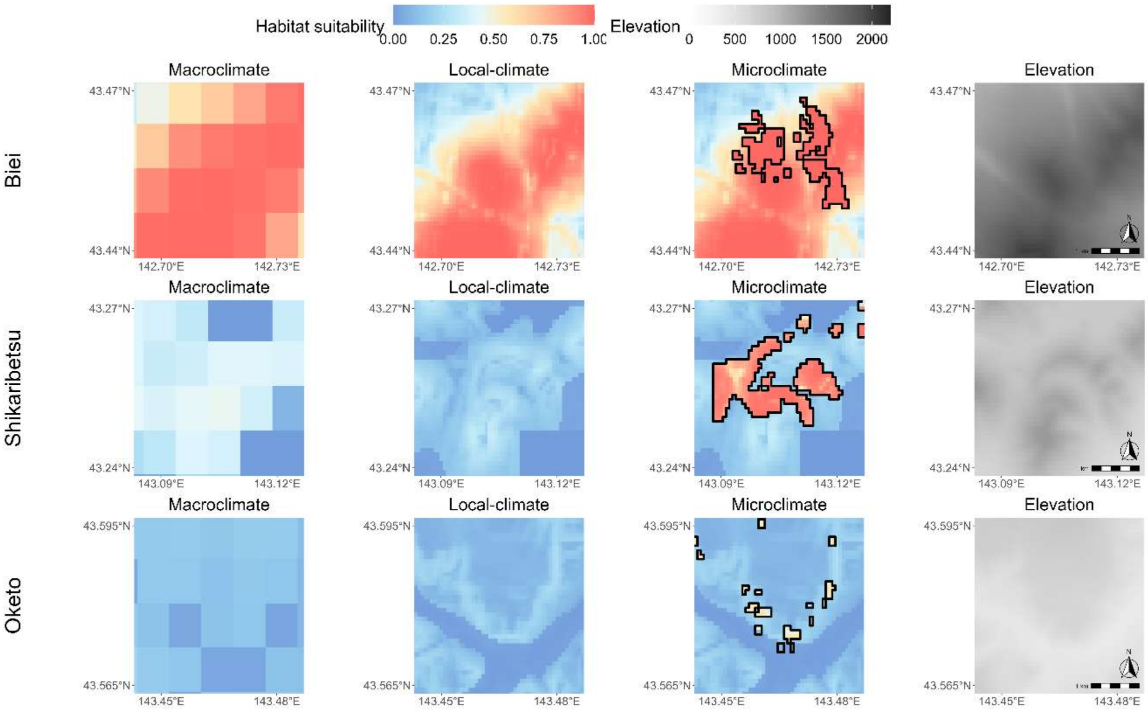


Fig. 5-4. Predicted habitat suitability of the northern pika in (starting from top row) the Biei, Shikaribetsu, and Oketo regions based on (starting from left column) the macroclimate, local-climate, and microclimate. Areas with rocky landforms are depicted by black lines in the microclimate panels. The elevation for each region is shown in the last column.

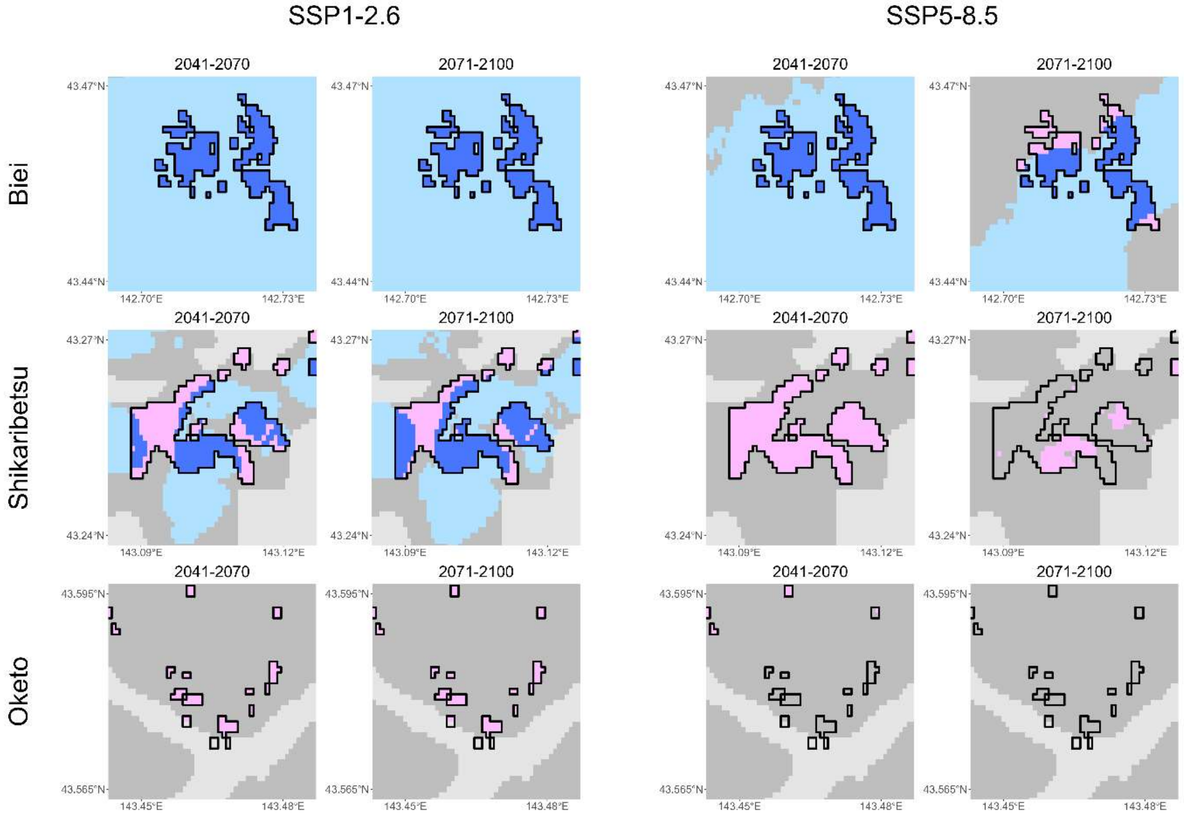


Fig. 5-5 Predicted future distribution of the northern pika in the Biei, Shikaribetsu, and Oketo regions based on the consensus approach. The 1st and 2nd columns represent predictions for the 2041–2070 and 2071–2100 under the SSP1-2.6 scenario, and the 3rd and 4th those under the SSP5-8.5 scenario. Dark gray areas represent areas suitable for the baseline period that are predicted to become unsuitable in the future, while light gray areas represent areas unsuitable for the baseline period. Areas with rocky landforms are depicted by the black lines. The light blue areas represent suitable habitats supported by the local climate outside rocky landforms. Within rocky landforms, the dark blue areas represent suitable habitats supported by both the local-climate and microclimate, whereas the pink areas represent those supported only by microclimate.

Chapter 6: Does fine-scale species distribution model contribute to a more realistic prediction of species range shifts?

Abstract

Species distributions are frequently modeled using environmental factors that are larger than the spatial scale experienced by the focal species. Since fine-scale environmental conditions are not reflected in the predictions, typical coarse-scale models are known to overestimate changes in distribution over time. To prevent this overestimation, fine-scale distribution models are being developed, but there have been few studies that have assessed the predictive accuracy of these models in predicting the distribution changes over time. In this chapter, I validated the predicted distributions of the northern pika (*Ochotona hyperborea*) for the years 2021-2025 based on the models developed in Chapter 5 by using observed occurrence information obtained in Chapters 3 and 4. This practice revealed that a prediction using fine-scale climate data was the most accurate based on AUC, although its difference with the prediction based on traditional, coarse-scale climate data was relatively small. Based on the true positive rate, the microclimate incorporated prediction was the most accurate. This suggests that accounting for microclimates reduced omission errors by reducing the overestimation of the distribution changes over time. However, the disadvantage of this approach was that it also exhibited higher false positive rates, indicating that it increased commission errors. Application of these predictions to conservation will require acknowledging the advantages and disadvantages of each prediction and a thorough discussion of the ideal balance between the omission and commission errors between practitioners and modelers.

Introduction

Climate change is causing species redistributions around the globe, with latitudinal and elevational range shifts being documented for a wide variety of species (Chen et al., 2011; Lenoir & Svenning, 2013). As these shifts have implications for range shifts of other species as well as ecosystem services and functions (Pecl et al., 2017), implementing effective conservation and management requires accurate predictions of future range shifts (Urban et al., 2016). One of the most widely used tool for this purpose is the species distribution model (Elith & Leathwick, 2009; Franklin, 2023). This model statistically links species occurrence with the environmental data and thereby enables predicting habitat suitability onto geographic space. By inputting future climate data for the prediction, SDMs enable understanding how the species distribution might change along with climate (Deb et al., 2020; Rissanen et al., 2021; Zhang et al., 2020).

Predicting range shifts accurately however remains a difficulty in SDMs (Araújo & Rahbek, 2006). One of such problems is the overestimation of species range shits, a case where the predicted shift of a species tends to be larger than the observed shift (Maclean & Early, 2023). Widely discussed following this phenomenon is that the spatial resolution of the environmental data is too coarse to capture the local-scale environmental heterogeneity, thus simplifying the species responses to the environment (Potter et al., 2013; Thuiller et al., 2005). This is particularly problematic in the context of assessing climate change impacts because thermal conditions are strongly influenced not only by the broad-scale factors (e.g., latitude, elevation), but also by local-scale factors (e.g., topography, vegetation, distance to rivers) (Morelli et al., 2016; Sears et al., 2011). Consequently, many predictions ignore the possibility that local-scale environments facilitate species to survive despite the warming trends at the broader-scale (Moritz & Agudo, 2013; Thuiller et al., 2005). Indeed, observations show evidence that many species have not demonstrated expected shifts and instead are found in original warmer locations (Chen et al., 2011).

In this light, many researchers are now refining the spatial scale of the SDMs to predict at scales relevant for the focal species by developing high resolution climate data (Haesen et al., 2023; Stickley & Fraterrigo, 2023). These studies have shown that models incorporating local-scale environments predict more accurately than the coarse-scale model (Stickley & Fraterrigo, 2023). However, this evaluation is based on a set of distribution data from the same time period as that for fitting the model (i.e., baseline period). Therefore, there is still a lack of evaluating whether incorporating local-scale environments provides predictions of species distributions that are accurate over time. In other words, whether fine-scale species distribution modeling effectively fills the overestimated gap between observed distribution changes and predictions based on traditional, coarse-scale model is unknown. This is because future distribution data for testing the predictions is apparently unavailable. Still, it is possible to test the predictive accuracy if past distribution data is available, by building the model based on the past data to predict the present distribution and testing the prediction by conducting a ground-truth survey. This approach should facilitate understanding predictive accuracy for species range shifts and considering further improvements for assessing climate change impacts.

In this chapter, I integrate results obtained through Chapters 3, 4, and 5 to assess whether the current northern pika distribution is predicted accurately by accounting for fine-scale climates in SDMs. The current occurrence of the northern pika in Hokkaido was surveyed in Chapters 3 and 4. The species distribution model was built in Chapter 5 based on the distribution information for the years 1981–2010. Thus, the habitat suitability for present (2021–2025) was predicted using this model and its accuracy was evaluated using the current occurrence information. An accurate prediction will be characterized by predicting the occupied sites with higher suitability or predicting unoccupied sites with lower suitability or both.

Materials and Methods

Occurrence information

I conducted occupancy surveys of the northern pika in Hokkaido in Chapters 3 and 4. The occurrence information recorded in these chapters represents well the current distribution of the northern pika in Hokkaido. Therefore, I used this information to evaluate the accuracy of the SDMs built in Chapter 5 in predicting distributions over time. Briefly, in Chapter 3, habitat resurvey was conducted at 61 sites that have been reported to be occupied by the northern pika in Hokkaido before 2010. In Chapter 4, I surveyed the occurrence of the northern pika at 37 sites in the Daisetsuzan National Park and its peripheries. In both chapters, the occurrence was assessed during 2021–2023 by using the playback (Sakiyama & García Molinos, 2023). Prior to the analysis, I removed some sites that lacked rocky landforms in the surveyed sites in Chapters 3 from the analysis. Considering the overlap in the study sites between these chapters, 74 unique sites were used for this study. This covered the whole elevational range of species (i.e., 60–2,210 m) as well as the large proportion of its geographical range in Hokkaido. Detailed explanations for both surveys are provided in each chapter.

Species distribution modeling

I provide the detailed explanation for the species distribution modeling in Chapter 5. Briefly, I first compiled species distribution data from previous literature reporting presence locations of the northern pika during 1981–2010. While I found 305 points in the literature, these were further reduced to 80 points considering spatial autocorrelation for the analysis. For environmental data, I considered the effects of mean summer temperature, mean summer diurnal thermal range, slope angle, and geology. For thermal variables, I used the climate data provided from the chelsa-cmip6 R package (Karger et al., 2023). Climate data for the years 1981–2010 was used for the model fitting (i.e., baseline) and that for years 2021–2025 under the SSP5-8.5 scenario in 4 global circulation models (GCMs) was used for predicting the present distribution.

I prepared two model settings differing in spatial resolution: the macroclimate model was analyzed at 30 arcsecs to consider the effect of ambient thermal conditions at a scale larger than an individual home range, while the local-climate model was analyzed at 3 arcsecs to consider the effect of ambient thermal conditions at the scale of an individual home range. The original climate data from chelsa-cmip6 was used for the macroclimate setting. For the local-climate setting, I statistically downscaled these data to 3 arcsecs based on elevation and used them for the analysis. I further considered the microclimate setting to assess how thermal conditions in rock interstices at the scale of an individual home range affect habitat suitability. For this setting, I predicted thermal conditions in rock interstices based on the modeled relationship between rock interstice and ambient temperatures measured in the field by using thermal data for the local-climate setting as the input. However, since the spatial distribution of rocky interstices was unknown for the whole study-area, I predicted the rock interstice thermal conditions for locations that I conducted the occupancy survey of the northern pika. Here, the assumption was that the thermal buffering effect by the rocky landforms exists universally in all sites surveyed since previous studies have shown this effect for most areas surveyed (Sakiyama et al., 2021; Sakiyama & García Molinos, 2024).

I then performed the distribution modeling analysis of the northern pika in Hokkaido using maximum entropy (MaxEnt; Phillips et al., 2006). Modeling was conducted separately for macroclimate and local-climate settings. After model tuning, the present habitat suitability was predicted for both the macroclimate and local-climate settings. The habitat suitability for the microclimate setting was predicted using the local-climate model by replacing the local-climate thermal data with rock interstice thermal data in the predictors. Thus, I obtained habitat suitability predictions for three settings and four GCMs.

Evaluation of the predictive accuracy

To evaluate the accuracy of SDMs to predict distributions over time, I first extracted the habitat suitability value at each site for each combination of prediction settings and GCMs. I then plotted these values with the observed occurrences and compared the predictions visually across settings.

I also evaluated the predictive accuracy quantitatively by computing the true positive rate (TPR) and false positive rate (FPR) for each prediction. I did this by binarizing the predictions to presence or absence along a moving threshold from 0 to 1 with 0.01 intervals and comparing the predicted occurrence with the observed occurrence. TPR represents the proportion of correctly predicted presence (i.e., proportion of predicted presence within observed presence), and FPR represents the proportion of falsely predicted presence (i.e., proportion of predicted presence within observed absence). Thus, a higher TPR is desired as it implies fewer omission errors (i.e., instances of misclassifying present sites as absent sites), while a lower FPR is desired implies fewer commission errors (i.e., instances of misclassifying absent sites as present sites). I further computed the area under the receiver operator characteristic curve (AUC), which takes both TPR and FPR equally into account to evaluate the overall predictive accuracy. An AUC value can range from 0 to 1 and values translate to: $AUC < 0.5$ as no predictive ability, $0.5 < AUC < 0.6$ as fail, $0.6 < AUC < 0.7$ as poor, $0.7 < AUC < 0.8$ as fair, $0.8 < AUC < 0.9$ as good, and $0.9 < AUC$ as excellent (Araújo et al., 2005). After computation, TPR, FPR, and AUC values were compared across predictions.

Results

Within the 74 sites surveyed during 2021–2023, I detected the presence of the northern pika at 54 sites (73.0 %). The other 20 sites were considered absent sites since I could not detect presence despite surveying multiple times. Absent sites were found all from low- to mid-elevations, spanning a wide elevation of 60 to 1,550 m (Fig. 6-1).

As reported in Chapter 5, mean summer temperature was the most important factor affecting the distribution of the northern pika, which exhibited a negative influence on the occurrence probability in both the macroclimate and local-climate models. Consequently, the predicted pattern in habitat suitability was relatively similar between the macroclimate-based and local-climate based predictions, with higher elevations predicted to be suitable areas. However, the predicted habitat suitability was heterogenous in the local-scale model because it reflected the complex terrain (Fig. 5-2; 5-4 in Chapter 5). As I incorporated rock-interstice microclimate into the local-climate model, the predicted habitat suitability rose from the local-climate prediction at most parts of the study area. The increase in the habitat suitability varied over space, but it was more prominent in low- to mid-elevations than in higher elevations (Fig. 5-4 in Chapter 5).

The habitat suitability at the survey sites varied among the prediction settings, but it was generally higher at present sites than at absent sites (Fig. 6-2). Comparing the habitat suitability among the prediction settings for a given site, I detected various patterns (Fig. 6-2). First, between the macroclimate- and local-climate based predictions, the former was slightly higher than the latter at many sites. However, there were some sites with similar or higher habitat suitability in the local-climate based prediction than the macroclimate-based prediction. Second, between the local-climate and microclimate-based predictions, the habitat suitability was generally higher in the latter, reflecting the aforementioned increase in suitability associated with incorporation of microclimates. Still, unexpectedly there were a few sites that exhibited lower habitat suitability in the microclimate-based prediction. Third, between the macroclimate and microclimate-based predictions, the latter was higher in most of the sites. Thus, the lines connecting the habitat suitability for each site exhibited a slight V-shape at many sites, plummeting in the local-climate based prediction (Fig. 6-2).

Quantitative evaluation of predictive accuracy based on TPR and FPR revealed that the microclimate setting generally had the highest values for both measures across the moving threshold (Fig. 6-3). Both TPR and FPR responded similarly in the macroclimate and local-climate settings, but the latter generally had lower values in both measures (Fig. 6-3). AUC was the highest in the local-climate setting (mean ± SD: 0.88 ± 0.01), but the macroclimate setting also had a similarly high AUC (0.87 ± 0.01) (Table 6-1; Fig. 6-4). Conversely, AUC was the lowest in the microclimate setting (0.84 ± 0.02), although the difference was relatively small with the other two settings. Thus, all settings performed well in predicting the species distribution over time with relatively small differences.

Discussion

In this study, I evaluated whether ongoing changes in the northern pika distribution are predicted accurately by SDMs incorporating fine-scale climates. The results indeed show that incorporation of downscaled climate as well as microclimate provide accurate predictions of the current distribution, as indicated by high AUC values. However, these AUC values were comparable to that of the traditional predictions based on macroclimate. This suggests that the overall accuracy was not necessarily improved significantly by incorporating fine-scale climates into species distribution predictions. Nevertheless, I detected various responses for TPR and FPR among prediction settings. The microclimate setting exhibited highest TPR and FPR values, suggesting that it is highly accurate in reducing omission errors although with the cost of increasing commission errors. Conversely, the local-climate setting generally had lower values for both TPR and FPR than the macroclimate setting across the binarization threshold, suggesting that the local-climate model is more accurate in reducing commission errors than the macroclimate model although with the cost of increasing omission errors. These patterns imply that fine-scale predictions vary in their strengths from the traditional, macroclimate-based predictions either by reducing omission or commission errors.

While AUC balances commission and omission errors equally, the ideal balance (i.e., relative importance) between these errors has been a matter of debate (Araújo & Peterson, 2012; Lobo et al., 2008). This is because the implications of balancing these errors vary strongly among contexts and objectives (Guisan et al., 2013, 2017; Peterson, 2006). For instance, in a general case of selecting reserves for species conservation, commission errors lead to conserving areas where species are not found while omission errors lead to smaller arears than required for conservation, thus indicating a trade-off (Rondinini et al., 2006). Nevertheless, commission error has traditionally been considered unacceptable because resources available for conservation are often limited (Araújo & Peterson, 2012), and consequently, applications of SDMs in conservation planning has been relatively conservative (Araújo et al., 2011). In the context of climate change impact assessments, however, there are perspectives that warrant overall balance between the commission and omission errors (Peterson, 2006), while others think consensus has yet been reached (Araújo & Peterson, 2012). In this study or other studies developing fine-scale SDMs, the initial motivation of microclimate incorporation was to prevent the models from overestimating species range shifts (e.g., Maclean & Early, 2023). Considering that this corresponds to weighing more the reduction of omission errors, I believe that the incorporating microclimates into species distribution predictions was successful as it reduced these errors by predicting present sites with higher habitat suitability. This highlights the usefulness of incorporating microclimates into species distribution predictions to avoid neglecting extant populations. Here, microclimate increased the habitat suitability effectively because, while temperature exerted a strongest negative effect on the northern pika distribution, buffered temperatures in rock interstices facilitated providing hospitable conditions than other settings. Conversely, local-climate based prediction failed to reduce the omission error as it generally predicted present sites with lower habitat suitability, as have been discussed in Chapter 5. This suggests that just incorporating downscaled climates is not enough to prevent the overestimation, possibly because it is simply a fine-scale representation of the macroclimate and thus does not include any particular aspect that contributes to species persistence, such as the thermal buffering effect. However, its strength lies in minimizing both the omission and commission errors, as it exhibited the highest AUC. Thus, relying on the local-climate based prediction will contribute to balancing maximizing conservation areas and minimizing redundant resource use.

Instead, the microclimate-based prediction still requires care for practical use, such as in conservation planning, because it tended to incorporate more commission errors as indicated by the high FPR values. That is, most sites experienced an increase in habitat suitability owing to the thermal buffering effect in rock interstices, but its beneficial effect resulted in predicting the presence of the northern pika even at absent sites. I believe that this error could be minimized in practice by utilizing additional knowledge gained in previous studies, such as consideration on the importance of habitat size (Chapter 3) or microhabitat availability (Chapter 4). For instance, even though any area with rocky landform will be predicted to have higher habitat suitability based on the microclimate setting, a posterior assessment on if there is enough habitat size or microhabitat availability will hint its habitat functionality. As mentioned before, this step will likely lead to the conservative use of the predictions in actual conservation (Araújo et al., 2011).

In conclusion, this study showed that incorporation of microclimates into species distribution predictions results in obtaining predictions that do not overestimate the distribution changes, which was the typical case in traditional predictions. However, this raises another issue of considering the ideal balance between omission and commission errors. It is therefore imperative that conservation practitioners and modelers share the contexts and objectives of using species distribution predictions in practical settings to optimize conservation planning under climate change (Guisan et al., 2013). I also believe that the validation framework that I used in this study, to assess the predictive accuracy of species distribution predictions over time, is essential for understanding the advantages and disadvantages of applying the predictions for practical use.

Table 6-1. Mean and SD of the AUC for each prediction setting.

Model	Mean AUC	SD
Macroclimate	0.87	0.01
Local-climate	0.88	0.01
Microclimate	0.84	0.02

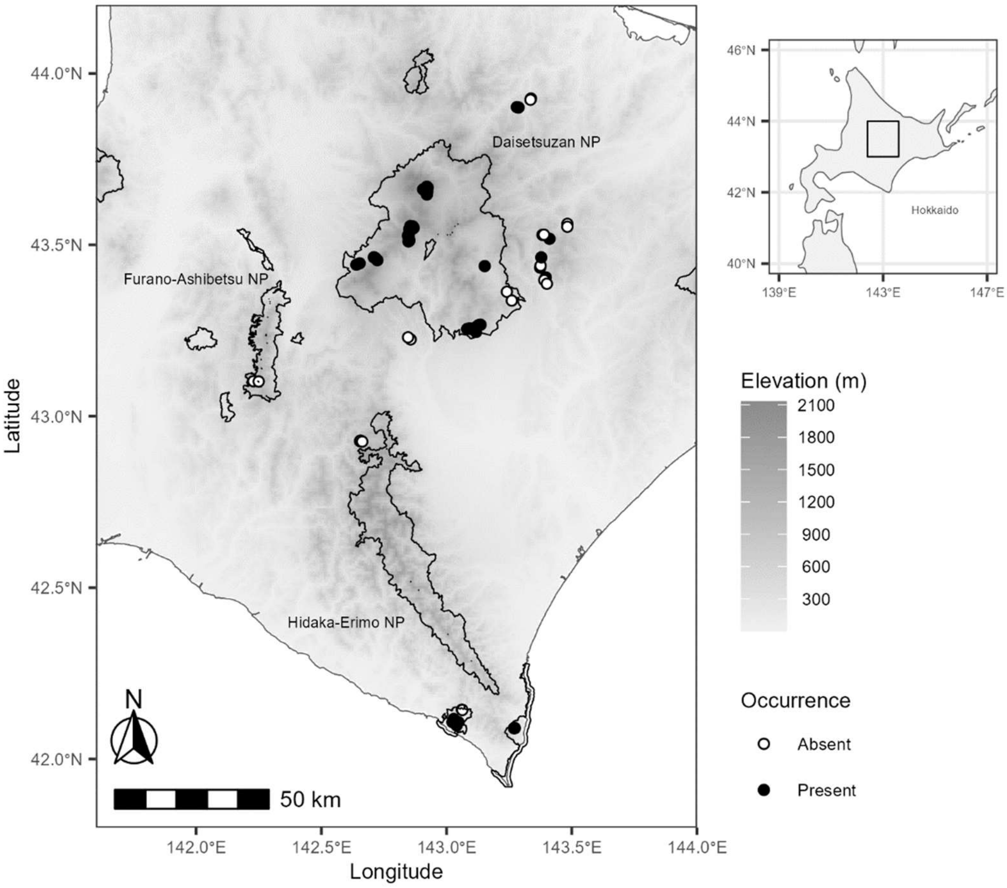


Fig. 6-1. Occurrence data used to validate the species distribution model predictions. This data was obtained in the occupancy surveys conducted in Chapters 3 and 4.

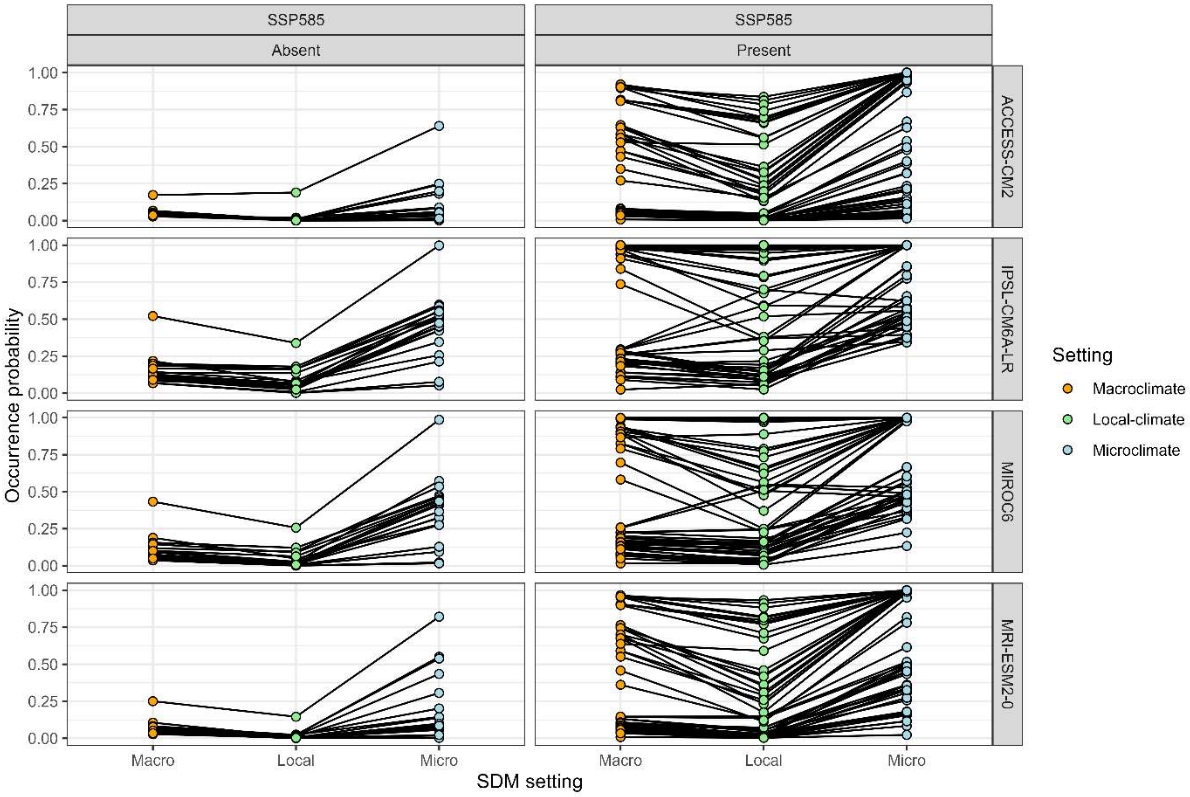


Fig. 6-2. Predicted occurrence probability at validation points. Each panel corresponds to differences in the observed occurrence at the points (present or absent) and the GCMs used for the prediction. The point colors represent the difference in the prediction settings (orange = macroclimate-based, green = local-climate based, blue = microclimate-based).

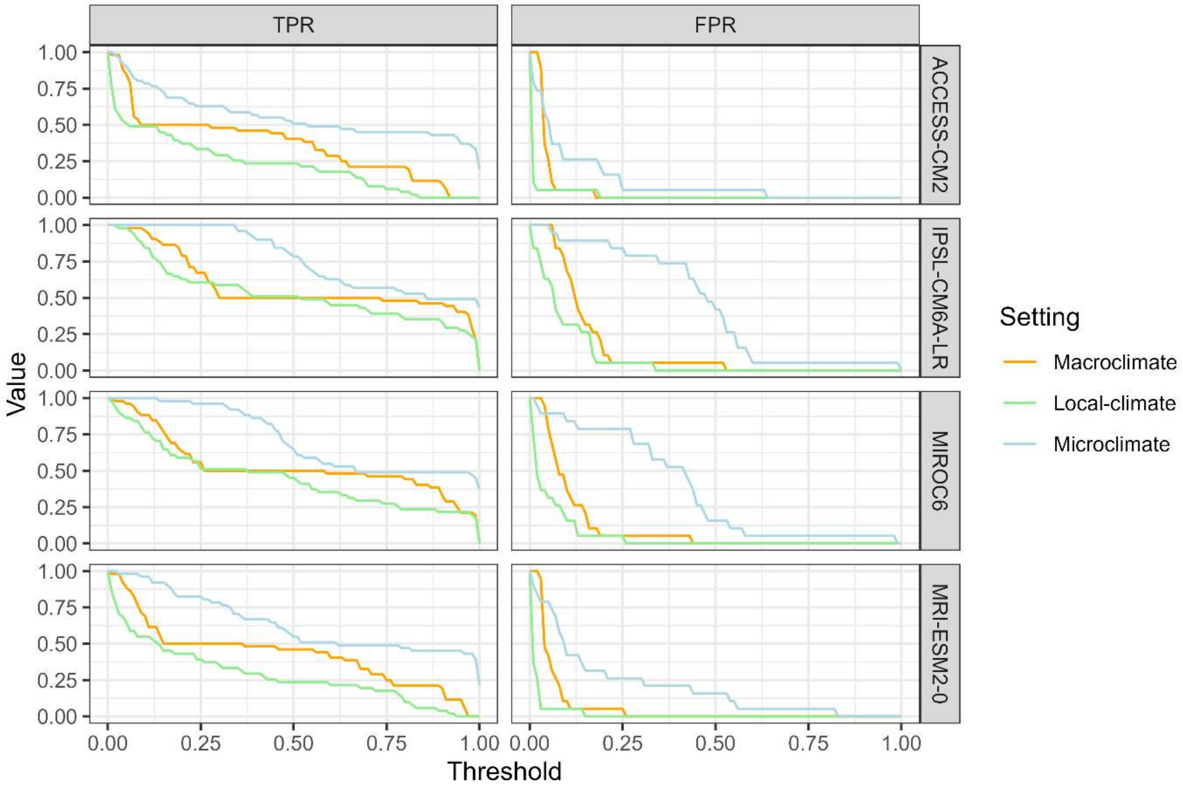


Fig. 6-3. Validation plot indicating the true positive rate (left) and false positive rate (rate) of the predictions based on four GCMs. Line colors represent the difference in the prediction settings (orange = macroclimate-based, green = local-climate based, blue = microclimate-based).

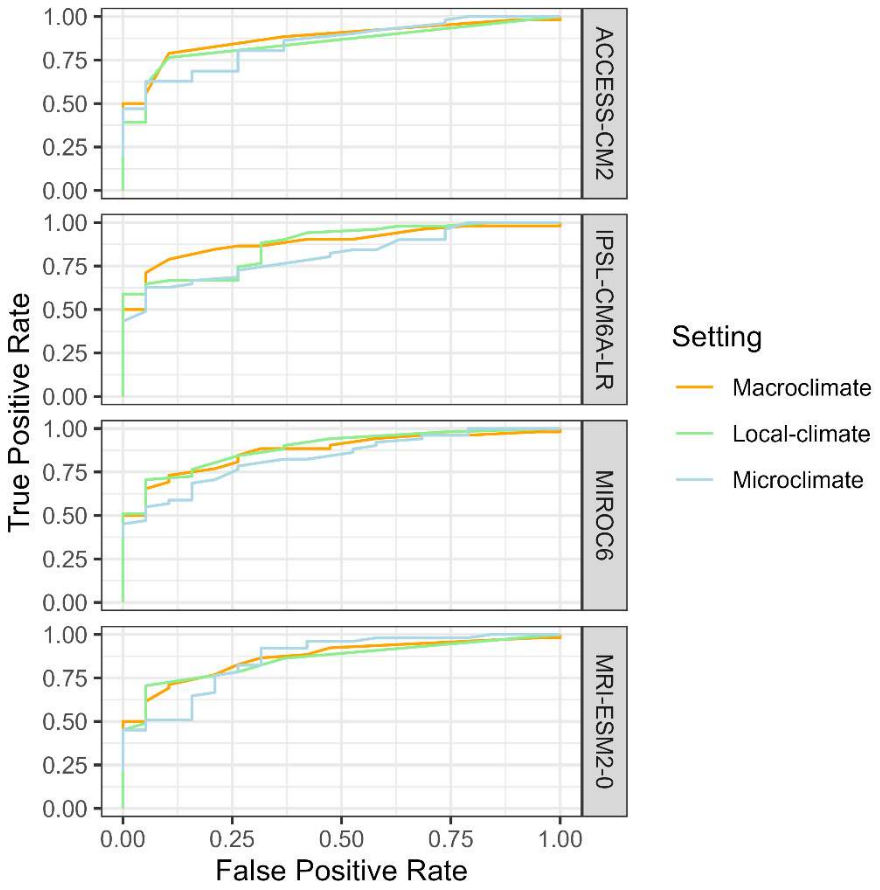


Fig. 6-4. Validation plot indicating the receiver operator curve. AUC is the area under this curve and thus represents the overall accuracy of the prediction by considering the balance between true positive rate and false positive rate. The four panels correspond to the prediction provided for each GCM and line colors represent the difference in the prediction settings (orange = macroclimate-based, green = local-climate based, blue = microclimate-based).

Chapter 7: General Discussion

The importance of microclimate in species range dynamics under climate change is increasingly being discussed as more studies indicate instances of species persistence in warmer regions (Chen et al., 2011; Lenoir et al., 2020). The potential mechanism is that individuals of a given species experience thermal conditions existing locally in their habitats and therefore might not be affected by the temperature increase occurring at larger spatial scales as negatively as expected (Moritz & Agudo, 2013). This suggests that traditional predictions of species range shifts based solely on coarse-scale climate data could oversimplify the picture of climate change impacts on species distributions and thus be problematic for conservation planning (Potter et al., 2013). Accordingly, environmental features generating thermal conditions that are locally buffered or decoupled from the regional scale trends are expected to be a key refugial resource for conservation (Morelli et al., 2016, 2020). However, evidence indicating the influence of microclimates on species range dynamics remains scarce in the literature. In this dissertation, I identified and addressed knowledge gaps regarding the role of microclimates in maintaining species distributions using the northern pika as the subject species since cool microclimates exist in its rocky habitats. In particular, I aimed to 1) expand the time frame of existing microclimate ecology studies, 2) understand the relative importance of microclimates with other environmental factors, and 3) evaluate the predictive accuracy of SDMs incorporating microclimates (Fig. 7-1 top). Here, I review the main findings of this study.

First, habitat resurveys revealed that a large proportion of the northern pika distribution has changed from the past at low- to mid-elevations (Chapter 3; Fig. 7-1 left). This result suggests that the Hokkaido regional population of the northern pika is becoming unstable under rising temperatures. Importantly, however, persistence of some local populations was observed in these warmer regions. As habitat size was found positively correlated with persistence, it is plausible that higher environmental heterogeneity in larger habitats, such as variations in thermal conditions, is important for maintaining the northern pika distribution over time.

Second, by measuring habitat thermal conditions along a wide elevational gradient (350–2,200 m), I evaluated their relationships with the northern pika occupancy at two nested spatial scales (Chapter 4; Fig. 7-1 middle). Analyses showed that rock interstice microclimate was not a significant factor at both the whole-distribution and range-edge (i.e., low-elevations) scale. Instead, other factors such as ambient thermal condition and microhabitat availability influenced occupancy at the whole-distribution scale, whereas presence of human land-use was strongly important at the range edge. Given thermal measurements did indicate that rock interstices effectively buffered ambient thermal conditions, my results suggest that the refugial effect of microclimates at the trailing edge could be overridden by other environmental factors (i.e., human land transformation) due to spatial hierarchy.

Third, Chapter 5 demonstrated how developing fine-scale SDMs led to distinct predictions from traditional, coarse-scale models through the incorporation of the thermal buffering effect of rock interstices that generally increased the predicted habitat suitability for the low- to mid-elevation areas (Fig. 7-1 right). Further, it was predicted that future distribution changes may be smaller if the northern pika could effectively utilize the rock interstice microclimate to reduce the thermal stress from rising temperatures through behavioral thermoregulation. Moreover, in Chapter 6, the validation analysis, which compared the predicted and observed distributions of the northern pika, indicated that incorporating microclimates led to accurate predictions of the current distribution of present sites as the omission error was the smallest (Fig. 7-1 right). This suggests that accounting for microclimate in SDMs provides more realistic predictions than that based on coarse scales or on ambient thermal conditions as overestimation of species range shifts was prevented.

Taken together, this dissertation provides evidence that complex topographies have the potential to maintain species distributions at the trailing edge under warming trends, but the refugial effect of microclimates is likely context-dependent given the influences of other environmental factors. Nonetheless, this study highlights the importance of considering the contribution of microclimates when predicting future range shifts under climate change to avoid overlooking potential suitable habitats. In this final chapter, I first discuss in what kind of situations microclimate will likely play an important role in maintaining species distribution. I then consider its implications for planning species conservation under climate change.

In what kind of situations will microclimate be effective for species persistence?

In Chapter 4, thermal measurements in northern pika habitats showed that rocky landforms harbor cool microclimates in rock interstices as ambient thermal conditions were buffered by over two degrees. However, occupancy analyses showed that the northern pika responded to ambient thermal conditions and microhabitat availability at the whole-distribution scale and human land-use at the range-edge scale, thus lacking evidence that microclimate supports occupancy. Despite these results, the non-uniform distribution change from the past at low- to mid-elevations in Chapter 3 resembles cases reported in previous studies, where local populations are persisting in unsuitable regions even under negative influences of climate (Chen et al., 2011; Moritz et al., 2008). Thus, in this section, I discuss in what kind of situations microclimate will be effective for species persistence.

This discussion first requires revisiting the spatial hierarchy in the relationship between species distribution and environment. In theory, different environmental factors operate to affect species distributions at different spatial scales. In other words, environmental factors operating at larger spatial scales are generally higher in the hierarchical level and environmental factors at smaller scales will operate given the environmental conditions at higher levels (Pearson & Dawson, 2003; Willis & Whittaker, 2002). Thus, for instance, it has been explained that climate is a dominant factor at larger scales (e.g., regional, continental, and global scales), while land-use will become more important at smaller scales (local, landscape, and regional scales) and microclimate may become more important at much smaller scales (micro, site, and local scales) (Pearson & Dawson, 2003). Applying this hierarchical structure to the results from Chapter 4, the extent differed between the whole-distribution and range-edge scale analyses while the resolution was the same. The whole-distribution and range-edge scales can therefore be regarded as assessing the distribution at regional-scale and landscape-scale, respectively. And as expected from the hierarchical theory, the result showed that actual regional thermal conditions (i.e., mean ambient temperature) explained well the whole-scale distribution. While the preference of the northern pika towards cooler conditions indeed reflects well their physiological constraints to warmer conditions, another possible interpretation is that the constraint by the ambient air was generally larger than the potential benefits by the rock interstice microclimate. I believe that this explanation by ambient temperature is robust as the analytical result from the habitat resurvey in Chapter 3 also indicated similar responses.

Then at the range-edge scale, the rock interstice microclimate was hypothesized to be a substitute of the thermal conditions preferred at the regional-scale (i.e., cooler conditions) and thus contribute to inhabiting unsuitable regions, although it occurs at a very small-scale (i.e., site scale) in reality. However, human land-use indicated an overwhelming effect, rejecting the hypothesis that microclimate supports local populations in the warmer, unsuitable regions by its buffering effect. Here, the important finding is that rock interstice microclimate did not function effectively as a substitute for environmental conditions operating at larger spatial scales as its potential benefit was possibly reduced by the overriding effect of another environmental factor (i.e., human land-use). Since human land-use operates strongly at the landscape scale (Pearson & Dawson, 2003), my results suggest that the effectiveness of microclimate at the trailing edge will likely depend on the habitat suitability based on higher hierarchical levels. In other words, the refugial effect of microclimate will likely be observed in landscapes with suitable conditions, such as in areas with less modification. While the limited number of study sites in Chapter 4 precluded analyzing this relationship in the northern pika, further studies are required to elucidate the factors underlying low-elevation populations. Moreover, it is imperative to obtain a general understanding of where microclimate fits in the hierarchical structure of various environmental factors and operate to support local populations in unsuitable regions by conducting investigations in other species. Importantly, Chapters 3 and 4 indicated the importance of habitat size or microhabitat availability on occupancy, respectively. This suggests the role of local-scale environmental heterogeneity in driving species distributions and it is possible that the higher thermal heterogeneity in larger habitats supported persistence of local populations. However, this study is limited in this aspect as thermal measurements were conducted only at one point for both the ambient air and rock interstice microclimate within each site due to limited resources. Thus, it will be interesting to assess the link between the habitat-scale microclimatic variability and occupancy in unsuitable regions in future research.

However, I note that it is also possible that microclimate was not related to species distribution at all for the northern pika at all scales. The lack of support by microclimates on species distribution have also been reported in previous studies (e.g., Kim et al., 2022). Yet, there are still few studies reporting this aspect, possibly due to a publication bias towards reporting the positive aspects of microclimates on species distributions. Thus, the situations where the support by microclimate is limited in driving species distribution also requires more discussion to characterize its importance. In case of this study, the limited microclimate availability at the landscape-scale may have affected the chances for the northern pika to inhabit the unsuitable regions successfully. This is because rocky landform patches were normally smaller than 10,000 m^2 (100 m x 100 m; Chapter 3) and occurred in low densities, thus covering only a small proportion of the landscape particularly in the lower elevations as forest ground and vegetation covered other proportions. This limited microclimate availability is in high contrast with studies assessing the effects of microclimates created by tree canopies in forest ecosystems (e.g., Frey et al., 2016), as its availability is seemingly high throughout the study area. Moreover, species traits could have influenced the species distribution in unsuitable regions. For instance, the ecological aspects regarding the movement of the northern pika may have affected its distribution, since movement is regarded as one of the fundamental factors affecting species distributions (Soberón & Nakamura, 2009). This is because the pika is a sedentary animal once it establishes its home range (Kawamichi, 1970), and the large-scale movements occur only during the natal dispersal event (Peacock, 1997). However, given that the dispersers move only within the natal habitat (Smith & Ivins, 1983) or relatively short distances (300m; Smith, 1974), and that the colonization process is more affected by the saturation status of the habitat patch rather than the habitat quality, the effect of microclimate on the spatial distribution of the pika may not be that large. Other traits of the northern pika, such as the strict habitat specialization towards rocky landforms, small number of litters, could also be related to the low occupancy observed in unsuitable regions. These aspects of the northern pika are in stark contrast to previous studies focusing on species with relatively higher movement abilities and/or higher reproduction abilities, such as in butterflies (Suggitt et al., 2015) and birds (Frey et al., 2016; Kim et al., 2022), to assess the importance of microclimates. Therefore, the effects of microclimate on species distribution will likely be more evident in systems where the microclimate availability is generally higher across the landscape, and the focal species have traits that facilitate them to access and utilize the microclimates more effectively. A viewpoint integrating these aspects on microclimate availability and species traits into a "microclimate ecological system" should be the key for future studies.

Implications for conservation under climate change

This study advanced the knowledge on the current population status of the northern pika in Hokkaido and therefore has general implications for their conservation. Importantly, the populations in higher elevations were stable, but those in low- to mid-elevations were suggested to be unstable. The observed change is in line with many of the climate change impacts observed for other species, as rising temperatures are affecting the local populations in warmer areas (Moritz et al., 2008). Establishing a continuous monitoring system is therefore needed to understand further changes. As higher elevations were predicted to support the species towards the future, these areas will continue to be important areas for the northern pika conservation. Indeed, most of the higher elevations in Hokkaido are already designated as protected areas with strong protection schemes, and therefore, these areas will be promising for persistence of the northern pika.

In contrast, conservation of populations in lower elevations is more problematic. This is because most of the land lacks protection despite the negative influence of human activities on the northern pika distribution demonstrated here (Chapter 4). Although microclimate is, in theory, anticipated to maintain species persistence in unsuitable regions or slow down the ongoing changes in species distribution under climate change, the direct negative impact by human activities suggests that human activities and land conversions in natural landscapes may exacerbate climate change impacts on local population by reducing the potential for microrefugia formation. Therefore, extant rocky patches providing cool microclimates in less modified landscapes should be first prioritized for conservation by considering protection at the landscape-scale. The efficacy of this approach is supported by the result in Chapter 3 in which protected areas were found to be important for the persistence of the northern pika. In highly modified landscapes, I believe that restoring landscape permeability should be a conservation priority if possible. Moreover, a factor largely absent from the current protection schemes is the viewpoint of acknowledging geodiversity and topographical complexity (Badgley et al., 2017; Morelli et al., 2016, 2020). Since these features are foundations of environmental heterogeneity, such as the provision of microclimates, laws restricting land conversions for human land-use should incorporate these elements for protection of biodiversity under climate change.

In this endeavor of protecting the geodiversity and topographical complexity, however, the large challenge still will be to map the geological and topographical features accurately at a scale required for biodiversity conservation (Amatulli et al., 2018). For instance, high-resolution spatial data of rocky landforms in current Japanese database is still limited, as the geological map is created at 1:200,000 (Geological Survey of Japan, National Institute of Advanced Industrial Science and Technology, 2017). Moreover, despite the topographical maps being created at high-resolutions at 1:25,000 (Geospatial Information Authority of Japan, 2023), their depiction of rocky landforms is relatively inconsistent as only those at higher elevations are depicted. In this light, remote sensing techniques may offer promising results (Zellweger et al., 2019), as it facilitates identification of rocky landforms from aerial images (Pu et al., 2021) as well as complex thermal measurements (Hoffrén & García, 2023).

While coarse-scale models often overestimate the change in distribution over time, this study also showed that incorporating microclimate into predictions enhanced the predictive accuracy by reducing omission errors. This was plausibly because accounting for environmental conditions occurring at fine scales enabled considering the possibilities that the northern pika thermoregulate through their behavior, as have been documented well based on field observations (Onoyama, 1991; Smith et al., 2016). I believe that this result has important implications for conservation because microclimate-based predictions will facilitate conservation planning that considers species behavioral adaptations under climate change. Compared to predictions based solely on ambient conditions, microclimate-based predictions indicated that more suitable habitats exist towards lower elevations and that such habitats may maintain local populations longer. This result advocates for expanding conservation targets from traditional approaches in order to avoid overlooking populations that may persist under warming conditions. For instance, accounting for microclimates expanded the predictions to include low- to mid-elevations as suitable areas, although such elevations are viewed hostile based on the traditional approach. Considering the strong assumptions of the microclimate-based prediction, validating the behavioral adaptation aspect based on the monitoring data may also become necessary. However, as discussed in Chapter 6, the use of species distribution model predictions largely depends on the contexts and objectives of conservation. Discussions on how we can protect species from climate change impacts are still scarce and it is imperative that we urgently establish more practical plans for future conservation.

In conclusion, this dissertation assessed the role of microclimate in maintaining species distributions. Although the direct assessment of its role did not clearly indicate its expected importance due to the influence of other environmental factors, this result point towards the fact that microclimates by themselves may not be sufficient to maintain local population in unsuitable regions in the face of climate change and other cooccurring human environmental impacts. However, this dissertation conveys an important message here of the importance of exploring and understanding the role of microclimate in the wider context of other environmental factors operating across spatial scales to ultimately being able to enhance and promote those situations where microclimates are more effective through appropriate conservation management practices.

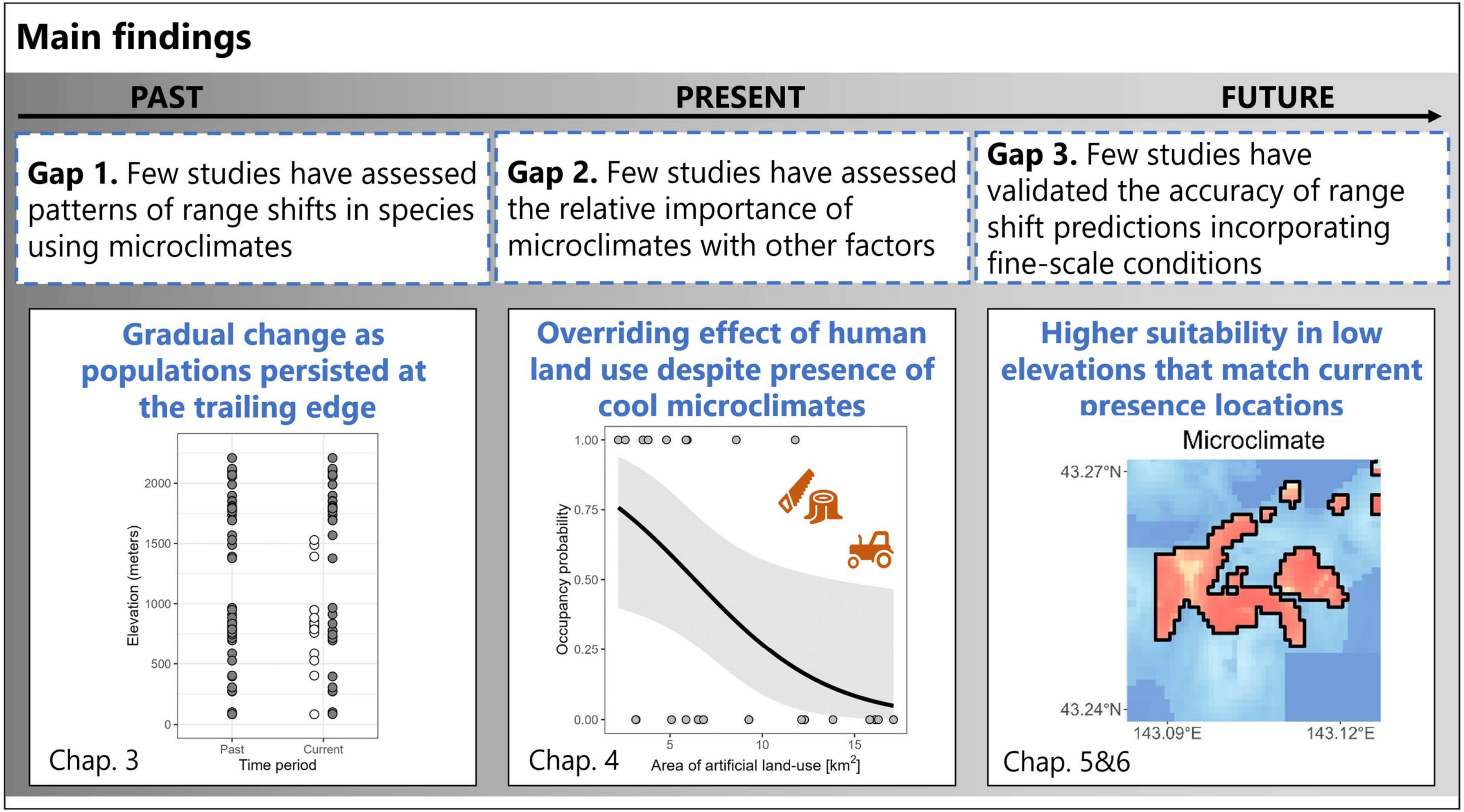


Fig. 7-1 Main findings from this study. (Top) Three knowledge gaps regarding the importance of microclimates in maintaining species distribution under climate change were identified in Chapter 1 General Introduction. (Left) In Chapter 3, I compared the current occupancy of the

northern pika in Hokkaido with historical records and showed that its distribution is changing in low- to mid-elevations. Despite this trend, many local populations were also found persisting in such warm regions. (Middle) In Chapter 4, although I expected the importance of cool microclimate for the trailing edge occupancy, it was best explained by the negative effect of human land use. This suggests that the refugial effect of microclimate at the trailing edge could be overridden by other factors due to spatial hierarchy. (Right) In Chapters 5 and 6, I developed fine-scale species distribution models (SDMs) for the northern pika by incorporating rock interstice microclimates into predictions. By validating range shift predictions with occurrence survey results, I showed that fine-scale SDMs are highly accurate in predicting current presence locations since some of the presence locations found in warmer regions were predicted with higher suitability than other predictions. This suggests that fine-scale SDMs have the potential to avoid overestimating range shifts and thus overlooking persisting populations at the trailing edge.

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Supplementary Materials

Chapter 2: 1 Table (S2-1), 5 Figures (S2-1 – S2-5), and Extended Methods S2

Chapter 3: 2 Tables (S3-1 – S3-2) and 1 Figure (S3-1)

Chapter 4: 3 Tables (S4-1 – S4-3) and 6 Figures (S4-1 – S4-6)

Chapter 5: 2 Tables (S5-1 – S5-2), 10 Figures (S5-1 – S5-10), and Extended Methods S5

Supplementary Materials for Chapter 2

Table S2-1. Detection results of the northern pika upon arrival at the site, after auditory observation, and after playback. “0” and “1” indicate absence and presence, respectively

Site	**Elevation (m)**	**Class**	**Upon arrival**			**Auditory observation**			**Playback**			**True occupancy status**
			Jul	**Aug**	**Sep**	**Jul**	**Aug**	**Sep**	**Jul**	**Aug**	**Sep**	
1	350	lower	0	0	0	0	0	0	0	0	0	0
2	350	lower	0	0	0	0	0	0	0	0	0	0
3	450	lower	0	0	0	0	0	0	0	0	0	0
4	450	lower	0	0	0	0	0	0	0	0	0	0
5	470	lower	0	0	0	0	1	0	0	1	1	1
6	510	lower	0	0	0	0	0	0	0	0	0	0
7	560	lower	0	1	0	1	1	1	1	1	1	1
8	590	lower	0	1	1	0	1	1	0	1	1	1
9	650	lower	0	0	0	0	0	0	0	0	0	0
10	900	higher	1	1	0	1	1	1	1	1	1	1
11	1,010	higher	1	1	1	1	1	1	1	1	1	1
12	1,010	higher	1	1	0	1	1	1	1	1	1	1
13	1,150	higher	0	1	1	1	1	1	1	1	1	1
14	1,160	higher	1	1	1	1	1	1	1	1	1	1
15	1,190	higher	1	1	0	1	1	1	1	0	1	1
16	1,420	higher	1	1	0	1	1	1	1	1	1	1
17	2,100	higher	0	0	0	0	0	0	0	0	0	0
18	2,220	higher	1	1	1	1	1	1	0	1	1	1

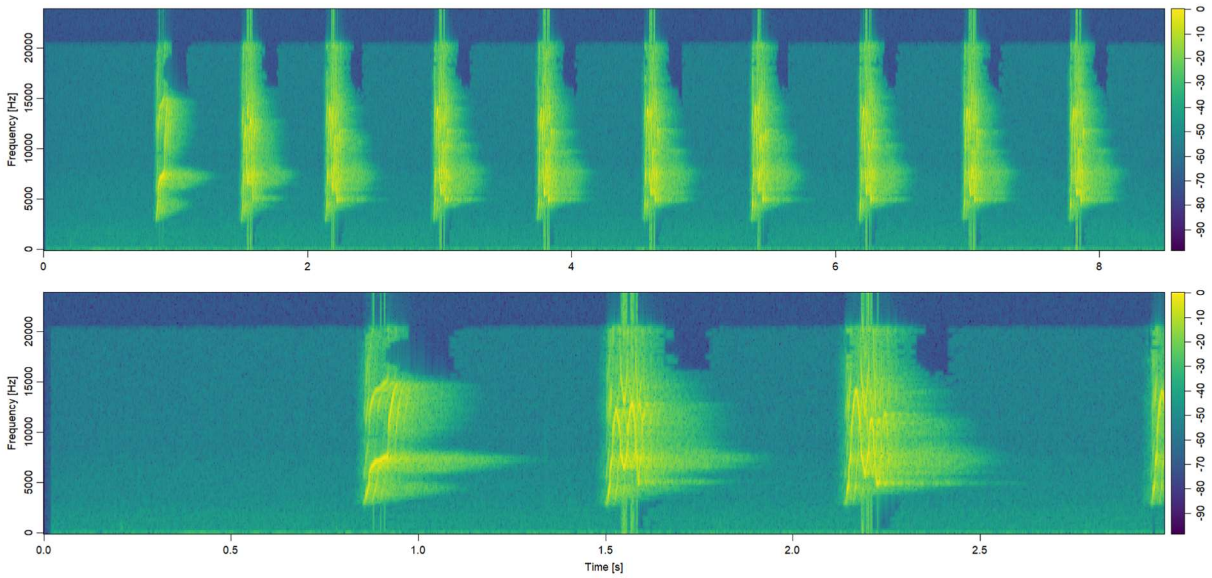


Fig. S2-1 Spectrographs of the audio file used in the playback survey, showing the whole length (top) and the first three seconds in zoom (bottom) of one “long call” or the “song” of the northern pika. Three repeats of this long call were broadcast from an audio speaker in the actual survey. The actual audio file used for the playback is archived as Supplementary Data SD2 in the published article of this research in Journal of Mammalogy.

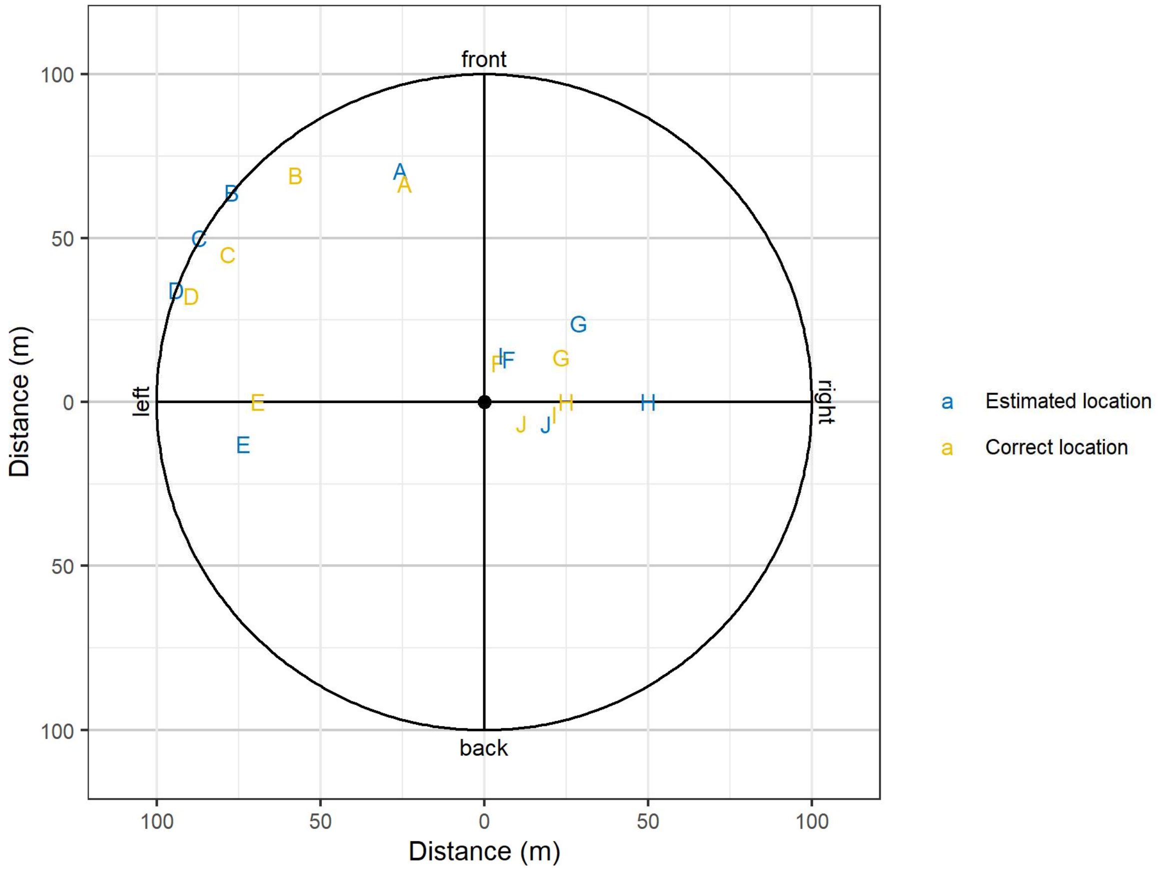


Fig. S2-2 I evaluated the auditory capability of the surveyor to detect the presence of the northern pika. Given that controlling the location of the animal vocalization is impossible, a survey assistant instead broadcast the northern pika vocalization from an audio speaker hidden at a random location in the talus patch and the surveyor estimated the distance and direction to the sound source from the site center. These records were then compared with the correct location of the sound source. The plot shows the estimated and correct location of the sound source, indicating that the surveyor was efficient in detecting the northern pika vocalization heard from various directions and distances.

Kawamichi 1981 **Study region: Hokkaido, Japan**	**Lissovsky 2005** **Study region: Russia**
Long call Explanation: Emitted in series, consisting of 4-16 cries. Given only by males in both reproductive and non-reproductive season. May function as territorial advertisement.	**Песня** English translation: song Explanation: Emitted in series, consisting of 1-23 modulated calls (модулированный сигнал). Used only by males for roll-calls and territory demonstrations.
Shown as A-D in Fig.1 in Kawamichi 1981	Shown as д (Sakhalin) in IV in Fig. 2 in Lissovsky 2005
Short call Explanation: Emitted singly or in series at irregular intervals. Produced by all individuals, irrespective of sex and age. Increase in the non-reproductive season and may be related with food storage.	**Предупреждающий об опасности сигнал** English translation: Alarm call Explanation: Emitted in series at irregular intervals, consisting of 1-20 cries. Produced both in response to an approaching danger: a person, a bird, or a rock fallen from a rock, and without any visible reason.
Shown as E-J in Fig.1 in Kawamichi 1981	Shown as г (Sakhalin) and д (Sikhote-Alin) in I in Fig. 1 in Lissovsky 2005
Trill Explanation: Produced by all individuals, irrespective of sex and age. Emitted singly when pikas quickly enter rock crevices.	**Стрекотание** English translation: Chirring, chirping Explanation: Consist of short chirp or a series of squeaks. Produced during a strong fright, when the animal unexpectedly collides with a human and rushes under rocks.
Shown as M and N in Fig.1 in Kawamichi 1981	Shown as a-г in V in Fig. 1 in Lissovsky 2005

Fig. S2-3 Matching vocalization types between Kawamichi (1981) and Lissovsky (2005).

Kawamichi 1981 **Study region: Hokkaido, Japan**	**Lissovsky 2005** **Study region: Russia**
No matching vocalization type.	**Трель** English translation: Trill Explanation: Produced both independently and in combination with other vocalization types. Used for territorial and mating demonstrations. Given only by males.
	Shown as a in IV in Fig. 2 in Lissovsky 2005
Submission call Explanation: Whining sound. Repeated several times. Used when an individual was approached or chased by another.	No matching vocalization type.
No spectrogram provided.	

Fig. S2-4 Unmatching vocalization types between Kawamichi (1981) and Lissovsky (2005).

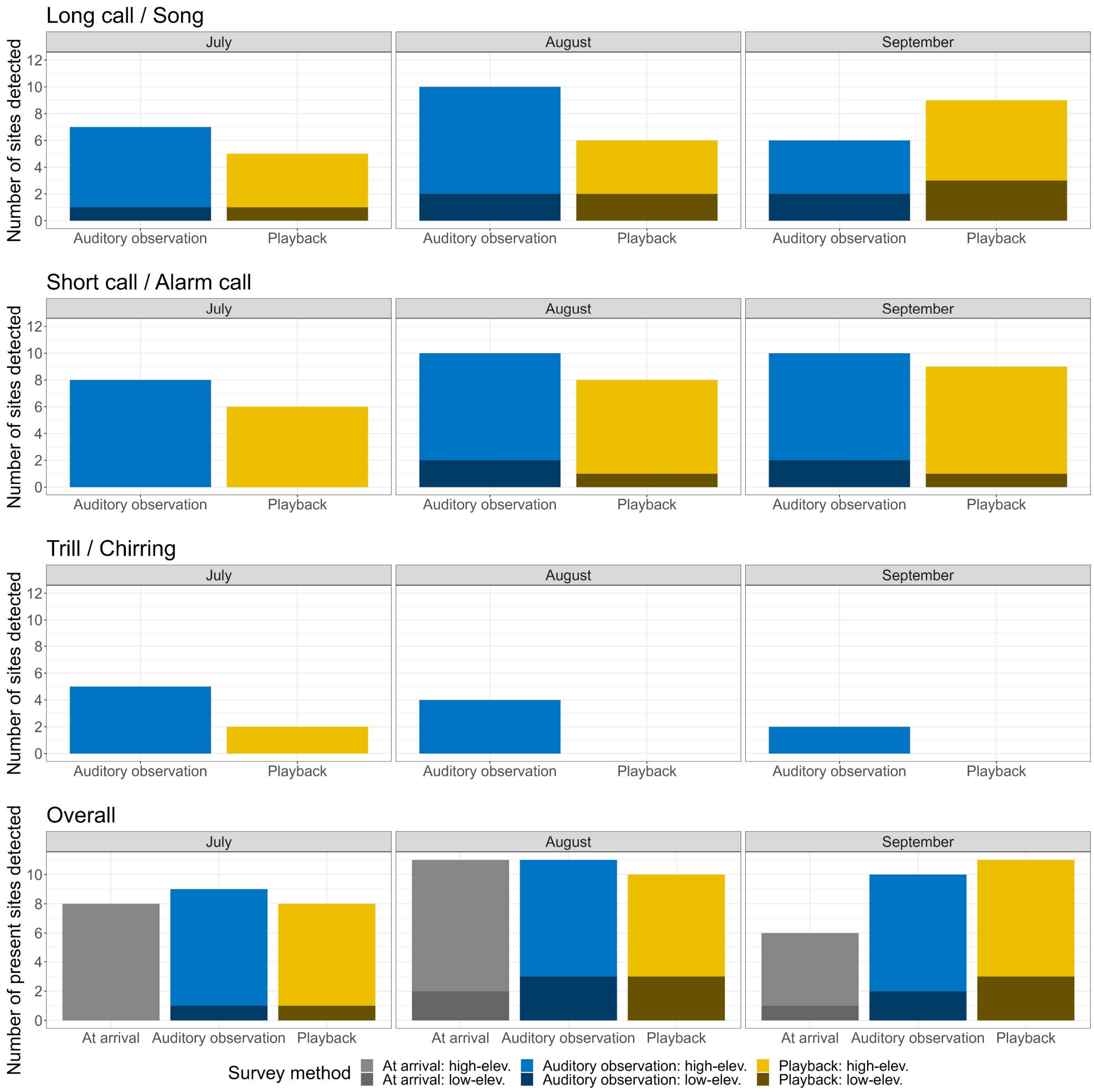


Fig. S2-5 Bar plots indicating the number of sites where each vocalization type was heard by using auditory observation (blue) and playback (yellow) methods. Overall result shows the number of present sites including detection at arrival (gray). Darker and lighter colors indicate lower- and higher-elevation sites, respectively.

Extended Methods S2

Various types of vocalizations are known to be used for specific functions in northern pikas, as described in detail in Kawamichi (1981) and Lissovsky (2005) (described in Russian). However, different terminologies were used between these literatures to describe the vocalization system of northern pikas. Moreover, since such terminological ambiguity remained untouched for unification, successive literature often refers to either terminological system for citation, which hampers comparison between studies. For example, Kojima et al. (2006) followed terminologies in Kawamichi (1981), whereas Lissovsky et al. (2021) followed Lissovsky (2005).

To reach a unified understanding of the vocalization system of the northern pika between Kawamichi (1981) and Lissovsky (2005), I referred to the characteristics and functions of each vocalization type and situations in which they are used for qualitative comparison. I also considered the spectrographs (= sonograms) of the vocalizations to enable quantitative comparison. Since large geographical variation are known to exist even within a same vocalization type in northern pikas (Lissovsky 2005; Lissovsky et al. 2021), I referred to geographically close population pairs between the literature for spectrograph comparison (i.e., Hokkaido, Japan in Kawamichi (1981) and Sakhalin and Sikhote-Alin, Russia in Lissovsky (2005)).

Various terms such as *long call*, *short call*, *trill*, and s*ubmission call* have been used in Kawamichi (1981) with reference to American pika literature. And *alarm call* (Предупреждающий об опасности сигнал), *song* (Песня), and *chirring* (Стрекотание) have been used in Russian terms in Lissovsky (2005), and *song* of the northern pika consist of vocalization elements such as the *trill* (Трель) and *modulated call* (модулированный сигнал) (Note that these Russian-English translations follow the English abstract of Lissovsky 2005). As I compared the qualitative and quantitative characteristics between the literature, I organized the vocalization terminology as follows (Fig. S2-3, S2-4): *long call* in Kawamichi (1981) matched with the *song* in Lissovsky (2005) because elements of the *long call* showed similar spectrographic shape of modulation with the *modulation call* of a *song* (W-shaped waves) and both are explained as being made by males only and for territorial demonstration; *short call* in the former matched with *alarm call* in the latter because both showed similar spectrographic shape (upward stroke) and are described as being emitted in single or multiple vocalizations with irregular intervals in response to an approaching danger or without any reason; *trill* in the former matched with *chirring* in the latter because both showed similar spectrographic shape (diminishing upward strokes) and are explained as being heard when the animal escapes into the rock under fright conditions. I could not obtain detailed information of function and spectrogram for *submission call* in Kawamichi (1981) and *trill* in Lissovsky (2005). The term *trill* was used differently between the literature, but I classified them as different vocalization types since the spectrographic shape and situation of their use were not resembling, suggesting that their use requires care (Lissovsky 2005).

Supplementary Materials for Chapter 3

Table S3-1. Correlation between model predictors.

Variable 1	**Variable 2**	***r***	***P***
Current mean temperature	Protection status	-0.590	< 0.001
Current mean temperature	Habitat size	-0.451	< 0.001
Habitat size	Protection status	0.532	< 0.001

Table. S3-2 Coefficient estimates of the selected models. Abbreviations correspond to Mean_temp = mean summer temperature, Protection = protection status, and Size = habitat size.

Model	Predictors	Estimate	SD	2.5 %	97.5 %	n_eff	Rhat
1	**Occupancy**						
	(Intercept)	0.444	1.240	-1.997	2.932	42,554	1
	Mean_temp	-1.570	1.020	-3.851	0.199	41,702	1
	Protectionyes	1.986	1.240	-0.292	4.625	52,992	1
	Size	2.479	1.200	0.457	5.197	36,373	1
	sigma[1|Area]	1.730	1.180	0.129	4.549	12,085	1
	Detection						
	(Intercept)	1.350	0.230	0.914	1.810	68,940	1
2	**Occupancy**						
	(Intercept)	1.320	1.220	-1.164	3.667	26,663	1
	Mean_temp	-1.990	1.060	-4.351	-0.149	40,338	1
	Size	2.290	1.030	0.519	4.557	36,745	1
	sigma[1|Area]	2.140	1.250	0.215	5.071	13,099	1
	Detection						
	(Intercept)	1.360	0.228	0.926	1.820	65,502	1
3	**Occupancy**						
	(Intercept)	-0.457	1.260	-3.010	1.993	50,497	1
	Mean_temp	-2.069	1.190	-4.680	0.016	40,660	1
	Protectionyes	2.167	1.250	-0.090	4.833	51,485	1
	sigma[1|Area]	2.873	1.210	1.060	5.775	29,904	1
	Detection						
	(Intercept)	1.370	0.230	0.926	1.830	80,085	1

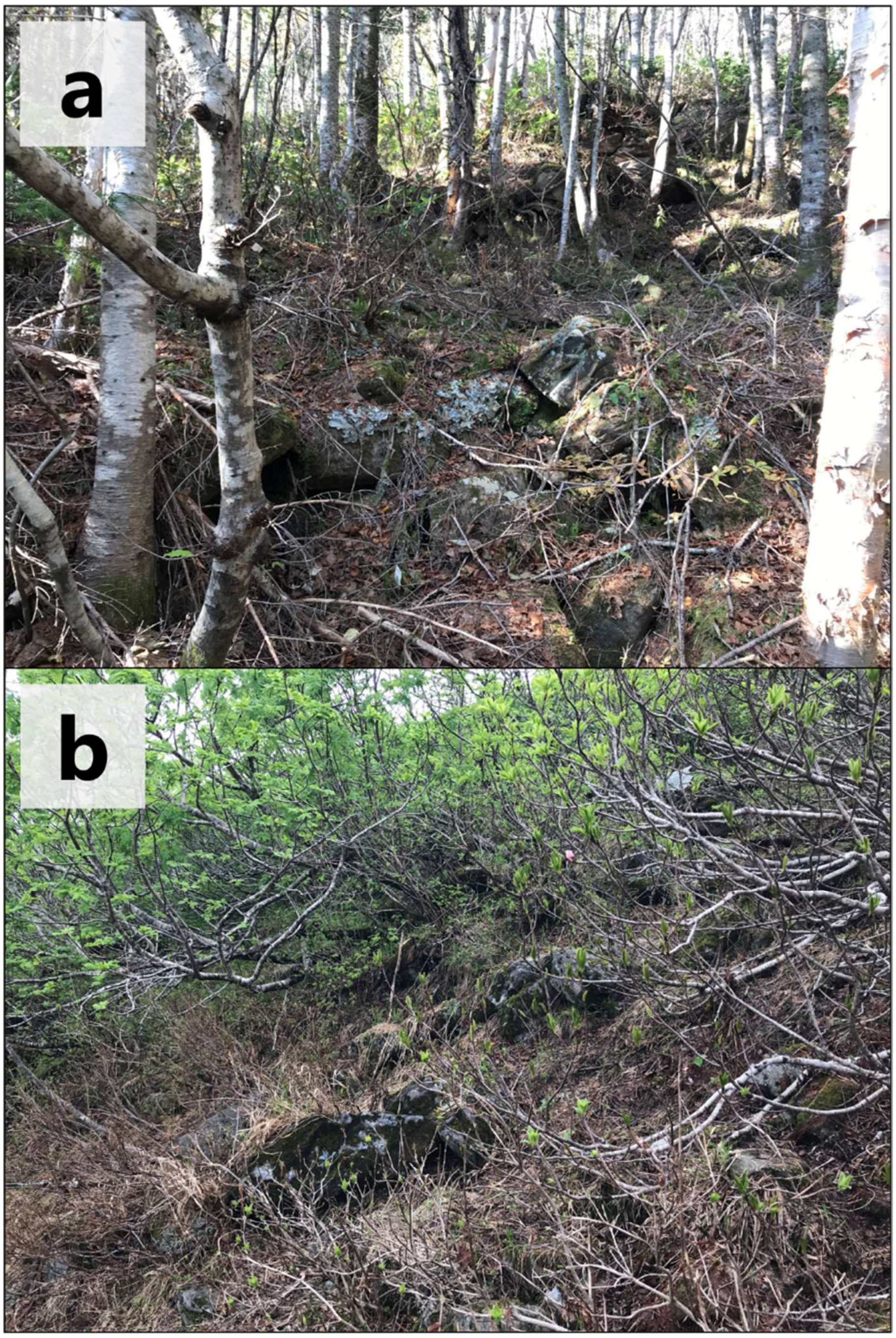


Fig. S3-1. Images of the resurvey sites that lacked clear signs of rocky landforms in (a) North Hidaka and (b) Yubari regions. Although the rocks were detected around the previously reported sites, rock interstices are covered by dense vegetation or soil.

Supplementary Materials for Chapter 4

Table S4-1. Detection data of the northern pika at 37 sites in Hokkaido, Japan, used in this study. Each site is listed with information about region and vegetation.

Year	Site	Region	Vegetation	Survey session					
				1	2	3	4	5	6
2021	1	Tokachi region	Forest	0	0	0	0	0	0
2021	2	Tokachi region	Forest	0	0	0	0	0	0
2021	3	Tokachi region	Forest	0	0	0	0	0	0
2021	4	Tokachi region	Forest	0	0	0	0	0	0
2021	5	Tokachi region	Forest	0	0	1	1	1	
2021	10	Daisetsuzan mountain range	Alpine	1	0	1	1		
2021	11	Daisetsuzan mountain range	Alpine	0	0	0	1*		
2021	15	Tokachidake mountain range	Alpine	1	1	1	1		
2021	16	Tokachidake mountain range	Alpine	1	1	1	1		
2021	20	Tokachi region	Forest	0	0	0	0	0	
2021	21	Tokachi region	Forest	0	0	0	0	0	
2021	23	Tokachi region	Forest	0	0	1	1	1	
2021	24	Tokachi region	Forest	1	1	1	1	1	
2021	31	Tokachi region	Forest-Alpine	1	1	1	1	1	
2021	32	Tokachi region	Forest-Alpine	1	1	1	1	1	
2021	34	Tokachi region	Forest-Alpine	1	1	1	1	1	
2021	35	Tokachi region	Forest-Alpine	1	1	1	1	1	
2021	36	Tokachi region	Forest-Alpine	1	1	1	1	1	
2021	37	Tokachi region	Forest-Alpine	1	1	1	1	1	1
2022	1	Tokachi region	Forest	0	0	0			
2022	2	Tokachi region	Forest	0	0	0			
2022	3	Tokachi region	Forest	0	0	0			
2022	4	Tokachi region	Forest	0	0	0			
2022	5	Tokachi region	Forest	1	1	1			
2022	6	Okhotsk region	Forest	0	0	0			
2022	7	Okhotsk region	Forest	1	0	0			
2022	8	Okhotsk region	Forest	0	0	0	0		
2022	9	Okhotsk region	Forest	0	0	0			
2022	10	Daisetsuzan mountain range	Alpine	1	1	1			
2022	11	Daisetsuzan mountain range	Alpine	1	1	1			
2022	12	Daisetsuzan mountain range	Alpine	1	1	1			
2022	13	Daisetsuzan mountain range	Alpine	1	1	1			
2022	14	Daisetsuzan mountain range	Alpine	1	1	1			

2022	15	Tokachidake mountain range	Alpine	1	1	1		
2022	16	Tokachidake mountain range	Alpine	1	1	1		
2022	17	Tokachidake mountain range	Alpine	1	1	1		
2022	18	Kamikawa region	Forest-Alpine	1	1	1		
2022	19	Kamikawa region	Forest-Alpine	1	1	1		
2022	20	Tokachi region	Forest	0	0	0		
2022	21	Tokachi region	Forest	0	1	0		
2022	22	Tokachi region	Forest	0	0	0	0	
2022	23	Tokachi region	Forest	1	0	0		
2022	24	Tokachi region	Forest	1	1	1		
2022	25	Tokachi region	Forest	1	1	0	0	
2022	26	Tokachi region	Forest	0	0	0		
2022	27	Tokachi region	Forest	0	0	1**	0	
2022	28	Tokachi region	Forest	0	0	0	0	
2022	29	Okhotsk region	Forest	0	0	0		
2022	30	Okhotsk region	Forest	0	0	0		
2022	31	Tokachi region	Forest-Alpine	1	1	1		
2022	32	Tokachi region	Forest-Alpine	1	1	1		
2022	33	Tokachi region	Forest	0	0	0	1	1
2022	34	Tokachi region	Forest-Alpine	1	1	1		
2022	35	Tokachi region	Forest-Alpine	1	1	1	1	
2022	36	Tokachi region	Forest-Alpine	0	1	1		
2022	37	Tokachi region	Forest-Alpine	1	1	1		

* : Presence detection by hearing a natural vocalization at site departure

** : Presence detection by hearing a natural vocalization during habitat environmental survey

Table S4-2. Combinations of predictor variables used in 22 candidate models to analyze the occupancy of the northern pika at the whole-distribution scale. The number of variables were constrained to one and two in observation and state models, respectively, to account for the limited sample size of my study. Abbreviations correspond to Ambient_mean = mean ambient temperature; Ambient_range = mean ambient thermal range; Interstice_mean = mean interstice temperature; Interstice_range = mean interstice thermal range; Rock_interstice = rock-interstice availability; and Date = Julian date of the survey.

No.	State process	Observation process
1	Interstice_mean + Interstice_range + (1|Site)	Date
2	Interstice_mean + Ambient_mean + (1|Site)	Date
3	Interstice_mean + Ambient_range + (1|Site)	Date
4	Interstice_mean + Rock_interstice + (1|Site)	Date
5	Interstice_range + Ambient_mean + (1|Site)	Date
6	Interstice_range + Ambient_range + (1|Site)	Date
7	Interstice_range + Rock_interstice + (1|Site)	Date
8	Ambient_mean + Ambient_range + (1|Site)	Date
9	Ambient_mean + Rock_interstice + (1|Site)	Date
10	Ambient_range + Rock_interstice + (1|Site)	Date
11	(1|Site)	Date
12	Interstice_mean + Interstice_range + (1|Site)	1
13	Interstice_mean + Ambient_mean + (1|Site)	1
14	Interstice_mean + Ambient_range + (1|Site)	1
15	Interstice_mean + Rock_interstice + (1|Site)	1
16	Interstice_range + Ambient_mean + (1|Site)	1
17	Interstice_range + Ambient_range + (1|Site)	1
18	Interstice_range + Rock_interstice + (1|Site)	1
19	Ambient_mean + Ambient_range + (1|Site)	1
20	Ambient_mean + Rock_interstice + (1|Site)	1
21	Ambient_range + Rock_interstice + (1|Site)	1
22	(1|Site)	1

Table S4-3. Model selection results for northern pika occupancy at the whole-distribution scale. The table lists models selected based on expected log predictive density (ELPD) and the null model, with indication of the mean and 95% credible intervals of the posterior distribution and $\hat{R}$ values for each parameter. Abbreviations correspond to Ambient_mean = mean ambient temperature; Rock_interstice = rock-interstice availability; and Date = Julian date of the survey.

Rank	**Process**	**Covariate**	**Beta**	**95 % CRI**	**$\hat{R}$**
1	State	Intercept	2.24	(0.84, 4.09)	1.00
		Ambient_mean	-2.58	(-5.13, -0.73)	1.00
		Rock_interstice	2.17	(0.75, 4.20)	1.00
	Observation	Intercept	1.68	(1.23, 2.17)	1.00
		Date	0.43	(-0.04, 0.94)	1.00
2	State	Intercept	2.27	(0.86, 4.11)	1.01
		Ambient_mean	-2.6	(-5.11, -0.71)	1.00
		Rock_interstice	2.17	(0.75, 4.21)	1.01
	Observation	Intercept	1.6	(1.17, 2.07)	1.00
Null model	State	Intercept	1.2	(-0.20, 2.93)	1.00
	Observation	Intercept	1.59	(1.16, 2.05)	1.00

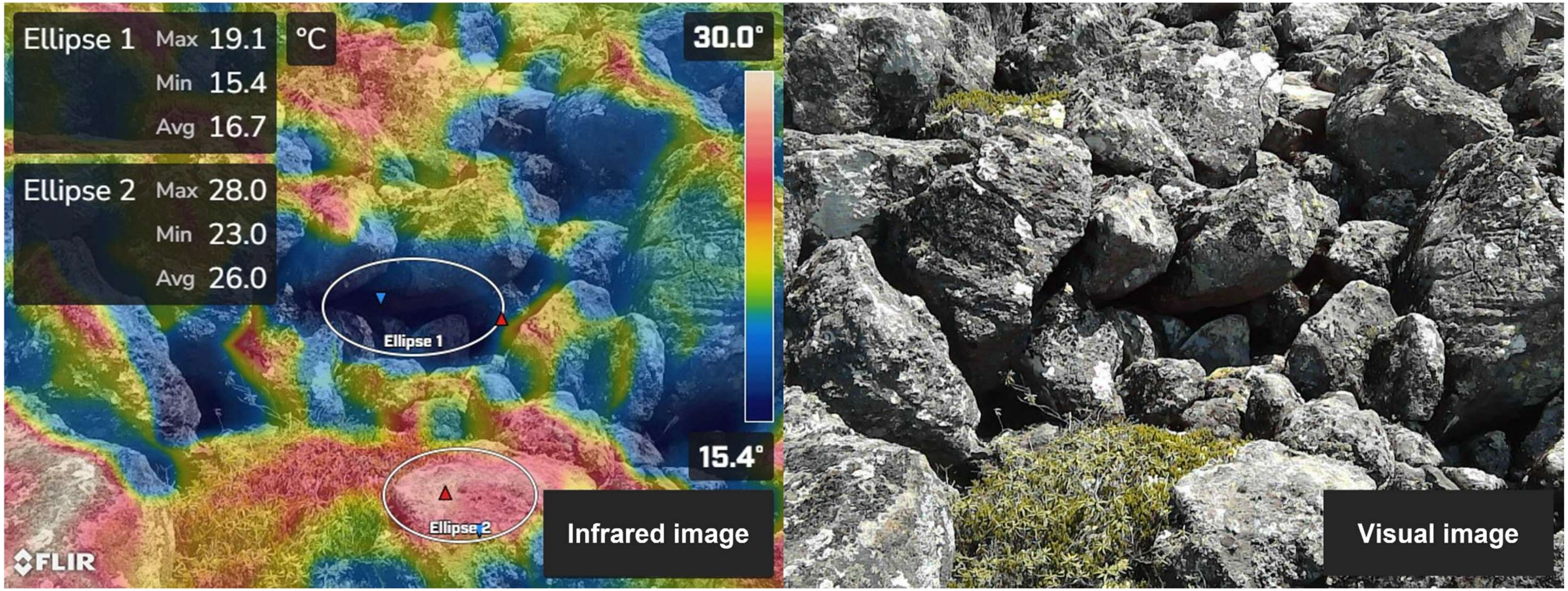


Fig. S4-1. Images of rock interstices in a typical northern pika habitat in Hokkaido, Japan taken by an infrared thermal camera (left) and a normal optic camera (right). In the infrared image, the rainbow color indicates the temperature. Thermal information is summarized for the rock interstice (Ellipse 1) and rock surface (Ellipse 2) in embedded boxes, with the corresponding locations of maximum and minimum temperatures indicated as red and blue triangles, respectively. Cooler temperatures are harbored inside the rock interstices. The size of the rocks in these images are 0.3–1.5 m.

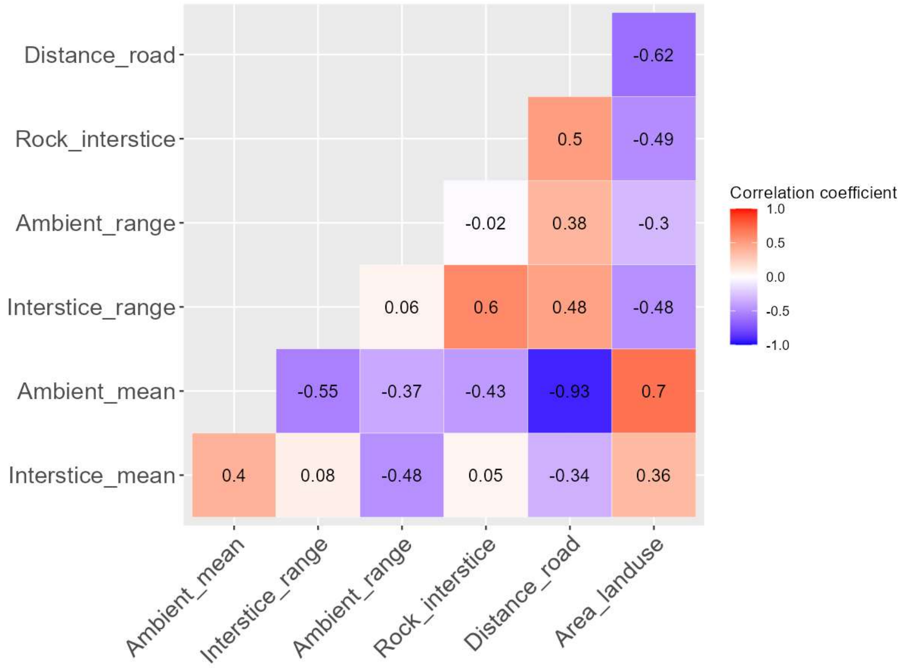


Fig. S4-2. Result of the correlation analysis for the predictor variables prepared for the whole-distribution analysis. Highly correlated predictors were considered as those with |*r*| > 0.7. Abbreviations correspond to Ambient_mean = mean ambient temperature; Ambient_range = mean ambient thermal range; Interstice_mean = mean interstice temperature; Interstice_range = mean interstice thermal range; and Rock_interstice = rock-interstice availability; Area_landuse: area of human land-use within 3-km radius; Distance_road: distance to the closest road.

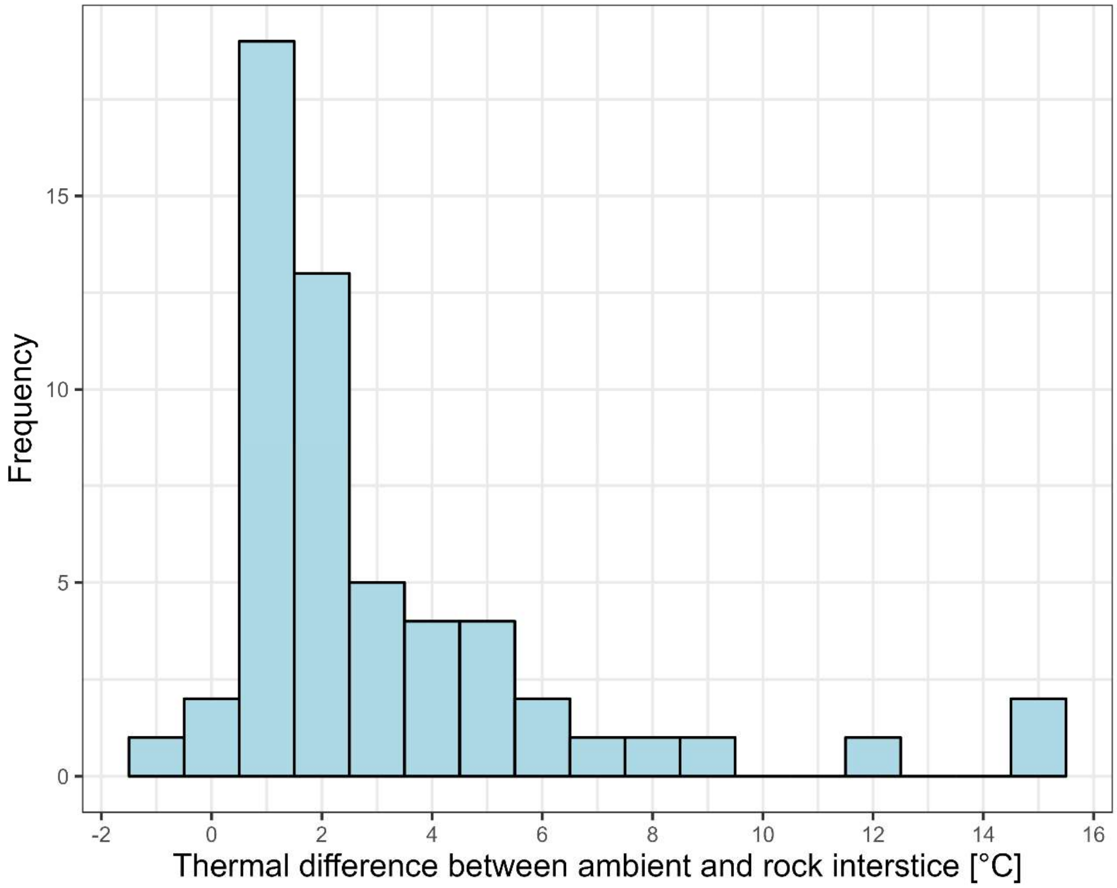
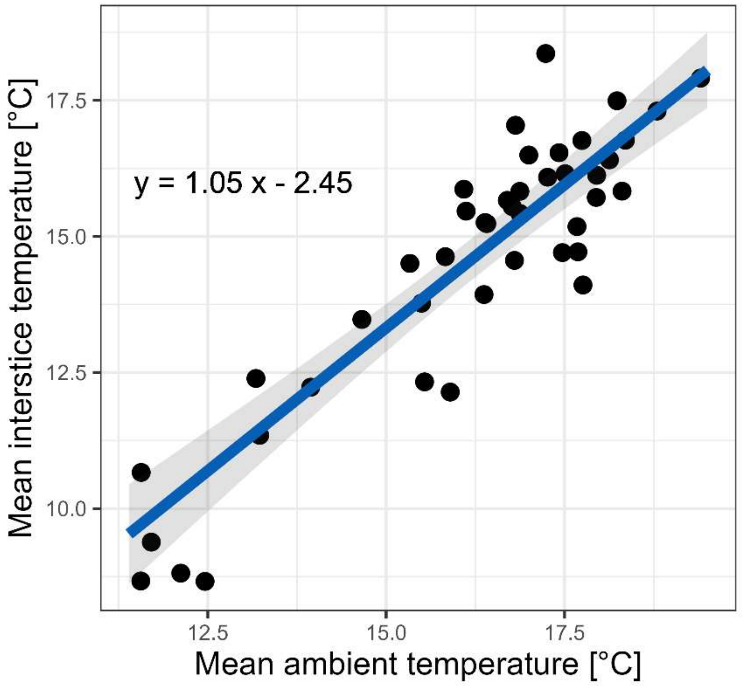


Fig. S4-3. Histogram showing frequency of sites based on thermal difference between ambient and rock interstice in northern pika habitats.



Fig, S4-4. Model prediction of mean interstice temperature as a function of mean ambient temperature based on actual thermal measurements. Since majority of the sites comprised a linear relationship between mean ambient and rock interstice temperatures, I built a linear mixed model to delineate this relationship by including sites with small thermal differences between the two locations (less than 4 °C) in the model, fitting site as the random effect. As a result, mean interstice temperature was formulated with estimated slope and intercept of 1.05 and -2.45, respectively (Standard error: 0.09 and 1.44, respectively), on the raw scale. Conditional and marginal R^2 values were 0.95 and 0.80, respectively, indicating a strong fit to the observed data.

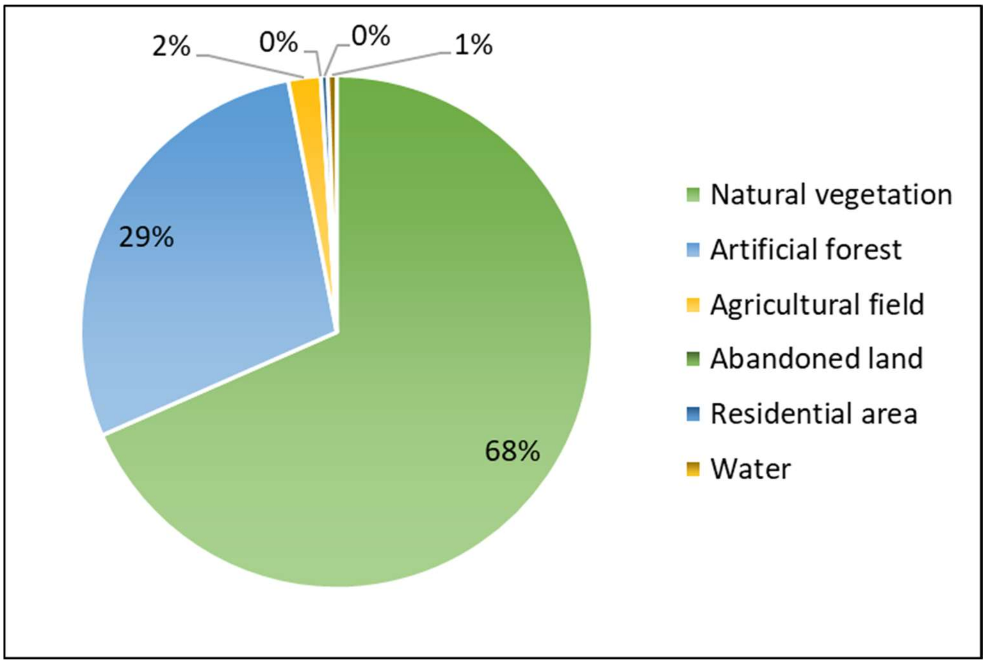


Fig. S4-5. Pie chart showing the average proportion of land-use types within the 3-km radius buffer generated from the study sites at the trailing edge of northern pikas in Hokkaido, Japan.

Fig. S4-6. An image of the remnants of rock removal practices for land levelling observed in agricultural fields close to my study area.

Supplementary Materials for Chapter 5

Table S5-1. List of previous literature reporting the northern pika distribution in Hokkaido that were used to obtain the presence data.

No.	Literature	Survey years	n	Map scale	Citation
1	Haga et al., 1979	1963-1978	109	1/50,000	Haga, R., Fujimaki, Y., & Onoyama, K. (1979). Mammals. In Hokkaido Government (Ed.), Survey Report of the Hidaka Mountain Ecosystem [Animals] (pp. 1–24).
2	Higuchi et al., 2006	2005	3	1/25,000	Higuchi, S., Yatsu, S., Ishiyama, K., & Yamamoto, E. (2006). Habitat of the pika (Ochotona hyperborea yesoensis) in the lava area of Mt. Tokachidake, Hokkaido. Journal of the Wildlife Research Society, 32, 20–26.
3	Ieiri & Yanagawa, 2009	2008	2	1/25,000	Ieiri, A., & Yanagawa, H. (2009). Habitat of northern pikas (*Ochotona hyperborea yesoensis*) in the low altitude area at the southern tip of the Hidaka Mountains. Res. Bull. Obihiro Univ., 30, 53–60.
4	Kawabe & Nakaoka, 2000	1996	1	1/50,000	Kawabe, M. (1989). Recent records of Northern Pika *Ochotona hyperborea* in Northern part of Tokachi District. Bulletin of the Higashi Taisetsu Museum of Natural History, 11, 19–22.
5	Kawabe, 1989	1985-1987	5	1/50,000	Kawabe, M. (1990). Northern pika *Ochotona hyperborea yesoensis* habitat at an altitude of 50m, Hokkaido. Bulletin of the Higashi Taisetsu Museum of Natural History, 12, 89–92.
6	Kawabe, 1990	1989-1989	5	1/50,000	Kawabe, M. (2002). The habitat of Northern pika *Ochotona hyperborea yesoensis* in Mt. Pishikatinai, central Hokkaido. Bulletin of the Higashi Taisetsu Museum of Natural History, 24, 61–63.
7	Kawabe, 2002	1991-2001	1	1/25,000	Kawabe, M., & Nakaoka, T. (2000). The southern limit of the habitat of Northern Pikas *Ochotona hyperborea yesoensis* in Hokkaido. Bulletin of the Higashi Taisetsu Museum of Natural History, 22, 9–11.

8	Kojima & Kawamichi, 2001	2000	5	1/50,000	Kojima, N., & Kawamichi, T. (2001). A population study of Japanese pika (*Ochotona hyperborea*) in Mt. Yubari. Wildlife FORUM, 6, 149–154.
9	Kurumada et al., 2010	2009	39	1/25,000	Kurumada, T. (2010). The habitat patches distribution and utilization of the northern pika in Mt. Nakayama, Hokkaido. Report of Hokkaido Institute of Environmental Sciences, 36, 65–69.
10	Kurumada, 2010	2004-2006	21	1/50,000	Kurumada, T., Inatomi, Y., & Asano, M. (2010). The habitat patches distribution of the northern pika at around Mt. Teshiodake, Hokkaido. Report of Hokkaido Institute of Environmental Sciences, 36, 70–76.
11	Oikawa & Matsui, 2009	2007-2008	6	1/50,000	Oikawa, N., & Matsui, M. (2009). Habitat status of the Japanese pikas in the University of Tokyo Hokkaido Forest. Northern Forestry, Japan, 61(10), 9–13.
12	Onoyama & Kato, 1991	1989	54	1/25,000	Onoyama, K., & Kato, D. (1991). Distribution in the Daisetsuzan Mountain Range. In Hokkaido Government (Ed.), Survey Report of Wildlife Distribution: Pika Ecology (pp. 1–24).
13	Onoyama and Miyazaki 1991	1988-1990	49	1/50,000	Onoyama, K., & Miyazaki, T. (1991). Distribution in Hokkaido. In Hokkaido Government (Ed.), Survey Report of Wildlife Distribution: Pika Ecology (pp. 25–55).
14	Sato et al., 2009	2007	4	1/25,000	Sato, S., Yanagawa, H., Ishiyama, K., & Yatsu, K. (2009). Use of small rock slides by the northern pika, *Ochotona hyperborea yesoensis* in low altitudinal areas of Taisetsu Mountains. Journal of the Japanese Wildlife Research Society., 34, 31–36.
15	Yamakawa & Shimizu, 2013	2009	1	1/25,000	Yamakawa, N., & Shimizu, C. (2013). Ice-Holes and Low-Temperature Phenomena in the Engaru District, Southern Part of the Kitami Mountains, Hokkaido. The Gakugei Chiri, 67, 47–56.

Table S5-2. Procedures and data sources explaining how environmental variables were generated for the species distribution model analysis.

Category	Variable	Macroclimate (30 arc sec.)	Local-climate (3 arc sec.)
Topographical **Data source: MERIT DEM*** **Original resolution: 3 arcsecs**	Slope	Computed in GIS after aggregating the MERIT DEM data to 30 arcsecs.	Computed in GIS using the MERIT DEM data.
Geological **Data source: Seamless Digital Geological Map of Japan** **Original resolution: 1:200,000**	Surface geology	The original polygon was converted to a raster with a resolution of 30 arcsecs. The raster cell value was assigned "1" if igneous and metamorphic rocks occurred in the cell and "0" if not.	The original polygon was converted to a raster with a resolution of 3 arcsecs. The raster cell value was assigned "1" if igneous and metamorphic rocks occurred in the cell and "0" if not.
Bioclimatic **Data source: chelsa-cmip6**** **Original resolution: 30 arcsecs**	Mean summer temperature	Created by using the original chelsa-cmip6 data.	Created after downscaling the chelsa-cmip6 data to 3 arcsecs.
	Mean summer diurnal range	Created by using the original chelsa-cmip6 data.	Created after downscaling the chelsa-cmip6 data to 3 arcsecs.

*Yamazaki et al. 2017 ** Karger et al. 2023

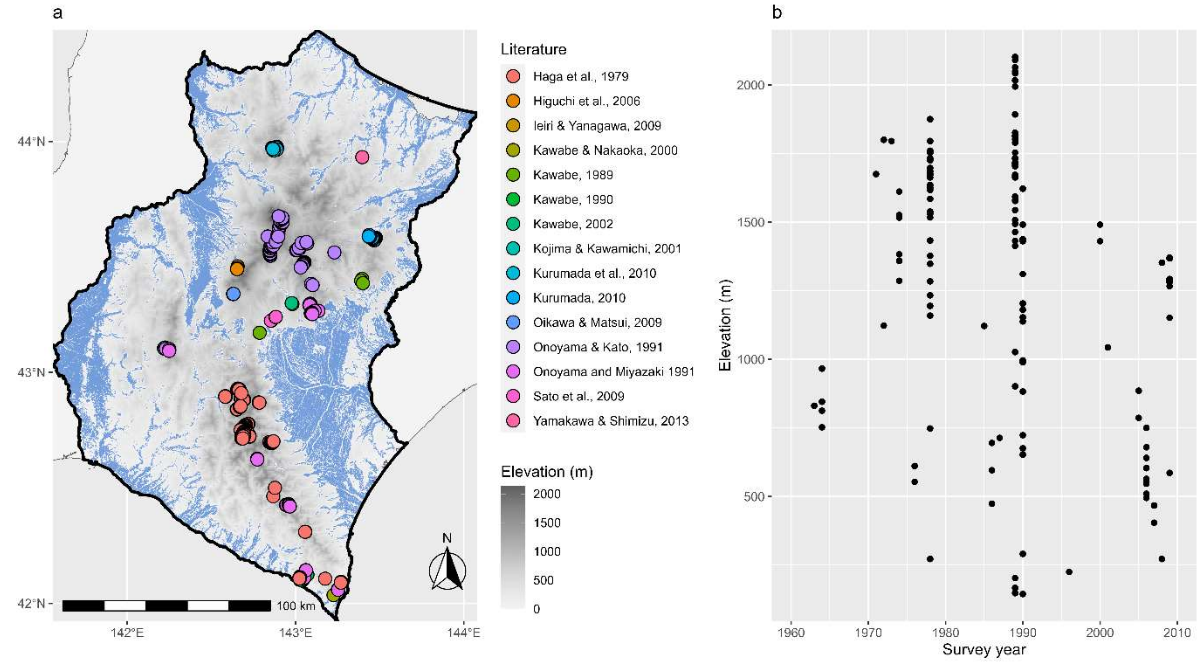


Fig. S5-1. Historical records of the northern pika distribution surveyed between 1963–2009. (a) Geographical map of the presence points that were selected in this study. The light blue area represents areas that were excluded from the analysis as they were considered land cover types irrelevant to northern pika distribution (e.g., agricultural and urban areas). (b) The relationship between elevation and survey year of the presence points.

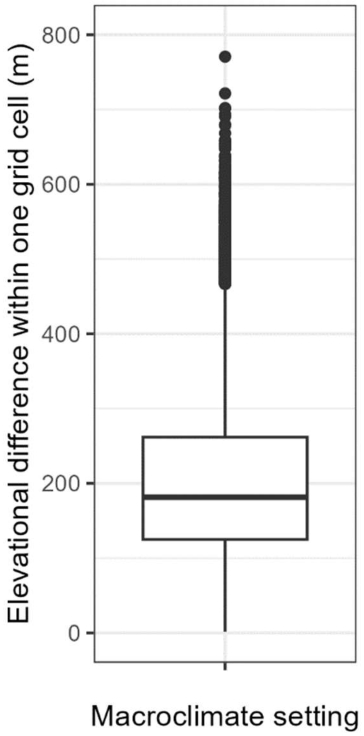


Fig. S5-2. A boxplot indicating the elevational difference within coarse-scale grid cells (30 arcsecs) calculated using 10 times finer (3 arcsecs) elevational data.

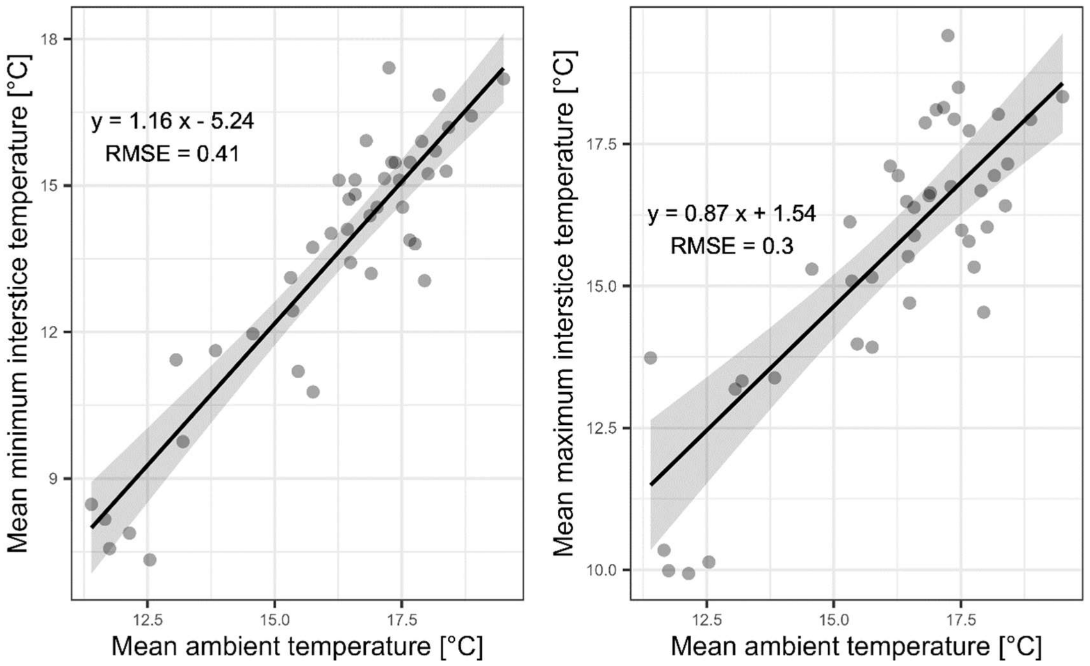


Fig. S5-3. Response plots of the linear regressions analyzing the relationship between mean ambient temperature and mean minimum (left) and mean maximum (right) interstice temperatures. These models were used to predict the rock interstice microclimates in my study area.

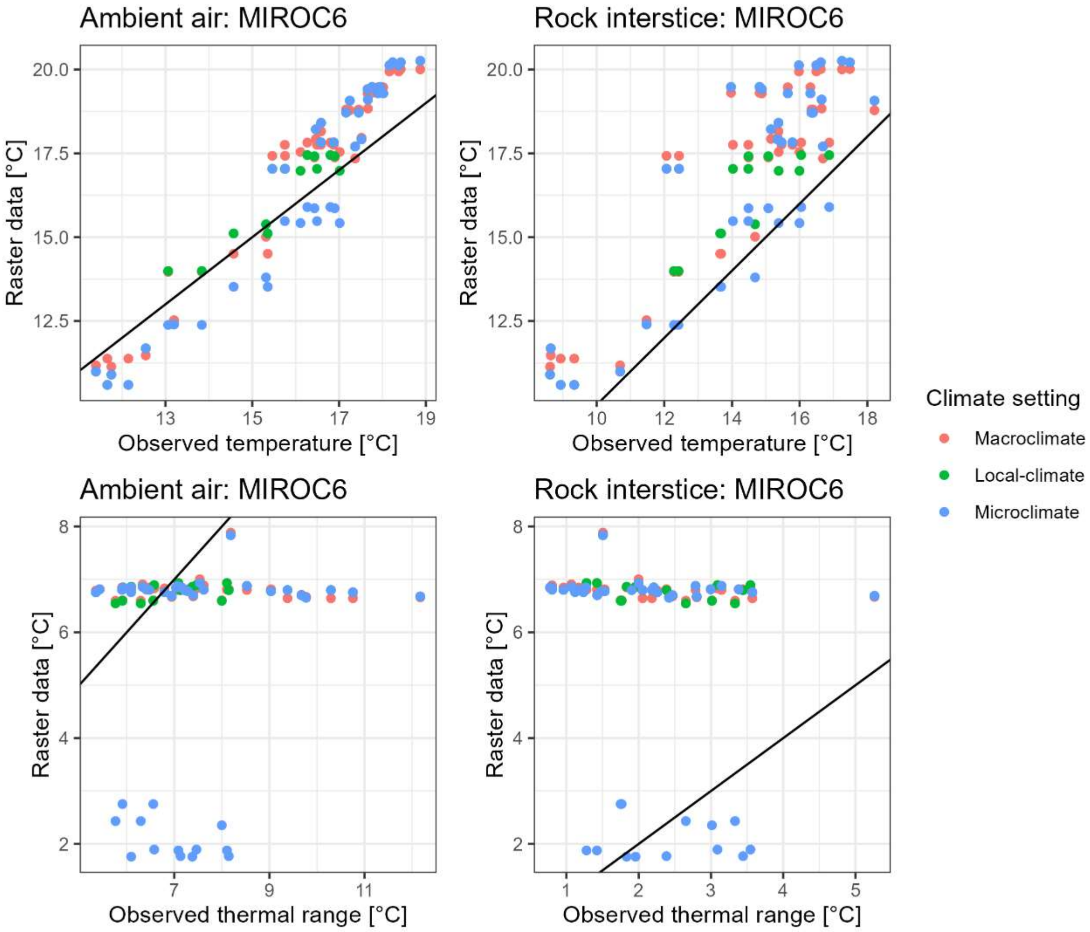


Fig. S5-4. Scatterplots showing the relationship between the bioclimatic variables (raster data used for the SDM analysis) and the observed thermal conditions. Plots are shown for the mean summer temperature (top) and diurnal thermal range (right) of ambient air (left) and rock interstice (right) with the bioclimatic variables computed based on the MIROC6 GCM. The black line is the 1:1 line and the point colors represent the climate settings for the bioclimatic variables. In this plot, the closer the points to the black line the more accurate the bioclimatic variable is in representing the actual observed data. The sum of the differences between the bioclimatic variables and the observed measurements for all GCMS is shown in Fig. S5-5.

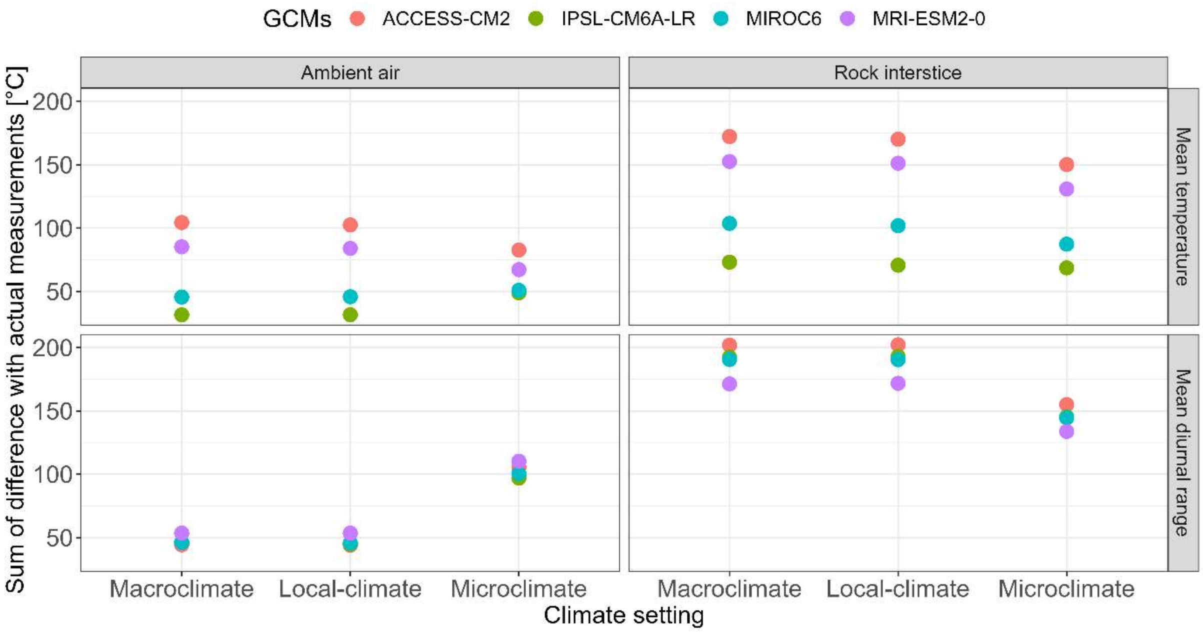


Fig. S5-5. Validation results of the bioclimatic variables used in the study. Y-axis is the sum of the thermal differences (*n* = 43) between the bioclimatic variables and the measured thermal conditions. The 1st and the 2nd rows show differences for mean temperature and mean diurnal range for ambient air (left) and rock interstice (right), respectively. Point colors represent the GCMs used to derive the bioclimatic variables. In this plot, the smaller the sum of difference the more accurate the bioclimatic variables are in representing the actual thermal conditions.

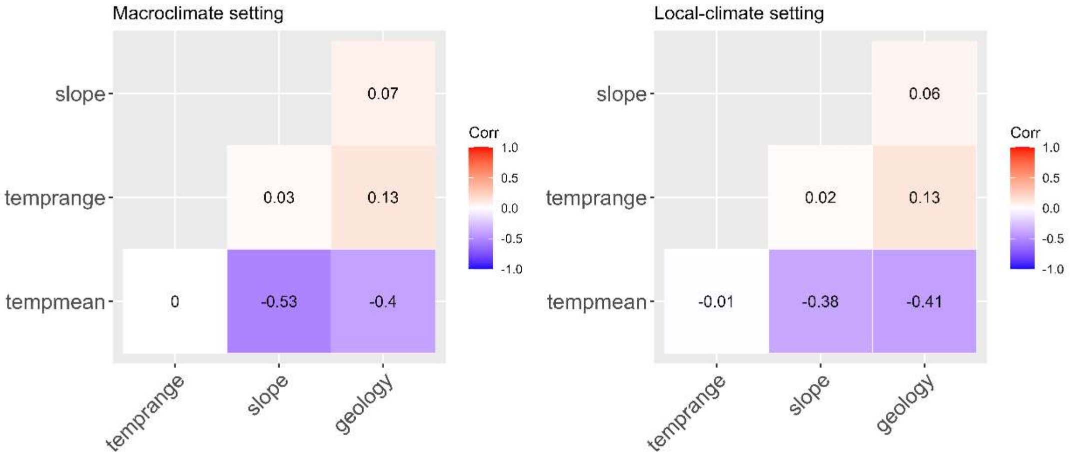


Fig. S5-6. Result of the correlation analysis for each model setting. Abbreviations correspond to: tempmean = mean summer temperature; temprange = mean summer diurnal range; slope = slope angle; and geology = surface geology.

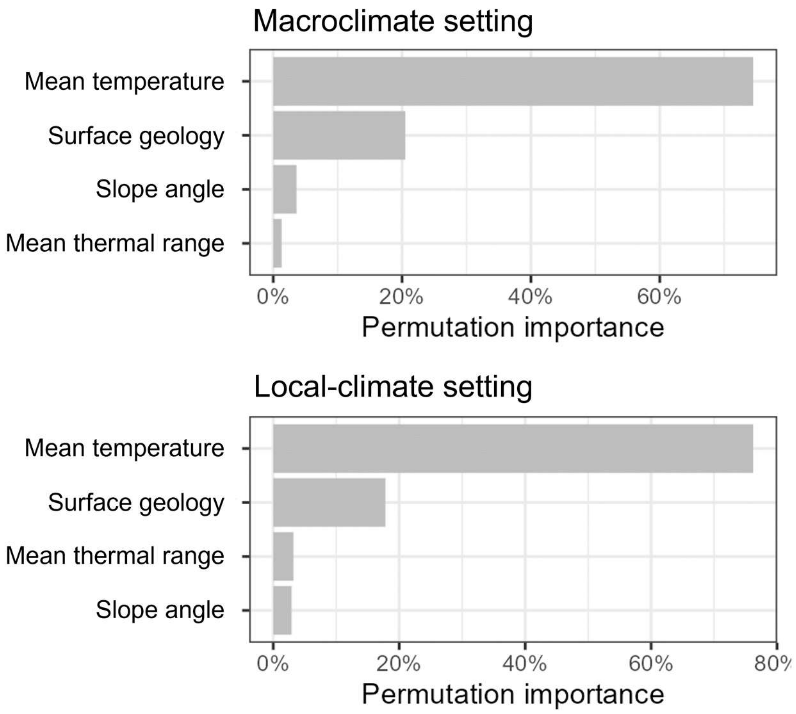


Fig. S5-7. Permutation importance of the model predictors for the best-fit macroclimate (top) and local-climate models (bottom).

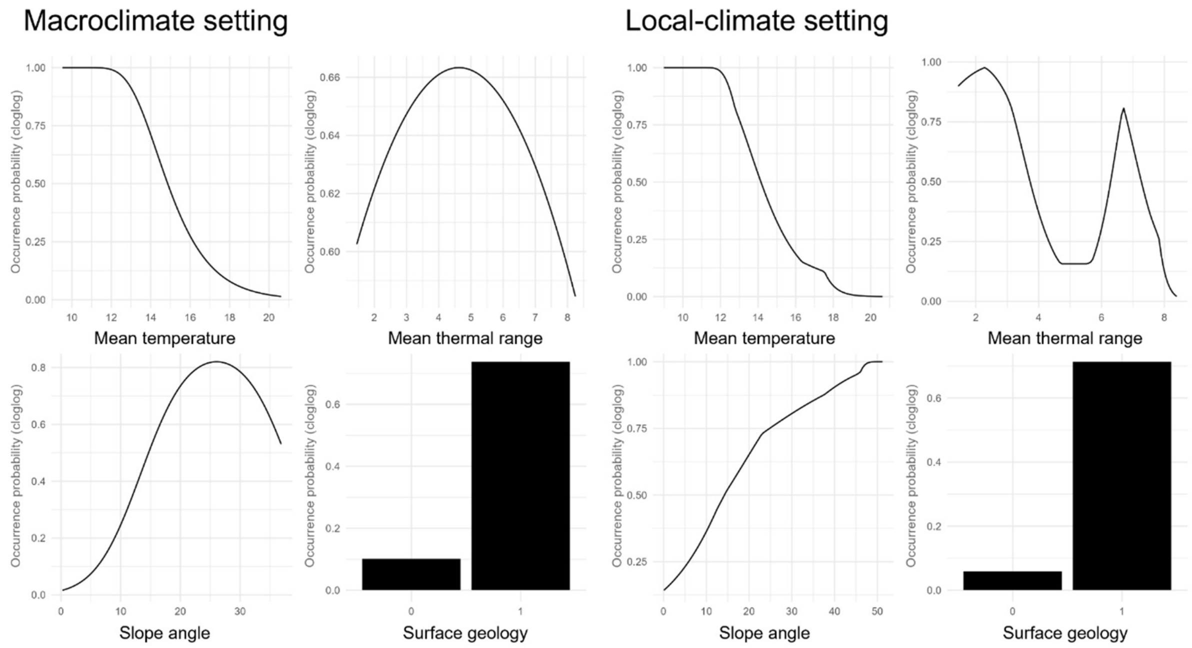


Fig. S5-8. Response plots of the model predictors for the best-fit macroclimate (left) and local-climate models (right).

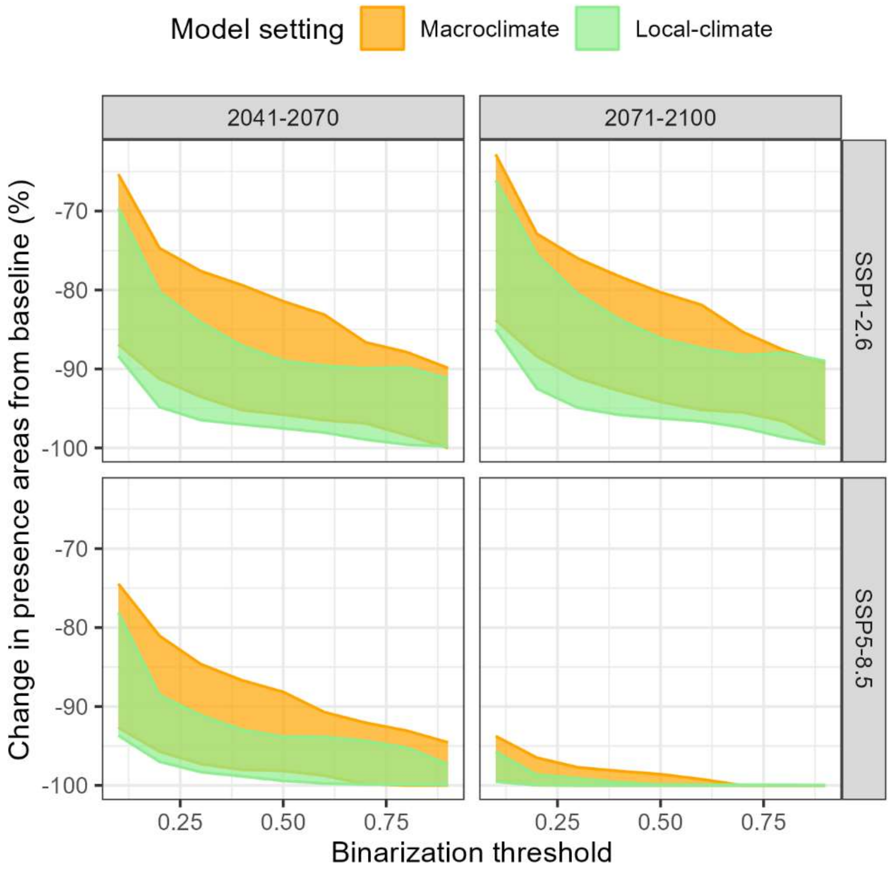


Fig. S5-9. Percentage of presence areas predicted to change in the future from the baseline period (1981–2010). Plots are shown for two time periods (2041–2070 and 2071–2100) and two emission scenarios (SSP126 and SSP585) and shades represent the range of the proportions predicted in the four global circulation models. Shade colors represent the difference in the model settings (orange = macroclimate and green = local-climate).

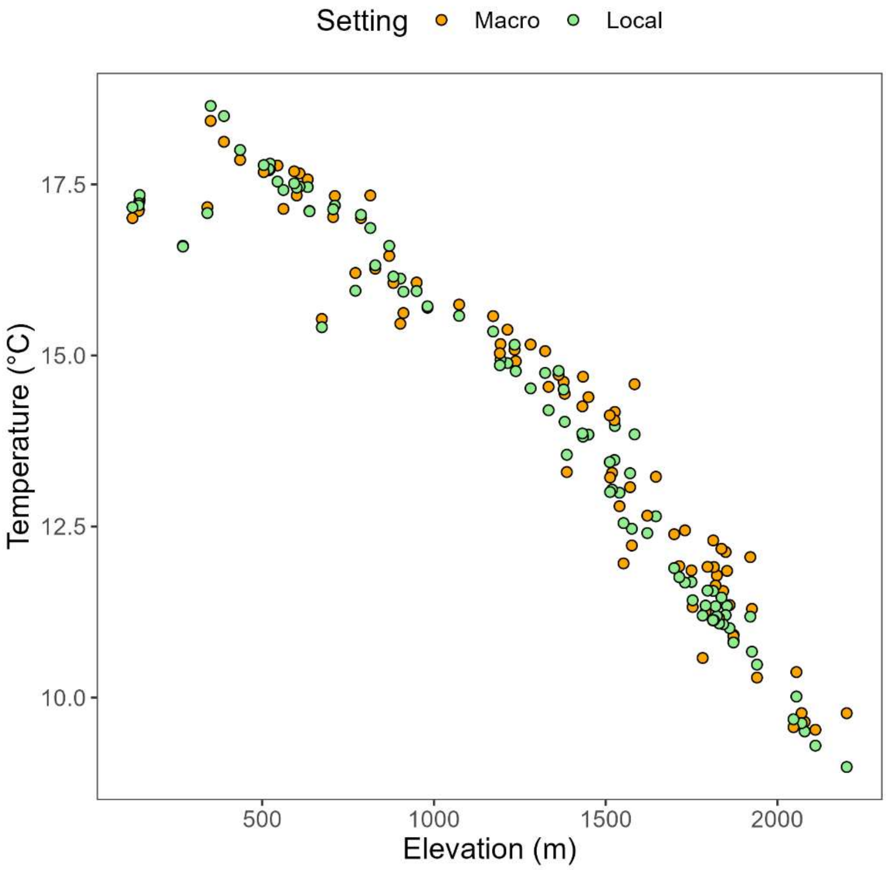


Fig. S5-10. Difference in elevation between the macroclimate and local-scale cells at the presence points used for distribution modeling.

Extended Methods S5

Derivation of the bioclimatic variables

In my study, I analyzed the effects of mean temperature and mean diurnal range during summer on the northern pika distribution. To represent the summer conditions of my study area, I considered the climatic conditions from July to August since these are the two warmest months in Hokkaido, Japan (Japan Meteorological Agency, 2023). To create these bioclimatic variables, I adapted the calculation formulas in the ANUCLIM framework (Xu & Hutchinson, 2013) to my season settings as explained below (Eqn. 1–3).

Mean summer temperature was calculated as the average of the mean daily minimum and maximum temperatures for the month of July and August over the different time periods considered in my study(Eqn. 1).

$$\text{Mean temperature} = ((t_{\text{min, Jul.}} + t_{\text{min, Aug.}})/2 + (t_{\text{max, Jul.}} + t_{\text{max, Aug.}})/2))/2 \quad \text{(Eqn. 1)}$$

Likewise, mean diurnal range was calculated as the average difference between the mean minimum and maximum temperatures for July and August (Eqn. 2).

$$\text{Mean diurnal range} = ((t_{\text{max, Jul.}} + t_{\text{max, Aug.}}) - (t_{\text{min, Jul.}} + t_{\text{min, Aug.}}))/2 \text{ (Eqn. 2)}$$

Where, $t_{\text{min, Jul.}}$, $t_{\text{max, Jul.}}$, $t_{\text{min, Aug.}}$, and $t_{\text{max, Aug.}}$ are the mean daily minimum and maximum temperature for July and August, respectively. These mean monthly minimum and maximum temperatures represent the average condition of each time period considered in my study. Note, however, that the input values depend on the climate settings, as explained as follows.

For the macroclimate setting, I used the raw climate data obtained from the chelsa-cmip6 R package (Karger et al., 2023) as the input for processing the bioclimatic variables, which had a spatial resolution of 30 arcsecs. These were the 7th (July) and 8th (August) layers in the “tasmin” and “tasmax” netCDF files.

To process bioclimatic variables for the local-climate setting, I downscaled the raw climate data used in the macroclimate setting to 3 arcsecs and used them as the input data. Monthly temperature data (“tasmin” and “tasmax” for July and August) were downscaled by performing a kriging analysis considering fine-scale elevation.

For the microclimate setting, I had the same spatial resolution as the local-climate setting. For temperature data, I considered that microclimates exist in rocky landforms, which could be beneficial for northern pikas. To reflect this situation, I modeled the thermal relationship between the ambient air and interstice microclimates and applied this relationship to areas that possess rocky landforms for predicting potential microclimates. First, I modeled based on thermal measurements how mean ambient air temperature is related with mean minimum and mean maximum interstice temperatures for July and August. Linear mixed models were used, with mean minimum and mean maximum interstice temperatures as the response variable, mean ambient temperature as the explanatory variable, and site as the random effect. As a result, I found that both mean minimum and mean maximum interstice temperatures can be modeled as a linear function of the mean ambient temperature (Eqn. 4–5; Fig. S5-3).

$$t_{\text{min interstice, July-Aug.}} = 1.16 \times t_{\text{mean ambient, July-Aug.}} - 5.24 \text{ (Eqn. 4)}$$

$$t_{\text{max interstice, July-Aug.}} = 0.87 \times t_{\text{mean ambient, July-Aug.}} + 1.54 \text{ (Eqn. 5)}$$

Then, I used this relationship to predict the interstice temperatures across the study area where rocky landforms exist by using the local-climate setting’s mean summer temperature, which represents the ambient thermal condition, as the input. After obtaining the minimum and maximum interstice temperatures, I used these as inputs for Eqn. 1 and 2 to predict the mean temperature and mean diurnal range in rock interstices. For areas without rocky landforms, I used the same temperature data as the local climate setting data.

Validation of the bioclimatic variables

While I downscaled thermal data to create bioclimatic variables at a high spatial resolution for the local-climate setting and those incorporating microclimates for the microclimate setting, these variables might not reflect the actual conditions well. Therefore, I validated the thermal variables by comparing them with actual thermal measurements of ambient air and rock interstice in northern pika habitats. For this aim, I used thermal measurements conducted at 14 sites in 2021 and 29 sites in 2022. While the rock-interstice microclimate was predicted only for the three selected regions for the analysis, for this validation procedure, I also predicted the microclimate for the places I conducted my measurements.

Particularly, I first visualized the relationships between the bioclimatic variables and thermal measurements on a scatterplot and then computed the sum of the differences between them for each model setting. I interpreted that bioclimatic variables generated for the local-climate setting reflected well the true conditions if the sum of the differences with measured ambient conditions were the smallest among the three settings. For the microclimate-setting, I interpreted that the bioclimatic variables reflected well the true conditions if their differences with measured interstice conditions were the smallest. Since field thermal measurements were conducted in the summer of 2021–22, I created bioclimatic variables using the CHELSA CMIP6 climate data for the years 2021–2025 to match the temporal settings. Identical to the main analysis, I considered four GCMs (ACCESS-CM2, IPSL-CM6A-LR, MIROC6, and MRI-ESM2-0), although considered only the SSP5-8.5 scenario as the current society is still a highly fossil-fuel based society.

As a result, for the mean ambient temperature, the sum of difference was the smallest in macroclimate and local-climate settings, despite these two settings also having the largest sum (Fig. S5-5). The microclimate setting fell in between, indicating that none of the model settings was clearly more accurate than others in reflecting ambient temperature. However, the scatterplot showed that the bioclimatic variables for all bioclimatic variables were plotted along the 1:1 line (Fig. S5-4), and therefore, I interpreted that the bioclimatic variables derived for the local-climate setting is moderately accurate in reflecting the actual conditions. For the rock interstice temperature, the microclimate setting had the smallest sum of difference for each GCM (Fig. S5-4, S5-5), suggesting that it is highly accurate in reflecting the actual microclimate conditions.

In the case of thermal range, the local-climate and microclimate settings were among the most accurate in reflecting thermal conditions for ambient air and rock interstices (Fig. S5-5). However, the scatterplot showed that all bioclimatic variables did not reflect the observed conditions well, with the bioclimatic variables exhibiting a bimodal distribution with minimal variation for each peak while the observed thermal conditions were distributed in a scattered manner (Fig. S5-4). This suggests that the thermal ranges of the bioclimatic variables are relatively similar throughout the whole study area while variations actually exist. Given that most of the points from all climate settings overlapped with each other, this inaccuracy was likely due to the source climate data (i.e., GCMs) having low capabilities to reflect actual conditions. Considering that the derivation process of the bioclimatic variables actually led to minimizing the sum of the differences for both the ambient air and rock interstices, I decided to use these bioclimatic variables for the analysis.