How Climate Influences Occupancy and Behavior of Pikas in Alaska

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Abstract

Collared pikas (*Ochotona collaris*) are cold adapted alpine lagomorphs of western Canada and Alaska that are vulnerable to direct and indirect effects of climate change. However, we do not yet know to what extent they can adapt to these changing climates. Collared pikas do not hibernate, so they spend the entire summer season foraging and caching vegetation within rock dens to survive winter. Our objectives were to 1) determine whether territory-specific microclimate and microhabitat characteristics influence occupancy of individual collared pika dens across years, and 2) characterize daily and seasonal foraging patterns of collared pikas to identify thermal limitations and understand how warmer conditions may affect food acquisition. We recorded den occupancy and territory characteristics, and placed temperature loggers within pika dens across 3 study areas with contrasting climate gradients in southcentral and interior Alaska, USA, during 2017-2022. We also conducted behavioral observations of collared pikas in these study areas across varying weather conditions and times of day to determine when pikas were foraging during July and August 2020-2021. We evaluated climatic conditions and habitat features to test hypotheses on den occurrence and used these data to estimate territory persistence with a Bayesian dynamic occupancy model. We tested hypotheses on proportional daily foraging activity as a function of both temporal and thermal explanatory variables through linear mixed-effects models. Daily maximum temperature during summer and winter best predicted collared pika occupancy rates, and dens with larger rocks remained cooler during summer. Foraging patterns of collared pikas were dependent on temperature, wind, and time of day, and caching behavior was dependent on a narrower range of conditions compared to grazing. These results demonstrate that specific microclimate requirements within collared pika territories, during both summer and winter, can influence territory occupancy and foraging behavior, and habitat characteristics can buffer temperature extremes. This information can advance understanding about the mechanistic links between climate and population persistence for collared pikas under the rapidly changing arctic climate.

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Dedication

To my parents, Colleen and John Harrison, and grandmother, Gloria Ramos, who supported me through my wildest dreams. To all my family, friends, and baby girl Juanita (*Canis lupus familiaris*) who stood by me, inspired me, and kept the magic alive. And of course, to the pikas.

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Chapter 1: Microhabitat and microclimate influence seasonal territory occupancy of collared pikas (*Ochotona collaris*).

Abstract

Collared pikas (*Ochotona collaris*) are cold adapted alpine lagomorphs of western Canada and Alaska that are vulnerable to direct and indirect effects of climate change. However, we do not yet know to what extent they can adapt to these changes. Pikas are highly philopatric, and high rates of abandonment and low rates of colonization of individual territories may be an early sign of population declines. Our goal was to determine whether territory-specific microclimate and microhabitat characteristics influence occupancy of individual collared pika territories across years. We quantified both summer and winter thermal stresses, which have not often been tested in conjunction but are known drivers of pika extinctions. We recorded den occupancy and territory characteristics and placed temperature loggers within pika dens across 3 study areas with contrasting climate gradients in southcentral and interior Alaska during 2017-2022. We examined changes in pika den occupancy by estimating annual colonization and extinction rates with a Bayesian dynamic occupancy model with forage availability, rock size, and multiple den temperature metrics as the explanatory variables. Across all pika dens within our study areas over 5 years, the average colonization rate (0.47) was higher than the average extinction rate (0.38), and our top models indicated that daily maximum temperature during summer and winter best predicted pika occupancy rates. These results demonstrate that specific microclimate requirements within pika dens, during both summer and winter, can influence territory occupancy and habitat characteristics can buffer temperature extremes. This information can

advance understanding about the mechanistic links between climate and population persistence for collared pikas under the rapidly changing arctic climate.

Introduction

A key concept for assessing vulnerability to climate change is understanding the degree to which species can “persist in place” or “shift in space” under future climatic conditions (Thurman et al., 2020, Foden et al. 2019). Many species are expanding their ranges latitudinally or upwards in elevation to escape warming environments, while others must develop behavioral strategies and utilize habitat features to escape the heat (e.g., Stelzner and Hausfater 1986, Terrien et al. 2011, Milling et al. 2017, Mota-Rojas et al. 2021, Cunningham et al. 2021). Climate models often poorly predict changing species distributions, because they do not account for microclimate refuges, which allow species to persist in otherwise unsuitable environments (Sears et al. 2011, Beever et al. 2016, Milling et al 2018, Mitchell et al. 2018, Verzuh et al. 2023). Examining relationships between habitat features and microclimates can help determine where and how species may be able to persist into the future (Vanwalleghem & Meentemeyer 2009, Sears et al. 2011, Fuller et al. 2014, Briscoe et al. 2014, Mathewson et al. 2016).

Alpine ecosystems are especially susceptible to increasing temperatures associated with climate change due to melting ice and reduction of permafrost (Overland 2021), which in turn influence water availability, vegetation communities, and protective cover for species living beneath the snow (subnivean) (Pauli et al. 2013, Penczykowski et al. 2017, Overland et al. 2019, Yamanouchi and Takata 2020). Through a process known as Arctic amplification, temperatures in the Arctic are increasing at a rate 2-4 times that of the global average due to anthropogenic carbon dioxide released into the atmosphere (Overland et al 2019; Yamanouchi and Takata 2020; Jacobs et al. 2021, Rantanen et al. 2022). Extreme weather events are increasing in frequency and magnitude at northern latitudes (>59°N) as well, resulting in uncertainty for the future climates (Overland 2021). Therefore, it is increasingly important to monitor how Arctic wildlife populations are responding to these temperature changes and extreme weather events to inform conservation and management efforts in critical habitats and sensitive ecosystems.

Pikas (Ochotonidae) are members of a family of subnivean species known to be influenced by climate warming with a limited ability to "shift in space". (Yandow et al. 2015, Hafner 2018, Dahal et al. 2020). Pikas are small, cold adapted lagomorphs distributed in montane regions at high latitudes across the Northern Hemisphere (Smith et al. 2018, Feijó et al. 2020, Dahal et al. 2020). Pikas do not hibernate, have a small body size (mean of 150 grams) and live in extremely cold conditions, so they maintain a high metabolic rate to survive winter (Koju 2018, Westover 2019). American pikas (*Ochotona princeps*) have a low heat tolerance and will succumb to ambient temperatures between 25.5 to 29.4℃ within 2 hours without seeking thermal shelter beneath the talus (McArthur and Wang 1973, Wang and Wang 1996, Matsumoto 2005, Lee et al. 2008, Moyer-Horner et al. 2015, Stafl and O’Connor 2015). Moreover, the mean stable body temperature (40.1°C) and upper lethal temperature (43.1°C) of American pikas span only 3°C, which is notably narrower compared to that of most other mountain-dwelling mammals (MacAurthur and Wang 1973, Smith 1974, Otto et al. 2015). Most pika species live beneath talus where temperatures are moderated year-round (Dearing 1997, Galbreath et al. 2009, Gliwicz et al. 2006). Pikas are generalized herbivores that forage in the vegetation surrounding the talus edge (Wilkening 2007). Unlike other small alpine mammals, pikas cache their forage beneath boulders in large haypiles, which they subsist on throughout the winter rather than hibernating or moving downslope (Morrison 2009, Holtcamp 2010). Pikas are known to cache vegetation with specific chemical properties that preserve them through winter (Dearing 1997, Varner et al. 2023).

Collared pikas (*O. collaris*) are one of two pika species occuring in North America and distributed from western Canada through south and central Alaska (Lanier and Hik 2016) (Figure 1.1). They are also one of only two pika species (the other being the Northern pika, *O. hyperbolea,* that occurs in Russia) that live at latitudes above 59°N, which is where Arctic warming trends are especially prevalent. In contrast to American pikas, which have long been a focus of climate change research (e.g., Smith 2020, Grayson 2005, Pimm 2010), collared pikas are relatively understudied (Lanier and Hik 2016). Although morphologically similar to American pikas and only geographically separated by approximately 650 km, collared pikas live in colder climates and their physiological tolerance to temperature as well as their precise ecological niche remain unknown (Lanier and Olsen 2013, Lanier et al. 2015). Additionally, their slow dispersal rate (<300-1000m per year) limits their ability to simply shift northwards to cooler climates at higher latitudes (Lanier and Olsen 2009, Lanier and Olsen 2013, Zgurski and Hik 2014).

Some populations of collared pikas are declining or fluctuating with relatively low genetic diversity (Morrison and Hik 2007, Lanier and Olsen 2013) and several key knowledge gaps remain for this species, in particular its response to climate change (Lanier and Olsen 2013). In Alaska’s State Wildlife Action Plan and Canada’s Species at Risk Act, collared pikas are listed as a species of greatest conservation need because of their likely vulnerability to a rapidly changing climate (COSEWIC 2011, Alaska Department of Fish and Game 2015). Several hypotheses have been posited to explain how habitat and climatic conditions influence survival and territory occupancy by pikas. However, most of this research has focused on American pikas in warmer climates. Collared pikas may experience both direct and indirect effects of climate change related to excessive heat in summer, forage availability, and snowpack reduction. Moving forward, we define aspects of an area occupied by pikas as 1) a colony, a patch of contiguous talus that is occupied by pikas, separated by at least 300 meters with a neighboring talus patch, and with assumed low rates of dispersal between them (Smith 1974, Zgurski and Hik 2014), 2) a territory, a 50 meter diameter (on average) area of rocky hillside where 1 individual pika resides and caches vegetation beneath rocks, and 3) a den, the central location of a pika territory where they cache a majority of their forage for winter.

The microclimates allowing pikas to persist in extreme environments are created by two habitat features – rocks and snow (Bhattacharyya and Ray 2015, Sakiyama et al. 2021). The size of the rocks selected for dens, where they cache a majority of their forage, is an important characteristic of pika habitat. Pikas require talus with sufficient subterranean cavities to create movement corridors which are usually created by loose rockslides (Kawamichi 1968). However, the talus should also be stable enough to support pika dens through winter without snowpack, small slides, or spring run-off damaging their dens and haypiles (Kawamichi 1968). American pikas typically select talus with rocks between 0.2 – 1.0m in diameter, with some variation across ecosystems and substrate type (Moyer-Horner et al. 2016). They often cache their haypiles beneath and sit atop larger boulders within their territories (Smith and Weston 1990, personal observation) possibly because larger boulders a) provide more space to cache vegetation, b) are typically more stable on the slope, c) offer more protection from the elements and predators, and/or d) offer a better vantage point for guarding their territories. Additionally, pikas are known to occupy microhabitats with more stable temperatures beneath the talus (Rodhouse et al. 2017, Sakiyama et al. 2021). The talus interior creates a moderate and stable microclimate refuge that both cools the air in summer and warms the air in winter, and the subterranean conditions likely contribute to the persistence of pika populations (Morard et al. 2010, Millar et al. 2014a, Millar & Hickman, 2021). Wright and Stewart (2018) and Sakiyama et al. (2021) suggested that thermal refuge provided by talus will likely be important in a changing climate for both American pikas and northern pikas in Japan, but may only partially offset the effects of climate change for American pikas.

Pikas require a consistent snowpack to insulate their dens through the winter, ideally at a depth greater than 20 cm (Morrison and Hik 2007, Beever et al. 2010, Bhattacharyya et al 2014, Johnston et al. 2019). If weather conditions such as reduced snowfall, excessive wind, rain, or midwinter snowmelt reduce the insulative snowpack, they could be exposed to cold ambient temperatures (Penczykowski et al. 2017). Excessive moisture from rain or condensation significantly reduces the insulative capability of fur resulting in substantial heat loss in mammals (McArthur 1991, McArthur and Ousey 1996). In the face of climate change, winter temperatures will likely fluctuate more within pika dens especially if snowpack decreases earlier in the year resulting in a higher frequency of melt-freeze events (Berteaux et al. 2016, Johnston et al. 2019). On the other hand, milder and shorter winters with fewer extreme cold spells could be beneficial for pikas. Snowpack projections under current and increased emissions scenarios indicate that snowpack will decrease particularly during the beginning and end of the snow season at lower elevations, in all known areas of the collared pika range in Alaska (Littell et al. 2018).

For small endotherms in general, highly fluctuating temperatures are more challenging than extreme but stable temperatures (Briga and Verhulst 2015). Contrary to the conclusions of many studies on American pikas in the Sierra Nevada Mountains and Great Basin of Nevada on the warmer fringes of their range, American pika abundance in the North Cascades of Washington was more strongly influenced by winter, rather than summer weather conditions (Johnston et al. 2019). Pikas were most heavily affected by acute and chronic cold stress at mid elevations (1000-1400m) where temperatures were stressfully low (typically < -5°C) and the snowpack was not consistently adequate to provide insulation (Yandow et al. 2015, Johnston et al. 2019). Similarly, Northern pikas in Nepal living in areas of warmer average minimum temperatures in winter were in decline likely due to acute cold stress (< -5°C) from snowmelt reducing insulation beneath the talus rather than from heat stress in summer (Koju et al. 2021). Insulation provided by snow (specifically, snow depth) is particularly important during springtime to reduce cold stress for pregnant females because they typically breed in early spring, and timing of reproduction is directly linked to long-term variance of snowmelt (Smith 1987, Smith and Weston, 1990, Morrison and Hik 2007, Bhattaccharaya et al 2014). At low elevations, pikas may respond to cold stress by resorbing fetuses (Millar 1974) resulting in reduced reproduction rather than reduced adult survival following years of low snowpack (Johnston et al. 2019). Therefore, one metric that may be important for pikas and other small mammals is the daily (or diurnal) temperature range (DTR; Varner et al. 2015, Bonebrake et al. 2020), where high DTR indicates insufficient insulation beneath the talus. In response to either cold or heat stress, pikas may seek shelter deep beneath the talus where temperatures are more stable or move upwards in elevation if adequate habitat is available (Millar et al. 2014).

Pikas need adequately sized rocks and forage nearby, which limits upslope movement in response to a warming climate and they already reside near their upper elevational limits (Ray et al. 2012). American pikas in California moved about 150m up in elevation over a decade, averaging about 12m per year (Beever et al. 2010), but pikas' response to climate change is highly variable across bioregions (Millar and Hickman 2021). Talus size and subterraneous cavities are smaller closer to mountain peaks, specifically on mountains with a high slope degree angle (Behre 1933), which could further limit the potential for upslope movement. Another limitation to upslope movement is the lack of forage species available at higher elevations near mountaintops (Johnston et al 2019). Pikas must occupy dens near alpine plant communities to access forage while also avoiding predators in the safety of the talus (Huntly et al. 1986, Roach et al. 2001, Bhattacharyya et al. 2013). Therefore, the proximity of "foraging meadows" may be an important characteristic of continued den occupancy. Within an area occupied by pikas, relatively few territories are available to colonize each year, so competition for territories is often very high (Smith and Ivins 1983) and adults rarely disperse from their territories once they are established (Zgurski 2011).

We expected collared pika territories that remained occupied across years to differ from those that were abandoned over the course of the study, and we investigated a set of diverse factors influencing territory persistence. We used the microhabitat and microclimate features associated with pika territories to test three non-exclusive hypotheses about the relative importance of winter conditions, summer heat, and forage availability (Table 1.1). Additionally, because rock size may also influence microclimate within dens, we explored the relationship between rock size and several microclimate variables. High turnover and over-winter mortality rates in pika territories are common across many climate regimes (e.g., Peacock and Smith 1997, Jeffress et al. 2013, Kreuzer and Huntley 2013, Smith 2020), yet still relatively unknown for collared pikas living at higher latitudes (Morrison and Hik 2007). Due to this potentially high turnover rate, we were interested in evaluating territory persistence over time, which is a key benefit of using occupancy models. We tested three non-exclusive hypotheses:

H1: *Summer Den Temperature Hypothesis:* Dens that experience excessive heat during summer and high daily thermal fluctuations indicating poor insulation are less likely to remain occupied. Because den temperatures are correlated with ambient temperatures, we expect there to be a quadratic effect of temperature with an ideal mid-temperature range allowing for sufficient forage growth surrounding the territory but few days with excessive heat (>20-25°C; Yandow et al. 2015, Otto et al. 2015, Benedict et al. 2020). We predicted that dens that maintain a mid-range of temperatures and low DTR during summer (June 1 – September 1) are more likely to remain occupied.

H2: *Winter Den Temperature Hypothesis:* Pika dens lacking sufficient insulative properties through winter are less likely to remain occupied. We predicted that dens that have relatively low DTR during Nov 1 – Apr 1 are more likely to remain occupied. We also expected that dens are more likely to remain occupied when they remain at a stable temperature around freezing, rather than at consistently higher or lower temperatures during Nov 1 – Apr 1.

H3: *Forage Availability and Storage Hypothesis:* Dens with a greater storage capacity that are close to high quality vegetation are more likely to be persistently occupied because proximity to forage resources reduces energy and risk associated with haying, and storage of forage in haypiles is critical for overwinter survival. We predicted that dens with relatively large rocks, large haypiles, and proximity to foraging meadows will be more likely to remain occupied.

We used occupancy modeling to estimate den persistence as a function of environmental parameters. Occupancy modeling is a common approach to examining small mammal territory turnover dynamics driven by climate and habitat characteristics (e.g., Bajaru et al., 2019; Gomez et al., 2018; Gorosito et al., 2018; Infante et al., 2022; Thornton et al., 2013). We evaluated climatic conditions and climatic features to test our hypotheses on den occurrence and used these data to estimate territory persistence. Pikas have long been a focus of climate change research, especially regarding the effects of summer heat on population persistence and adaptation. However, few studies have focused on individual-level territory turnover rates to determine mechanistic variables driving persistence or declines during both summer and winter, and even fewer within collared pika habitat (Millar and Hickman, 2021). Our study examines mechanistic variables driving population persistence by linking them to occurrence of individual collared pika dens through time.

Methods

Study Areas – We conducted research in three study areas along a climate gradient in Southcentral and interior Alaska across 5 years (Figure 1.2). These study areas were selected from historically occupied sites that were monitored by the Alaska Department of Fish and Game (ADF&G) since 2018. The main distinctions among these areas are the vegetation communities and amount of shrub cover surrounding the talus, rock sizes within the talus, and climate conditions. (Table 1.2). Within each study area, we monitored multiple study sites, each with adistinct pika colony for a total of 12 sites/colonies across the 3 study areas.

The Denali study area was at the highest latitude (63.1 – 63.3°N) and had the widest range of elevations (930 – 1370 m) of the three study areas. It was situated within a tundra climate characterized by lower annual precipitation and colder winters compared to the other two study areas. Average monthly mean temperatures over the last decade (2010 – 2020) during the warmest months in summer (June – August) ranged from 12 to 17°C and widely ranged across years during the coldest months in winter (December-February) from -29°C to -8°C (Druckenmiller 2019, US Department of Commerce 2023). Annual precipitation from 2010 to 2020 ranged from 23 to 31cm and snow depth averaged 50 – 100cm (December – April) from 2014 to 2023 (US Department of Commerce 2023, Fielding Lake 1268 2023). The vegetation community was dominated by Ericaceous dwarf shrubs, graminoids, and tall shrubs (*Salix sp*.). This study area contained three distinct groups of study sites, or clusters of talus slopes occupied by pikas, separated by less than 10km, and assumed negligible rates of exchange among sites. The first group of sites were located along the Denali Highway, primarily in gently sloping talus patches near the road. The second group of sites were located 6-8 km from the main road and were unique in that they were entirely within large boulder-filled drainages rather than low-angle slopes. The third area was located along the Richardson Highway and consisted of one site with a south facing exposure and had the tallest and most abundant shrubs surrounding it. This site was occupied by a small number of individuals (<6 pikas) during the study.

The Hatcher Pass study area was located at 61.8°N and 1120 – 1190 meters (m) of elevation and was characterized by a maritime and continental transitional subarctic climate with mid-range temperatures and a diversity of forbs at the lower extent of the talus (Hayward et al. 2017). This study area supported an abundant population of pikas compared to our other study areas. Within the area, there were 4 sites with tagged individuals from a longer-term survival study conducted by ADF&G. Average monthly mean temperatures over the last decade (2010 – 2020) during the warmest months in summer (June – August) ranged from 12 to 17°C and widely ranged across years during the coldest months in winter (December – February) from -17°C to 0°C (US Department of Commerce 2023). Annual precipitation from 2010 to 2020 averaged 38 – 61 cm of rain and snow depth averaged 69 – 163 cm from December through April 2006 – 2023 (US Department of Commerce 2023; Independence Mine 1091 2023). The vegetation community within and surrounding the talus slopes occupied by pikas was diverse, consisting primarily of Ericaceous dwarf shrubs, forbs, graminoids, lichens and mosses with some tall shrubs (*Salix sp.* and *Alnus sp.*) interspersed. Hatcher Pass is a State Recreation Area that receives relatively high recreational use year-round including hiking, skiing, paragliding, 4-wheeling, and snowmobiling.

The third study area was located on the military base, Joint-Base Elmendorf Richardson (JBER), in Anchorage (Figure 1.2). Situated only 17 km from the coast but at 1040 – 1130 m of elevation and at 61.1°N, this study area had a maritime subarctic climate with cool summers, cold winters moderated by proximity to the ocean, and consistent cloud cover and fog. Average monthly temperatures over the last decade (2010 – 2020) during the warmest months in summer (June-August) ranged from 12 to 17°C and widely ranged across years during the coldest months in winter (December-February) from -16°C to -1°C (US Department of Commerce 2023). Annual precipitation ranged from 35 – 58 cm during 2010 to 2020 and snow depth was highly variable across years averaging 25 – 38 cm from December through April 1990 – 2021, ranging from a high of 91 cm in 1990 and 2006 and a low of 0 – 5 cm during mid-winter in other years (Alaska-Pacific RFC 2023). High winds within this study area likely contribute to the variability in snow accumulation. During our study, snow depth during mid-winter was relatively high ranging from 48 – 107cm at a nearby SNOTEL site (Eagle River 7.8 SE) at a similar elevation (Alaska-Pacific RFC 2023). The vegetation community at this site was sparse, primarily consisting of Ericaceous dwarf shrubs such as mountain heather (*Cassiope mertensiana*), graminoids, lichens and mosses. There were no tall shrubs and few forbs within or near these pika sites. We monitored one pika population in this study area over a large area of connected talus.

Pika Den Surveys – We recorded microhabitat and temperature measurements as well as occupancy status of pika territories from 2017 to 2022. During the first year of this study, we identified active pika territories by the presence of haypiles containing fresh vegetation and defined the den as the rocks immediately surrounding the largest haypile within a pika territory. Consequently, all dens that we monitored were occupied during the first year they were surveyed and re-visited each subsequent year. Dens were physically marked with a wooden stake placed beside the rock housing the largest haypile within that territory, and we recorded the location using a GPS to facilitate annual monitoring. Each summer season during June to August, we visited the den and recorded the number and size (length, width, height) of haypiles within the territory, the size of the rock sheltering the largest haypile (length, width, height), the distance of the den to the nearest foraging meadow (area >5 m^2), the dominant vegetation within that meadow (Ericaceous dwarf shrub, tall shrub, dry graminoid herbaceous, forb, moss/lichen), and the distance to the nearest tall shrub patch (>0.5 m tall) (Table 1.3).

Temperature dataloggers (Onset® HOBO MX2201 and Thermochron iButton) were deployed in a subset of pika dens across all of our study sites to monitor the temperature of their dens throughout the year during 2018 – 2022. The dataloggers were tied to a fist-sized rock with metal wire and placed within the largest haypile at each pika den, well out of direct sunlight approximately 20 – 30 cm from the entrance. Between 3 and 20 dataloggers were deployed at each site, depending on the size of the colony, and exchanged each summer to ensure that they continued logging throughout the year. HOBO loggers were set to record temperature every hour and iButtons every 4 hours. The temperature recording period was June 2018 to August 2022 and totaled 32 year-long den temperature readings during 2018 – 2019, 59 during 2019 – 2020, 74 during 2020 – 2021, and 89 during 2021 – 2022 (N=253). At each study site, we also assessed ambient temperature by placing one iButton temperature logger housed within a protective PVC pipe container above the expected snowpack (N=10) (Sakiyama et al. 2021, Varner and Dearing 2014). These ambient loggers recorded one temperature reading every 4 hours.

Statistical Analysis – We tested our hypotheses on the influence of microclimate and microhabitat variables on collared pika den occurrence across our 3 study areas using Bayesian hierarchical multi-season site occupancy models developed by MacKenzie et al. (2003), and Royle and Kéry (2007). Our study was set up to monitor active pika dens across years, so all dens were occupied during their first year ($\psi_{t=1}$ =1), which gave us a prediction of den persistence through time (MacKenzie et al. 2003). We therefore placed the effects of our covariates on the persistence term (Φ) rather than the den re-establishment term (γ) . We modeled subsequent turnover rate across 6 years, with a staggered entry of dens each year, beginning with 11 dens in 2017 and ending with 197 dens by 2022 that had at least 2 years of observations. Temperature data were collected at different intervals for durations spanning 1 – 2 years depending on the date temperature loggers were set and retrieved at each study area and site. Covariates related to weather and haypile size varied across years, whereas rock size and distance to tall shrubs were fixed across years.

We made several assumptions about our occupancy models that we believe are justifiable due to our sampling design. In contrast to most occupancy models, we assumed perfect detection of occupied pika dens (p = 1), and therefore modeled occurrence rather than occupancy. Pika occupancy, in general, can be confidently determined by the presence or absence of fresh vegetation within the den with a high detection probability (i.e., approximately 1; Kukka et al., 2020, Smith 2020, Beever et al. 2010, Rodhouse et al. 2010, Peacock 1997), although some studies have refuted this assumption in areas of sparse or dry vegetation (Goldman et al. 2023, Rodhouse et al. 2018, Millar & Hickman, 2021, Smith et al. 2016, Millar et al. 2018, Camp et al. 2020). We believe that this assumption is justified in our study for several reasons. First, all dens were occupied during the first year they were monitored, and dens were marked with a GPS point and stake to facilitate location in subsequent years, so we knew the exact location of all dens we were monitoring rather than randomly sampling across the site. Second, we monitored den occupancy using the presence of fresh vegetation in haypiles rather than detection of individual animals within the territory. Studies with lower detection rates monitored individual pika occupancy or survival rather than the occurrence of active dens, and typically within habitats characterized by dry climates at low elevations in the American pika range (Goldman et al. 2023, Shinderman 2015, Wilkening and Ray 2016. Additionally, we incorporated a 25 m search radius (average pika territory size; Smith 2008) around each pika den to find satellite haypiles, so even if a den had moved to another nearby rock within that territory, we would find it and the territory was recorded as occupied (this occurred only 9 times out of 723 total den visits). Third, we visited all study sites during later summer (late July – August) after pikas had already been foraging and building their haypiles for months making them easy to detect with confidence. Because we conducted some work during June and early July at the Hatcher Pass study area, we visited each den again in the later season during 2019-2021 to confirm that den occupancy was classified correctly. Finally, our study system is characterized by high rainfall and green vegetation was routinely cached by pikas, which made haypiles stand out against the rocks they were cached under and easy to discern a currently active den from an abandoned den (Figure 1.3). Although questionable for occupancy studies of other species, the assumption of perfect detection of occupied pika dens has been accepted and tested many times in the past and is more acceptable in areas of lush vegetation as opposed to sparce and dry areas where freshly cached vegetation is difficult to discern from haypiles made the previous year (Bhatccharaya et al. 2014, Beever et al., 2010; Rodhouse et al., 2010; Erb et al., 2011; Jeffress et al., 2013, Stewart et al. 2015, Ray et al. 2012).

Pikas typically display high site fidelity, low dispersal rates, and tend to remain within a small territory throughout the foraging season (Rodhouse 2018 (centrally placed foraging behavior), Peacock 1997, Smith 2008). On the rare occasion (< 10 observed and recorded across years) that a pika did switch dens within the same territory, we used measurements from the initial occupied den within that territory for analysis. However, due to the rarity of these events and proximity of a new den within the same territory (< 25m), this change likely did not significantly affect our results.

Variables included in our models represent metrics of microhabitat and microclimate features that could be important for collared pikas based on studies of American pikas and align with our three hypotheses (Table 1.3). Temperature trials on American pikas identified thresholds at which they begin to experience heat stress (> 25.5 to 29.4℃) and cold stress (< -5°C; Smith 1974). Consequently, we evaluated effects of temperature on occupancy by modeling intervals of 5°C below or above these thresholds similar to the approach used by Yandow et al. (2015) for American pikas. Due to the physiological similarity between American and collared pikas and the unknown thermal tolerance of collared pikas, we chose the same temperature intervals tested by Yandow et al. (2015) and Smith (1974), and added one colder interval (-10°C) to account for collared pikas' potential adaptation to a cooler climate. We also tested DTR (daily temperature range) which represents both chronic and acute thermal stress and was calculated by subtracting daily maximum temperature from daily minimum temperature from within dens (Varner et al. 2015, Bonebrake et al. 2020). Finally, we included the average daily maximum and minimum temperatures in summer and winter as metrics of chronic thermal stress within each season, which has been an important predictor of pika occupancy (Rodhouse et al. 2018, Monk and Ray 2022). We defined the winter season as November 1 – March 31 based on a study by the International Arctic Research Center, which defined the start of the winter season in the locale of my study area as early November and lasting 137 – 144 days on average (Walsh and Brettschneider 2019). We defined the summer season as June 1 – August 31 to encompass the warmest daily temperatures during the year without snowpack presence and the peak foraging season typically observed for Collared pikas (US Department of Commerce 2023, Alaska-Pacific RFC, Morrison & Hik 2008, Morrison et al. 2009). We normalized all variables with a z-transformation to compare them on the same scale and evaluated correlation among variables with Pearson's correlation coefficient.

We estimated model parameters with a Bayesian framework and Markov chain Monte Carlo (MCMC) samples of posterior distributions. We used JAGS (version 4.3.1), a program for Bayesian analysis with Gibbs sampling in the BUGS language through R version 4.2.2 and the R2jags package (Martyn Plummer 2003). We constructed additive models on the logit scale to test our hypotheses about the influence of covariates on dynamic territory occupancy (Royle and Dorazio 2008, Jeffress et al. 2013, Rodhouse 2018). We tested a quadratic effect on all variables for which a nonlinear trend could logically occur. Due to lack of variability in the data for the categorical variable “meadow type”, we did not include this variable in our models. Therefore, we could only assess microhabitat as distance to a foraging meadow, distance to tall shrubs, and rock size. For clarity in model interpretation, we re-defined several terms of the occurrence model to fit our system. We defined extinction rate as *den abandonment* rate and colonization rate as *den re-establishment* rate because all dens were initially occupied. Finally, the resulting survival rate is the *den persistence* rate, which is the probability that a den would remain occupied year after year.

We used uninformative, normally distributed priors Normal(mu=0, tau=0.01) for all variables except “distance to vegetation” and “distance to shrubs”, which we set to (mu=0, tau=0.05) for improved convergence. Tau (τ) represents the precision of the variable estimates and is equal to 1/variance. Priors for den re-establishment rate (γ) and 1- den-abandonment rate (ψ) were set to dbeta (1,1). We selected uniform priors so that they would have little influence on the resulting inference and would instead be most informed by the data because we had no previous knowledge about the expected values of these variables (Northrup and Gerber 2018). Due to the highly variable climate regimes of our three study areas, we first set an index for study area on our priors for microclimate and microhabitat covariates, so missing data would be informed by covariate values from each study area separately. However, DIC values of these models were much higher than the same ones with no index for study area. Additionally, convergence was difficult to achieve with this method and required more data, so we did not use an index for study area in our final analysis.

We used a stepwise procedure to build our models due to the large number of parameters with varying temporal scales, correlation among microclimate parameters, and difficulty of convergence (Rodhouse 2018). We first ran univariate models of all microclimate variables with and without quadratic effects of some of those variables, and hypothesis driven additive models with microclimate covariates that were not correlated (e.g. summer and winter metrics). We selected the top 10 of these models with microclimate metrics based on the lowest deviance information criterion (DIC) value. Next, we repeated this process to build models containing only microhabitat covariates and selected the top 10 microhabitat models. We then built hypothesis driven additive models with the microclimate and microhabitat covariates that were within those top 20 models selected. The final model set contained the top 10 microclimate models, the top 10 microhabitat models, and the additive models with both sets of covariates. After running the final model set, we selected all models with a DIC value lower than the intercept-only model for further evaluation.

Posterior summaries of our models were based on 100,000 MCMC samples of the posterior distributions from 5 chains run simultaneously, thinned by a factor of 20, following an initial burn-in of 20,000 MCMC iterations. We assessed convergence of our results with traceplots, the Gelman-Rubin diagnostic (R-hat), and Geweke's convergence diagnostic. Convergence was reached for all parameters included in the top models according to the criteria R−1|<0.1 and Geweke statistic > +/- 0.05 (Ntzoufras 2009, Rodhouse et al. 2018, Geweke 1992a, Geweke 1992b). For all models that were ranked higher than the null model, we evaluated the traceplots and re-ran some models with wider priors and more MCMC iterations when convergence was questionable. We selected our final top models based on the lowest DIC value, the uniformity of the traceplots, and R-hat value <1.1. Finally, we tested relationships between covariates that we expected could be related (e.g., haypile size and temperature as a function of rock size) using linear regression models to help interpret model results. Finally, we evaluated the effects of each covariate on den persistence using covariate means from the top models in a stable equilibrium equation:

$$\psi_t^{(eq)} = \frac{\gamma_t}{\gamma_t + (1 - \phi_t)}$$

In this equation, terms are defined as stable equilibrium of den occupancy probability through time ($\psi_t^{(eq)}$), annual den re-establishment rate (γ_t), and annual den abandonment rate (ϕ_t). Results of this equation gave use the estimated probability of den persistence at the full range of observed values of the most influential covariates, while holding all others constant (Royle and Dorazio 2008).

Results

We surveyed 197 individual pika dens over 5 years, beginning with 20 occupied dens in 2017 with additional dens monitored in subsequent years (Table 1.4). No new dens were added in 2022. Proportions of pika dens that were occupied varied across the 5 years (Table 1.5). Given that all dens were active during the first year they were monitored, and new active dens were added each subsequent year, sample sizes changed annually and likely contributed to a nonlinear trend in occupancy across the study years. The raw proportion of dens that were occupied for at least 2 subsequent summer seasons ranged from 0.74 in 2018 to 0.47 in 2022.

Occurrence probabilities varied slightly along bioclimatic gradients represented by each study area (Table 1.4). The microclimate and microhabitat metrics varied more among than within study areas, which complicated estimation of these effects (e.g., rock size, distance to shrubs, DTmax-w) (Figure 1.4). Temperature loggers inside pika dens in the Denali study area consistently recorded lower daily temperatures during winter and higher fluctuations in temperature during summer compared to both the Hatcher Pass and JBER study areas.

Our Bayesian hierarchical occupancy models allowed us to estimate the effects of microclimate and microhabitat on annual den persistence. Based on the intercept-only model re-establishment and abandonment rates varied annually with a higher re-establishment than abandonment rate in all but the last transition year (2021 – 2022) (Table 1.5). However, our study was primarily designed to estimate rates of persistence as a function of abandonment rather than re-establishment due to the initially occupied status of all dens during their first year. In all but the second transition year (2018 – 2019), abandonment rates were consistently below 50% with an average of 38.4%, and persistence rates were consistently above 50%, with an average of 61.6% (Table 1.5).

Our model results supported our *summer den temperature hypothesis* and were contrary to the expectations of our *winter den temperature* hypotheses. The top two models (ΔDIC < 2) both contained the microclimate covariates *average daily maximum temperature* (DTmax) in both summer (β = -0.11, CRI = -0.26, -0.02) and winter (β = 0.17, CRI = 0.03, 0.41) as a quadratic effect with credible intervals that do not overlap 0 (Table 1.6, Figure 1.5). No microhabitat covariates had a significant influence on den persistence, contrary to the expectations of our *Forage Proximity and Storage* hypothesis. The probability of a den remaining occupied year to year (den persistence) peaked when DTmax in summer was between 20 and 22°C, and was lowest at our lowest observed DTmax-s of 1.9°C, based on results of the stable equilibrium equation (Figure 1.6). As expected, the DTmax in summer positively influenced den persistence at moderate temperatures only, and den persistence declined under extremely warm summer temperatures, although uncertainty was high. During winter, den persistence was lowest when DTmax was between -1.5 and -3.0°C and was highest at our lowest observed value of -11.7°C (Figure 1.7).

We explored the relationship between rock size and several microclimate variables and haypile volume in a post hoc analysis because rock size likely influenced microclimate and storage capacity within dens. Linear regression models suggest a relationship between rock size and summer temperature values of DTmax-s ($p = 0.03$) and DTR-s ($p = 0.02$) with a slight but significant negative trend. These results suggest that larger rocks had relatively cooler and more stable den temperatures across all study areas during the summer. Rock size did not have a significant effect on winter den temperatures and contrary to our expectations, pikas did not cache greater amounts of vegetation under larger rocks.

Discussion

Our study revealed mechanistic connections between climatic features and den persistence over time for collared pikas. Our work demonstrated that both summer and winter temperatures and the insulative capacity of dens influenced persistence rates of collared pika dens. However, contrary to our expectations, daily temperature fluctuations were not strongly related to den persistence. Additionally, rocks and particularly large rocks, appeared to buffer den temperatures during summer but not winter, and this habitat feature might facilitate the persistence of populations of collared pika under warming Arctic conditions. While most studies of pikas focus on populations, our research focused on the success or failure of individual pika dens, which helps identify the mechanisms underpinning population extirpation or persistence. The hierarchical Bayesian framework allowed us to specify which parameters changed through time, accounted for more uncertainty than a frequentist approach, and facilitated use of the entire dataset even when covariate values and occupancy status were missing across years, which allowed for a larger sample size (Rodhouse et al. 2018). These results advance ecological understanding about how climate influences collared pika den occupancy and can inform management for a species of concern across western Canada and Alaska by helping to identify habitat areas where conservation efforts may be especially beneficial.

In accordance with expectations from our *summer den temperature* hypothesis, pika dens had a higher probability of persistence at moderate *average daily maximum temperatures in summer*. This temperature range was centered around 21°C, and probability of persistence decreased above and below this temperature, although there was greater uncertainty at the high end of our temperature gradient. A comparable temperature range correlated with den occupancy of American pikas in California and Nevada, even though we suspected collared pikas would be adapted to cooler summer temperatures (Millar et al. 2016; Yandow et al. 2015). However, higher temperatures up to 25.5°C were reported in occupied dens of American pikas in Lava Beds National Monument (Rodhouse et al. 2016). We placed our temperature sensors in haypiles beneath the largest rock in the territory, 20 – 30 cm from the entrance. Our recorded temperatures may have been warmer and more similar to the ambient temperature than those reported by researchers who placed sensors deeper within the talus (>1m) where subsurface ice maintains a more stable and cooler microclimate (Smith et al. 2016, Millar et al. 2014).

We expected a quadratic effect of summer heat due to the importance of warm temperatures for growth of forage species, and low maximum temperatures tolerated by pikas while foraging aboveground. Fossil records of American pika occurrence and current occupancy of collared pikas suggest a strong reliance on a permafrost layer within their habitat to maintain cool temperatures throughout the year (Hafner 1994, Zgurski 2011). The importance of the metric, average daily maximum summer temperature within dens rather than daily temperature range (DTR), suggests that chronic rather than acute temperature measurements are better predictors of collared pika den persistence. This conclusion is consistent with the findings of thermoregulatory research on American pikas which demonstrated that chronically high maximum temperatures during summer had a stronger influence on pika extirpations and foraging behavior than acute temperature metrics (Wilkening et al. 2011, Beever et al. 2010).

We expected the most suitable winter den temperatures to hover around 0°C, indicating a sufficiently insulative snowpack, but that is not the trend we observed. Dens with average temperatures just below freezing had lower probabilities of persistence than those with colder temperatures, which might reflect den abandonment due to moist conditions within dens due to periods of snowmelt above the insulative layer. Indeed, other subnivean species rely on temperatures below 0°C during winter to sustain dry microclimates (e.g., tundra voles, *Microtus oeconomus* (Aars and Ims 2002), wolverines, *Gulo gulo* (Glass et al. 2022), wood frogs, *Rana sylvatica* (Pauli et al. 2013)). For example, a study of willow grouse (*Lagopus lagopus*) burrows beneath snow during winter in Finland (at a similar latitude to our study areas, >60°N) revealed that when burrows reached –4°C, the snow began to melt, and the birds would get wet (Melin et al. 2020). Wet conditions within pika dens resulting from freeze-thaw events during winter can reduce survival even more than purely cold conditions due to both acute cold stress and degradation of haypiles (Haga 1960, Wilkening et al. 2011, Ray et al. 2012, Gergel et al. 2017, Lute et al. 2015, Yandow et al. 2015, Rodhouse 2018, Johnston et al. 2019, Koju et al. 2021). Colder pika dens in our study could have been more successful for indirect reasons such as a consistently deep snowpack for a longer period, minimal freeze-thaw events, and less condensation within dens, which could be less costly from a thermoregulatory standpoint (Korhonen 1980, Courtin et al. 2018, Shipley et al. 2019). Contrary to our expectations, DTR in winter did not influence den persistence. However, den temperatures did not fluctuate much during winter (< 1°C on average) in any study area across the four winter seasons (Figure 1.4).

Climate data indicate that winter temperatures in Alaska and western Canada have increased 3-4°C on average over the last 50 years and are continuing to increase more rapidly than summer temperatures (Overland et al. 2019). The winter of 2018 was the second warmest winter on record in the Arctic (+6°C; above 60°N; within our study areas) (Overland et al., 2019), and it was also the year with the lowest den persistence rates (0.46) and highest den abandonment rates (0.54) within our study (Table 1.5). A study of American pikas in the southern Rocky Mountains, USA, documented that DTmax of ambient air in winter months was higher on average than historical temperatures, and this trend was more pronounced under the talus within pika dens (Monk & Ray, 2022). Warmer winters in Alaska (Overland et al., 2019) could negatively affect collared pikas, especially because talus does not adequately buffer pika dens from temperature change during winter without a sufficiently deep snowpack (Morrison and Hik 2007, Beever et al. 2010, Bhattacharyya et al 2014, Johnston et al. 2019)

We did not find support for a strong influence of forage availability based on proximity to meadows or forage storage (as assessed via haypile and rock size) on persistence of pike dens. However, the average rock size and range at our Denali study site were consistently smaller (Figure 1.8), and these differences may have influenced model results and contributed to the large variance in the parameter estimates for rock size. With a separate linear model, we tested whether haypiles were larger at dens with larger rocks, but we found no significant trend. Combining linear models with occupancy models is a common approach that can help interpret occupancy results and assess habitat selection by small mammals (Gorosito et al., 2018). Despite the lack of evidence supporting our models with microhabitat variables, we do not discount the importance of forage availability and microhabitat quality to den persistence, and we suggest that future research include additional forage and habitat metrics at a fine scale.

Shrub expansion associated with warming climates in alpine ecosystems is known to threaten alpine tundra obligate species due to habitat loss and predation risk (Martin 2017, Ge et al. 2012, Krebs et al 2014, Myers-Smith 2007, Myers-Smith 2011, Kukka et al. 2020). Anecdotal evidence of collared pika site occupancy indicates that extensive woody vegetation is a limiting habitat feature for collared pikas (Cannings et al. 2019). However, within both Denali and Hatcher Pass study areas, tall shrubs were typically surrounded by other palatable leafy green plants that pikas cached at high densities in their dens (personal observation). Therefore, although we expected to observe a negative effect of proximity to tall shrubs on den persistence, the distance from tall shrubs may have been a proxy for distance to foraging areas with a higher diversity of forage species, which could confound interpretation of this variable.

Rock characteristics likely influence pika den occupancy in numerous ways relating to den temperature and haypile protection. Post hoc analyses suggested that rock size was important for den temperature regulation. A linear model of raw temperature and rock size documented a correlation between rock size and summer temperature, in which dens with larger rocks were slightly cooler (lower DTmax-s) and had more stable (smaller DTR-s) temperatures. Therefore, rocks selected for dens may play a role in temperature regulation and haypile protection. American pikas living in Lava Beds National Monument rely on the cool lava rock tunnels to protect them from otherwise inhospitable heat and select for a particular rock type, which provides more stable temperatures through summer (Rodhouse et al. 2016). In contrast to collared pikas, American pikas in warmer and drier climates like the Great Basin, Sierra Nevada, and the Salmon River Mountains of Idaho, often create haypiles in the open without direct protection from rocks (Millar and Hickman 2021, Slichter 2020, personal observation 2023). However, collared pikas cache haypiles consistently beneath boulders, protected from rain and snow, and they appear to select for rocks of a minimum size (>50cm) (Cannings et al. 2019, Kukka et al. 2020). Therefore, collared pikas may be even more reliant on the rocks sheltering their haypiles to protect them during winter and from excessive moisture from precipitation that could affect quality of stored vegetation. Larger rocks may also provide a better vantage point for pikas to protect their territories from pilferers and more space to hide their haypiles, as well as a larger area to hide from arial predators (Smith and Weston 1990). Finally, larger rocks are typically more stable on the slope and may provide more protection from destruction of the den in weather events such as avalanches and excessive drainage during snowmelt (Kawamichi 1968).

We identified several limitations and related assumptions in our occupancy models, which we believe had minimal impact on our results. First, in contrast to traditional occupancy models that explicitly estimate detection probability, we assumed perfect detection of pika dens, and we modeled den occurrence rather than occupancy. We believe that extensive search effort coupled with green vegetation apparent in haypiles supports this assumption. Second, our sampling of microhabitat features did not accommodate shifts in the location of a den within an active territory, however, such shifts were rare. Third, we did not incorporate the spatial relationships among dens within a site into the occupancy models, but do not believe this would significantly influence den re-establishment rates due to strong competition for territories and the fact that most were within dispersal distance from occupied dens. Fourth, because juveniles likely have lower survival rates than adults, and they frequently move to new territories (Franken 2004), age class could influence den persistence estimates. Although we did not have consistent data on age classes within each year to model, we estimated that about 30% of the dens we monitored were inhabited by juveniles. Consequently, our models potentially underestimated actual rates of den persistence. Finally, we selected study sites that reflect a gradient of habitat conditions across the range of collared pikas in Alaska, but we did not use study area-specific priors within our models because limited data within each study area*year resulted in a lack of model convergence, and we obtained more robust estimates by pooling data across study areas.

Shifting ranges to higher elevations where temperatures are colder and, importantly, snowpack is deeper and less likely to melt may be beneficial for pikas as warming trends continue. For example, American pika occurrence shifted 145m up-slope on average over the last decade in the Sierra Nevada mountain range in California (Beever et al. 2011). However, there are several limitations to this solution for pikas, such as reduced forage availability and smaller rock sizes at higher elevations that may dampen the positive effect of upwards movement to escape warmer temperatures (Yandow et al. 2015). Rocks, with their ability to moderate summer heat, could be a key component in the ability of pikas to persist in place rather than shift in space in areas of suitable talus, but pika populations may still be constrained by warming winters. Larger boulders are typically located at the highest densities from a mountain's base to mid-way upslope, primarily due to the influence of gravity; farther up the mountain, the talus becomes progressively composed of smaller rocks, eventually transitioning into scree (Kirkby and Statham 1975). Temperatures inside the talus are increasing more rapidly than ambient air temperatures, which may restrict the effectiveness of this thermal refuge during the summer (Monk and Ray 2022). However, geological research on the thermodynamics of talus interiors in Norway concluded that the lower part of talus slopes maintains a cooler temperature due to convective heat transfer and may remain cooler despite increasing ambient air temperatures with climate change (Wicky and Hauck 2017). The contrasting nature of these patterns deserves further attention for research on pikas and other talus-dwelling species in the face of warming summers and winters, to determine where they might be able to persist and where they are likely most vulnerable.

There is a tremendous need for focused studies on microclimate and microhabitat to understand how broad-scale climatic conditions are affecting species in heterogeneous ecosystems such as mountainous habitats (Sakiyama 2021, Benedict et al. 2020, Rodhouse 2018, Varner and Dearing 2014). To advance understanding of factors influencing den occupancy by collared pikas, we suggest fine-scale examination of snowpack characteristics, humidity beneath the talus during winter, and forage quality and availability. Further exploration of the relationship between rock size and temperature could help managers identify habitats that may be most suitable in the future. Finally, exploring the effects of microclimate on foraging behavior during summer could provide a better understanding of the mechanisms driving population persistence or declines with increasing summer heat.

How local climate constrains a species' ability to persist in place is an important question to consider for wildlife management in a changing climate, especially in highly sensitive ecosystems. The magnitude of climatic variability increases with latitude and elevation (Chan et al. 2016), so collared pikas theoretically live in some of the most variable climates despite their low heat tolerance. At the rapid rate that winters are warming, collared pika dens may become increasingly less suitable, resulting in increased over-winter mortality and higher turnover rates of territories. Our models indicated that intermediate summer den temperatures and colder winter den temperatures were most suitable for collared pikas. As a result, pikas in areas of consistently high summer temperatures exceeding 20°C and diminished snowpack in winter may be vulnerable, although our results had a high degree of uncertainty at the upper end of summer temperatures. Large rocks could moderate the thermal environment of dens and help managers identify where pikas may be buffered by warming summer temperatures. Identifying local-scale mechanisms driving population persistence is important for determining areas that may be suitable for pikas, especially when analyzing species distribution models for the future (Mathewson et al. 2017, Sakiyama et al. 2021). Mechanistic variables identified as important metrics for collared pika occupancy within our study can strengthen these models that landscape level covariates cannot and are important to consider for pika and small mammal management in a changing climate.

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Tables

Table 1.1. Hypotheses and predictions for the effects of microhabitat and microclimate on seasonal territory occupancy of collared pikas across all study areas in Alaska, USA during 2017-2022.

Hypothesis	Description	Predictions
H1: Summer Den Temperature	Dens lacking sufficient insulative properties through summer are less likely to remain occupied.	**P1**: Dens that maintain a mid-range of temperatures and low DTR during June 1 – September 1 are more likely to remain occupied. **P2:** Dens that maintain a low DTR during June 1 – September 1 are more likely to remain occupied.
H2: Winter Den Temperature	Dens lacking sufficient insulative properties through winter are less likely to remain occupied.	**P1**: Dens are more likely to remain occupied when their average temperature is consistently close to 0°C during November 1 – April 1. **P2:** Dens that have relatively low DTR during November 1 – April 1 are more likely to remain occupied.
H3: Food Availability and Storage	Dens with a greater storage capacity that are close to high quality vegetation are more likely to be persistently occupied because proximity to forage resources reduces energy and risk associated with haying, and storage of forage in haypiles is critical for overwinter survival.	**P1**: Dens with relatively large rocks, large haypiles, and proximity to foraging meadows will be more likely to remain occupied.

Table 1.2. Description and habitat characteristics of each study area where collared pika den occupancy was monitored from 2017 to 2022 in Alaska, USA.

Study Area Name	**Hatcher Pass**	**Denali Hwy**	**JBER**
Location	Hatcher Pass State Recreation Area	Talus slopes along the Denali and Richardson Highways	Near Tanaina Lake and Snowhawk Valley within Training Area 427 and 431
# of Sites	4	8	1
Latitude (°N)	61.8	63.1-63.3	61.1
Elevation Range (m)	1120-1190	930-1370	1040-1130
Climate Type	Continental subarctic	Tundra	Maritime subarctic mountains
2010-2020 Dec-Feb Monthly Mean Temps (°C)	-17 to 0	-29 to -8	-16 to -1
2010-2020 June-Aug Monthly Mean Temps (°C)	12 to 17	12 to 17	12 to 17
2010-2020 Annual Rainfall (cm)	38 to 61	23-31	35-58
2010-2020 Dec-April Mean Snow Depth (cm)	69 to 163	50-100	25-38 (highly variable)
Vegetation Community	Diverse: Ericaceous dwarf shrubs, forbs, graminoids, lichens and mosses, and some tall shrubs *(salix sp.* and *alnus sp.*)	Dominated by ericaceous dwarf shrubs, graminoids, and tall shrubs (*salix sp.* and *alnus sp.*)	Ericaceous dwarf shrubs such as mountain heather (*Cassiope mertensiana*), graminoids, lichens and mosses. No tall shrubs within or near these pika sites and very few forbs.
Additional Information	Most abundant pika populations. Heavy recreation year-round	3 distinct groups of sites with different aspects and talus slope configurations	1 site spanning a large area of connected talus

Table 1.3. Descriptions of explanatory variables tested within models of collared pika den occurrence and persistence during 2017-2022 in Alaska, USA.

	Covariate Name	**Description (proximate to or within den)**
Temperature Covariates	Tmax	Maximum temperature within den (by year)
	Tmin	Minimum temperature within den (by year)
	ratio-5	Ratio of temperature recordings < -5°C (by year)
	ratio-10	Ratio of temperature recordings < -10°C (by year)
	ratio+20	Ratio of temperature recordings > 20°C (by year)
	ratio+24	Ratio of temperature recordings > 24°C (by year)
	DTR-s	Mean diurnal temperature range in summer (Daily Tmax - Tmin)
	DTR-w	Mean diurnal temperature range in winter (Daily Tmax - Tmin)
	DTmax-s	Mean daily maximum teperature in summer
	DTmin-s	Mean daily minimum teperature in summer
	DTmax-w	Mean daily maximum teperature in winter
	DTmin-w	Mean daily minimum teperature in winter
Habitat Covariates	Distance to shrubs	Distance (m) to nearest tall shrub patch
	Distance to meadow	Distance (m) to nearest foraging meadow
	# Haypiles	Total number of haypiles found in 25m radius (average pika territory size)
	Total Haypile Volume	Additive volume (cm^3) of all haypiles
	Max Haypile Volume	Volume of largest haypile (cm^3)
	Rock Size	Volume of the rock (cm^3) sheltering the largest haypile

Table 1.4. Summary of Collared pika den survey activity and occurrence within each study area in Alaska, USA during 2017-2022.

Study Area	**2017**	**2018**	**2019**	**2020**	**2021**	**2022**
			Total dens surveyed			
Hatcher Pass	20	40	68	82	92	98
Denali		28	50	56	75	68
JBER				11	18	17
TOTAL	**20**	**68**	**118**	**149**	**185**	**183**
			Proportion of occupied dens			
Hatcher Pass	1	0.75	0.4	0.66	0.6	0.43
Denali		1	0.57	0.42	0.62	0.51
JBER				1	0.64	0.53
TOTAL	**1**	**0.74**	**0.49**	**0.59**	**0.61**	**0.47**

* All dens were occupied during the first year they were surveyed, and additional dens were added to the survey each year. Proportions were calculated from dens that were occupied during at least 2 sampling seasons, so dens were not included in the proportion if it was the first year they were surveyed.

** Study Areas were comprised of 13 separate study sites of varying aspects and elevations (see Methods). Four sites were monitored in Hatcher Pass, six in Denali, and one large site at JBER.

Table 1.5. Null occurrence model results of annual re-establishment, abandonment, and persistence probabilities of collared pika dens for each transition year during 2017-2022 in Alaska, USA. Den re-establishment (γ) is the proportion of dens that transitioned from unoccupied to occupied, not including the first year they were monitored because all were initially occupied. Den persistence (φ) is the proportion of dens that remained occupied from one year to the next, and den abandonment (1- φ) is the proportion of dens that transitioned from occupied to unoccupied from one year to the next.

Transition Year	**den re-establishment rate (γ)**	**den abandonment rate (1-φ)**	**den persistence rate (φ)**
2017-2018	0.50	0.29	0.71
2018-2019	0.82	0.54	0.46
2019-2020	0.40	0.38	0.62
2020-2021	0.33	0.26	0.74
2021-2022	0.32	0.45	0.55
Average	**0.47**	**0.38**	**0.62**

Table 1.6. Specifications of the 5 top occurrence models ranked by DIC value. The top 2 models were of equal rank (ΔDIC < 2) but the microhabitat variables (Dist Shrub and Rock Vol) in the second model displayed are not significant. Priors were uninformative and normally distributed at (0, 0.01) for all parameters in the models displayed except for Dist Shrub which was set at (0, 0.05) for convergence.

Model Rank	**Model**	**DIC**	**Number of iterations**	**Burn-in**
1	DTmax-s+DTmax-s^2+DTmax-w+DTmax-w^2	425.1	1,000,000	30,000
1	DTmax-s+DTmax-s^2+DTmax-w+DTmax-w^2+ Dist Shrub+Dist Shrub^2+Rock Vol+Rock Vol^2	425.2	1,000,000	30,000
2	DTmax-w+DTmax-w^2+DTRs+Dist Shrub+ Dist Shrub^2+ Rock Vol+Rock Vol^2	479.6	100,000	20,000
3	DTmax-w+DTmax-w^2+DTR-s	495.3	100,000	20,000
4	Ratio 10°C+Ratio 10°C^2+DTR-s	515.6	100,000	20,000
5	Ratio 10°C+Ratio 10°C^2+DTR-s+Dist Shrub+Dist Shrub^2+ Rock Vol+Rock Vol^2	531.7	100,000	20,000
15	Intercept-only	698	100,000	20,000

Figures

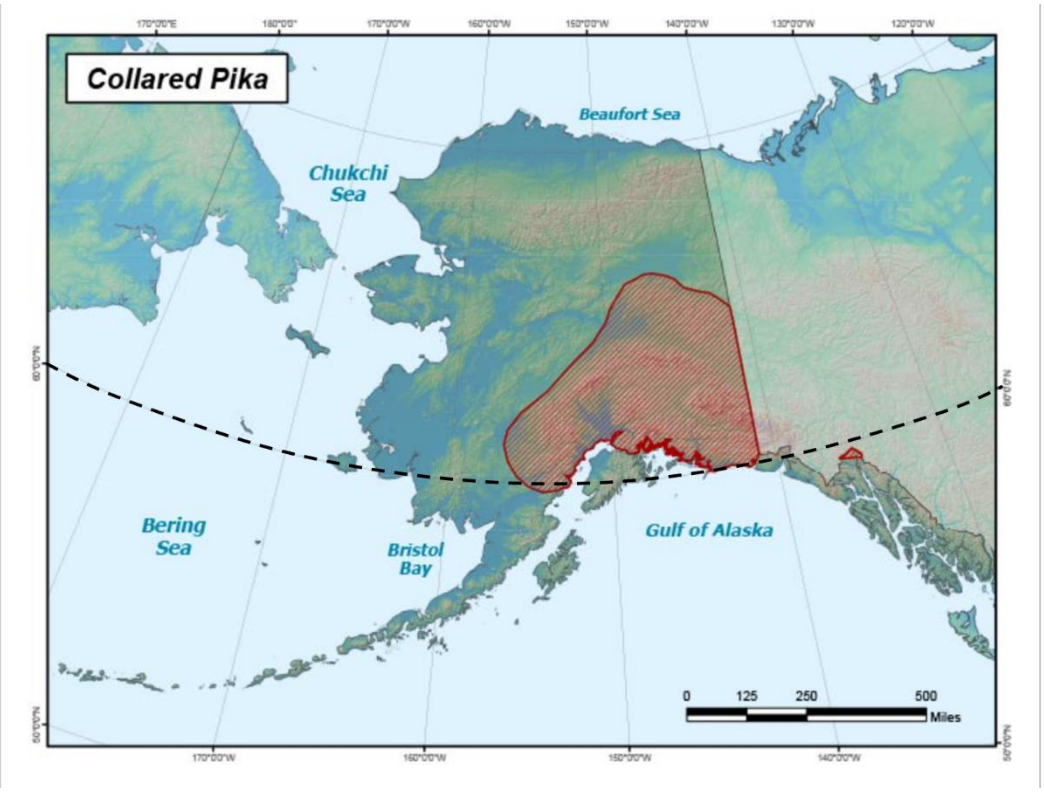

Figure 1.1. Collared pika distribution across Alaska, USA (©Alaska Department of Fish & Game). The dashed line emphasizes the 60°N mark, where climate scientists have observed arctic amplification resulting in more pronounced temperature increases compared to regions south of this latitude.

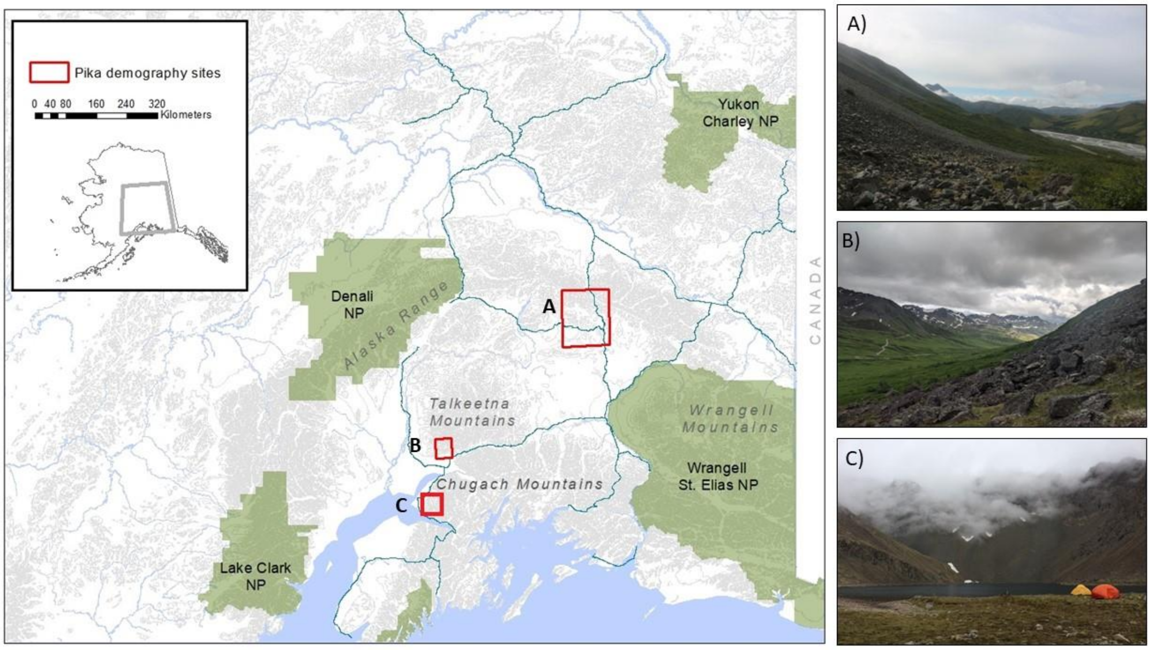

Figure 1.2. Study area locations in southcentral Alaska, USA. A) Denali Highway, B) Hatcher Pass, C) Joint-base Elmendorf Richardson (JBER). For reference, the green areas highlight National Parks and the red box encompassing the JBER study area (C) is within the city limits of Anchorage.

Figure 1.3. Comparison of A) occupied and B) abandoned collared pika dens in the field in Alaska, USA. Occupied dens routinely had large quantities of cached fresh vegetation, which remained green throughout the summer season, while abandoned dens had exclusively old brown vegetation from the previous year.

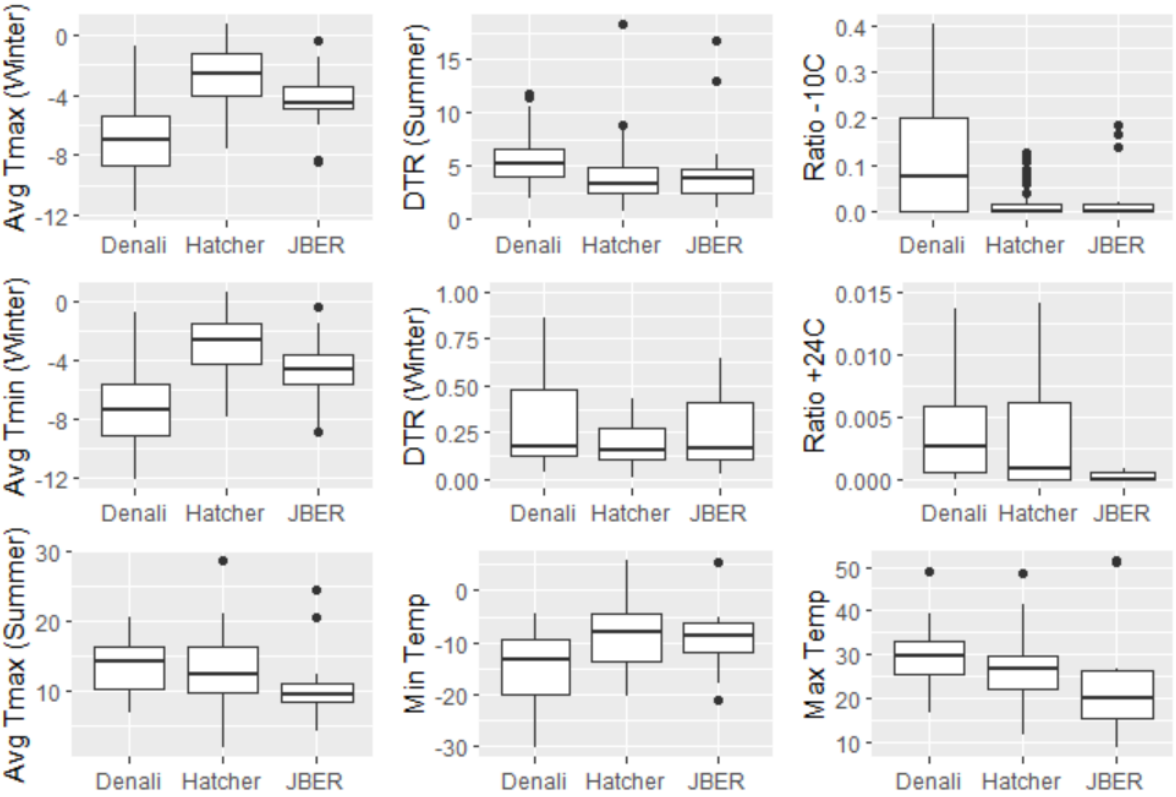

Figure 1.4. Boxplots comparing microclimate metrics within collared pika dens among each of three study areas in Alaska, USA, during 2017-2022.

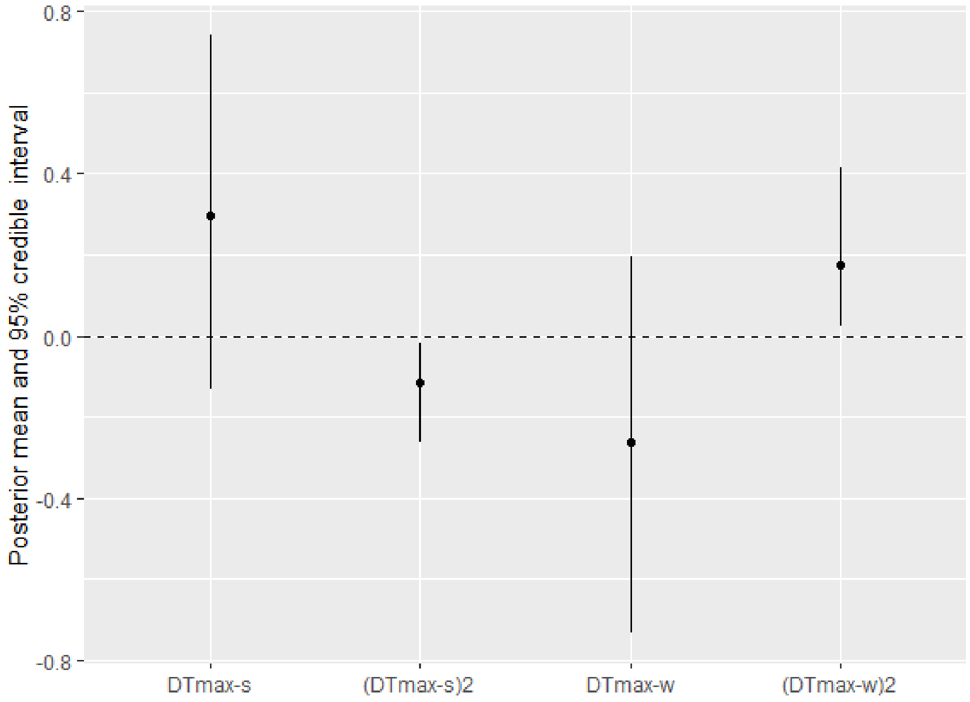

Figure 1.5. Estimated effect sizes of the average daily maximum temperature during summer (DTmax-s) and winter (DTmax-w) (± 95% credible interval) on persistence probabilities of collared pika dens across all study areas in Alaska, USA during 2017-2022 from the top occurrence model. The credible intervals of the quadratic term DTmax^2 of each covariate did not overlap 0 and best explained persistence probabilities over solely linear terms.

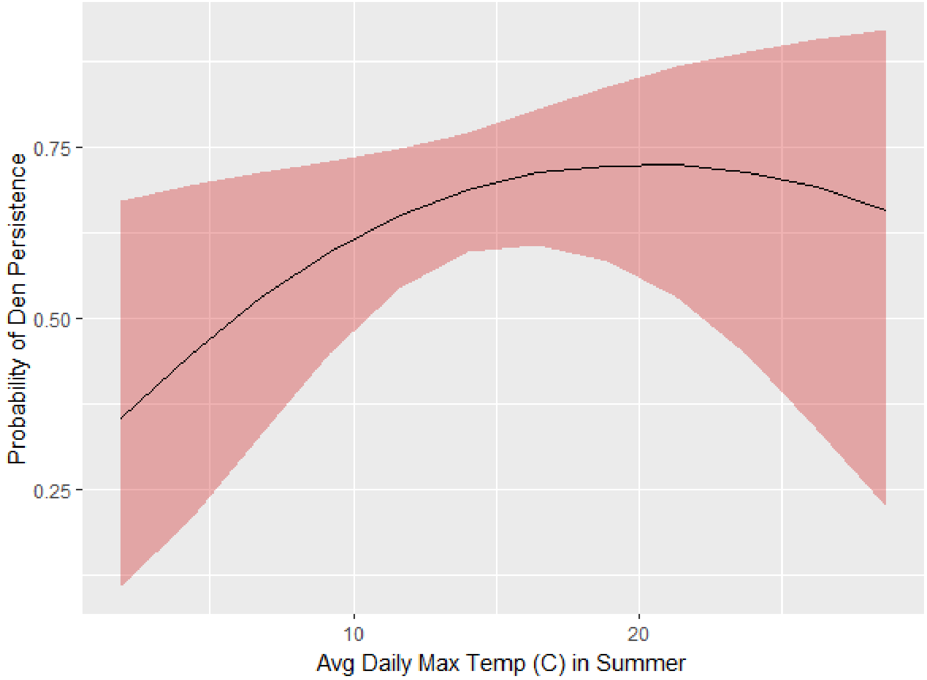

Figure 1.6. Estimated probability of persistence (± 95% confidence interval) of collared pika dens at the full range of observed values of average daily maximum temperature in summer (2 - 27°C), June-August 2017-2022 in Alaska, USA. Results are based on the beta estimates and the 95% credible intervals of linear and quadratic terms of this variable from our top occurrence model.

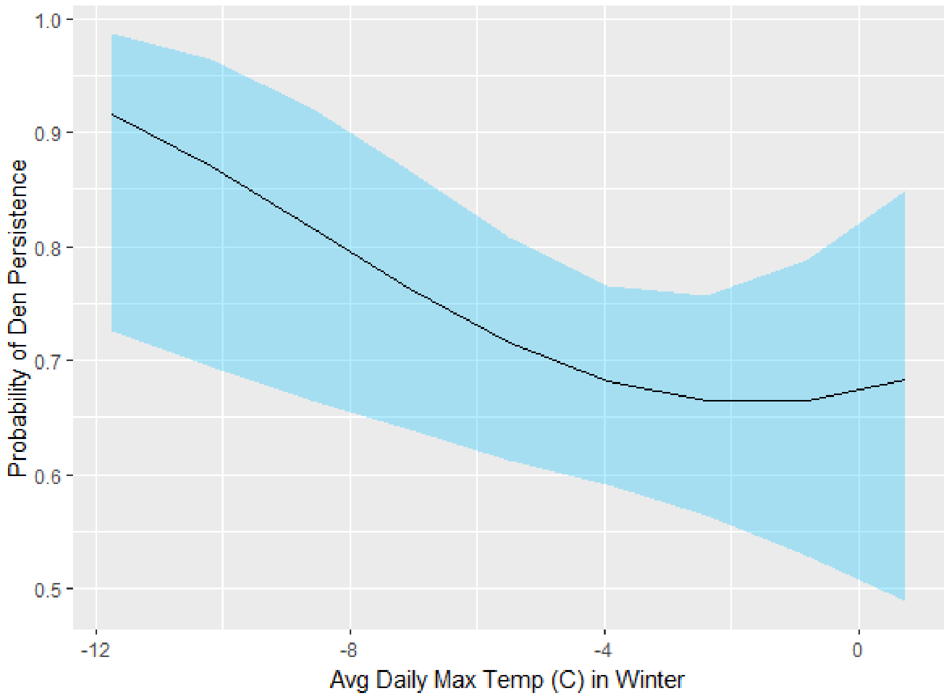

Figure 1.7. Estimated probability of persistence (± 95% confidence interval) of collared pika dens at the full range of observed values of average daily maximum temperature in winter (-11 - 1°C), November – April 2017-2022 in Alaska, USA.

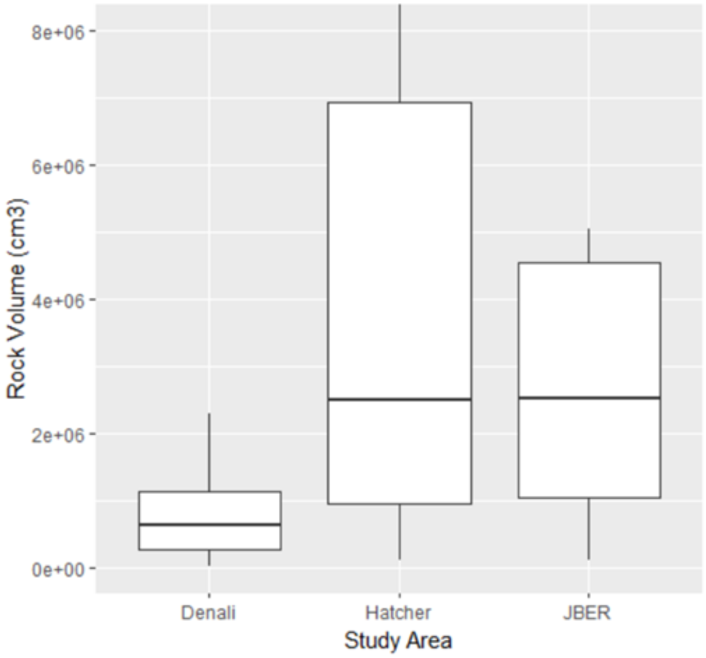

Figure 1.8. Boxplots comparing the distribution of rock sizes at collared pika dens within each study area in Alaska, USA from 2017-2022. Rocks selected for dens in Denali were 2-8 times smaller on average than in the other two study areas.

Chapter 2: Pika behavioral response to climate during the summer foraging season at high latitudes

Abstract

At high northern latitudes, the summer foraging season for herbivores is relatively short and changing with rapid temperature increase in the Arctic. Although summer may be getting longer, forage species may senesce before the season is over and excessively warm temperatures may limit daily foraging time. Collared pikas (*Ochotona collaris*) of western Canada and Alaska do not hibernate, and they spend the entire summer season foraging and caching vegetation to survive winter. Our objectives were to characterize daily and seasonal foraging patterns of collared pikas to identify thermal limitations and understand how warmer conditions may affect food acquisition. We conducted behavioral observations of collared pikas to determine when pikas were foraging at multiple sites in southcentral and interior Alaska during July and August 2020-2021. We tested the hypothesis that heat influences foraging behavior at diel and seasonal time scales by examining proportional daily foraging activity as a function of both temporal and thermal explanatory variables. Foraging patterns of collared pikas were dependent on temperature, wind, and time of day, and caching behavior was dependent on a narrower range of conditions compared to grazing. This is the first study to distinguish between specific foraging behaviors of collared pikas and evaluate environmental factors that influence them. We use these results to assess how this species of concern might be influenced by changing climactic conditions in alpine ecosystems.

Introduction

Animals have developed a wide range of adaptations and behaviors to address the daily challenge of acquiring food. Optimal foraging theory, first developed by MacArthur and Pianka (1966), states that natural selection favors animals using behavioral strategies to maximize net energy intake per unit of time spent foraging. Potential tradeoffs among time and energy spent traveling to and foraging for quality food items, missed opportunity costs, metabolic state, and risk of predation also shape foraging strategies (Brown et al. 1999). Thermal conditions also can constrain foraging by increasing the amount of energy required to search for high quality food (Owen-Smith 1998, Bozinovic et al. 2000, du Plessis et al. 2012, Carr and Lima 2014, Semenzato et al. 2021). Additionally, many non-hibernating small mammals spend substantial time searching for and caching high-quality food to last through winter, which can reduce the time available for feeding and also increase exposure to predation (Dally et al. 2006, Steele et al. 2014, Robin and Jacobs 2022).

Pikas (Ochotonidae) are small lagomorphs of alpine ecosystems that do not hibernate and exhibit a central place foraging strategy (Huntly et al. 1986). Pika species living in talus are generalist herbivores that forage in vegetation surrounding the talus edge (Wilkening 2007). Unlike any other alpine mammal, pikas spend the entire summer caching large amounts of vegetation with specific chemical properties beneath boulders in large *haypiles* to sustain them through winter (Dearing 1997, Galbreath et al. 2009, Gliwicz et al. 2006, Holtcamp 2010). Due to this caching or “haying” behavior, pikas influence the ecology of alpine ecosystems by contributing to seed dispersal, nutrient cycling, and soil development (Aho et al. 1998, Wesche et al. 2007, Zhang et al. 2016, Yu et al. 2017).

Research on American pikas (*Ochotona princeps*) demonstrated they have the capacity to adapt to warming summer conditions by altering their behavior (Johnston et al. 2019, Smith 1974), but to what extent? American pikas have a low heat tolerance and will die within 2 hours if exposed to ambient temperatures between 25.5 to 29.4°C without shedding heat beneath the talus, so they avoid activity during excessive summer heat (McArthur and Wang 1973, Smith 1974, Yandow et al. 2015, Moyer-Horner et al. 2015, Smith 2020, Benedict et al. 2020). Additionally, the difference between American pika mean stable body temperature (40.1°C) and upper lethal temperature (43.1°C) is only 3°C, which is a much narrower range than that of most other montane mammals (MacAurthur and Wang 1973, Smith 1974, Otto et al. 2015). American pikas retreat to a thermal refuge during midday heat in low elevation areas (e.g., Great Basin National Park, Nevada, USA; Smith 1974) and use habitat features to dissipate heat in areas that would otherwise be inhospitable (e.g., Lava Beds National Monument, California, USA; Ray et al. 2016). They make up for lost foraging time during warm days by foraging into the night (Smith 2020).

Collared pikas (*O. collaris*) of western Canada and Alaska, USA, live at higher latitudes than American pikas, and although the specific threshold at which they experience heat stress is unknown, they are adapted to cool climates (Figure 2.1). Under current climate conditions, the arctic (>60°N) is warming at a rate between 2 to 4 times that of the rest of the planet (Overland et al 2019; Yamanouchi and Takata 2020; Jacobs et al. 2021, Rantanen et al. 2022), so collared pikas are likely to experience a more pronounced temperature increase across most of their range than their southern relatives (Figure 2.1). Therefore, even though their climate is currently cooler, collared pikas may experience heat stress during the summer as temperatures continue to rise. A behavioral strategy to reduce heat stress that has been observed for talus-dwelling pika species is to retreat to their rock dens during the midday heat (Smith 1974, Bhattacharyya et al. 2014, Millar et al. 2014, Ray et al. 2016). At northern latitudes like Alaska, the window for pikas to gather food is relatively narrow due to long periods of snow cover. As summer temperatures are increasing with the current climate change trajectory, foraging time lost while waiting out the midday heat could have a significant impact on pika survival if they do not have enough time to build up their haypiles (Morrison et al. 2009). While warmer temperatures during late spring could result in a more productive growing season and potentially longer foraging period during summer, the peak availability of quality forage may occur earlier than the peak in haying activity for pikas due to their breeding cycle (Huntly 1991, Yandow et al. 2015).

Collared pikas may adjust their foraging patterns in response to climatic conditions to ensure that they cache sufficient forage for winter, but doing so may impose risks. In a study of collared pika foraging behavior, Morrison (2007) found they made more haying trips in the early morning and late evening in June but increased their haying rate at midday in July and August (during peak forage growth)and were consistently haying during all hours of daylight (18-21 hours per day). Similar patterns have been documented in other pika species, *O. Macrotis* (Kawamichi 1971) and *O. Princeps* (Smith and Weston 1990). Greater time spent foraging at night and longer or more frequent periods of rest during midday suggest that a thermal constraint could be imposed by rising temperatures. Additionally, it remains uncertain whether pikas can maintain their overall foraging time on warm days by adjusting their foraging schedule or if they adhere to a consistent temporal routine and lose foraging time.

Haypiles are a critical food resource for pikas during winter, especially for populations at high latitudes. For collared pikas, survival was highest when they began caching hay before July 31, suggesting that a long haying period allowed them to accumulate a sufficient cache to sustain them through the long winter, although the effect of this initiation date varied across years (Morrison et al. 2009). Similarly, survival rates of another northern pika species, the Durian pika (*O. dauurica*) of Mongolia (Zhong et al. 2008) indicated a heavy reliance on haypiles to survive winter, as determined by haypile removal trials and resulting population estimates the following spring. In contrast, haypile size of American pikas, which inhabit lower latitudes, was not a good predictor of reproductive success or over-winter survival, and they have been observed foraging for lichens, cushion plants, shrubs, tree bark and evergreen trees during the winter (Millar 1974, Conner 1983, Dearing 1997, Gliwicz et al. 2006). Therefore, the reliance on haypiles by pikas and correlation with winter survival may be region-specific and dependent on forage species availability through winter, and annual weather conditions (Gliwicz et al. 2006, Zhong et al. 2008, Smith and Millar 2018).

Along with increasing temperatures, weather patterns in the arctic mountains are changing (Serreze and Barry 2011, Thoman et al 2020), which could affect foraging and haying by pikas. One of the most apparent effects of climate change is the increase in and severity of extreme weather (Seneviratne et al. 2012). Wind affects the ability of pikas to hear approaching predators and to communicate with other pikas vocally, which has adverse effects on survival (Hayes and Huntly 2005, Zhou et al. 2023, Speakman et al. 2021). Heavy rainfall also poses risks such as the deterioration of haypiles, mold development, and thermal costs associated with wet fur (Moore 1987, Varner et al. 2023). Finally, solar radiation in the absence of cloud cover increases the effect of warm ambient temperatures during foraging and reduces the efficacy of talus as a thermal refuge (Smith 1974, Varner and Dearing 2014, Millar et al. 2016, Speakman et al. 2021, Zhou et al. 2023).

The objective of this study was to evaluate how temperature and weather conditions influence foraging by collared pikas. Specifically, we aimed to identify minimum and maximum temperatures at which pikas stop grazing (i.e., immediate consumption) and haying (i.e., harvesting and caching). We developed four non-exclusive mechanistic hypotheses to explain foraging responses of pikas (Table 2.1).

H1: Summer heat – On warm days, pikas are less active aboveground and remain closer to their dens when it is hottest because they are small-bodied endotherms that are constrained by a low tolerance to heat and behaviorally thermoregulate by resting below the talus (MacAurthur and Wang 1973, Smith 1974, Huntly et al. 1986, Otto et al. 2015, Varner et al. 2016). We predicted that on warm days, foraging activity would decrease as ambient temperature increased (P1), and the maximum distance that pikas are observed from their den would be negatively correlated with ambient temperature (P2).

H2: Weather conditions – Pikas are less active during inclement weather, potentially as a predator avoidance strategy (Hayes and Huntly 2005) and/or to conserve energy during cold and wet conditions (Moore 1987, Hayes and Huntly 2005, Zhou et al. 2023). We predicted that foraging activity would decrease during periods of rain, high wind speeds, and low temperatures which typically precede rain.

H3: Time of day – Pikas have a circadian foraging pattern that is independent of weather or temperature. We predicted pikas would hay and graze most frequently in the morning and late afternoon and rest during mid-day during all temperature and weather conditions.

*H4 Interaction between temperature * time of day* – Pikas modify daily foraging behavior in response to temperature (e.g., Pikas switch foraging activity to evening/night activity following hot days) (Smith 1974, Camp et al. 2020, Millar and Hickman 2021, Zhou et al. 2023). We predicted pikas would hay and graze more frequently during the early morning, evening or night on days with high maximum temperatures.

Evaluating how thermal constraints influence foraging and haying behavior by collared pikas can advance understanding of the mechanisms by which climate change could affect their population persistence. To our knowledge, this is the first study to address these questions for collared pikas, and our research can inform conservation strategies prior to population extirpations. Because species at high latitudes are experiencing rapid climate change, understanding behavioral responses and their fitness consequences will be important for conservation planning under different climate scenarios.

Methods

Study Areas - We conducted research in three study areas along a climate gradient in Southcentral and interior Alaska (Figure 2.2). The study areas were selected from historically occupied sites that were monitored by the Alaska Department of Fish and Game (ADF&G) since 2018. The main distinctions among these sites are the vegetation communities and amount of shrub cover surrounding the talus, rock sizes within the talus, and climate conditions. (Table 2.2). Within each study area, we monitored multiple study sites of distinct pika colonies for a total of 12 sites across the 3 study areas during July and August 2020-2021. Distinct colonies were identified by talus patches occupied by pikas and separated by ≥300 m with assumed low rates of dispersal (Zgurski and Hik 2014). Our study areas were situated at relatively high latitudes in the subarctic, above 59°N where global warming trends are most amplified (Overland 2021).

The Hatcher Pass study area was located at 61.8°N and 1120-1190 m of elevation and was characterized by a maritime and continental transitional subarctic climate with mid-range temperatures and a diversity of forbs at the lower extent of the talus (Hayward et al. 2017).This study area supported an abundant population of pikas. Within the area, there were 4 sites with tagged individuals from a longer-term survival study conducted by ADF&G.

Annual summer temperatures over the last decade (2010-2020) indexed as the average monthly means during the warmest months (June-August) ranged from 12°C to 17°C across years. Annual winter temperatures index as the average monthly means during the coldest months (December-February) varied widely across years from -17°C to 0°C (US Department of Commerce 2023). Annual precipitation during 2010-2020 averaged 38 – 61 cm of rain, and snow depth averaged 69 – 163 cm from December through April 2006-2023 (US Department of Commerce 2023, Independence Mine 1091 2023). The vegetation community within and surrounding the talus slopes occupied by pikas was diverse, consisting primarily of Ericaceous dwarf shrubs, forbs, graminoids, lichens and mosses with some tall shrubs (*Salix sp.* and *Alnus sp.*) interspersed. Hatcher Pass was a State Recreation Area that received relatively high recreational use year-round including hiking, skiing, paragliding, 4-wheeling, and snowmobiling.

The Denali study area, which was at the highest latitude (63.1 – 63.3°N) with sites across a range of elevations (930 – 1370 m), had a climate with lower annual precipitation and colder winters compared to the other two study areas. Annual summer temperatures over the last decade (2010 – 2020) indexed as the average monthly means during the warmest months (June-August) ranged from 12°C to 17°C across years. Annual winter temperatures index as the average monthly means during the coldest months (December – February) varied widely across years from -29°C to -8°C (US Department of Commerce 2023). Annual precipitation during 2010 – 2020 was 23 – 31cm, and snow depth averaged 50 – 100 cm during winter (December – April) from 2014 to 2023 (US Department of Commerce 2023, Fielding Lake 1268 2023). The vegetation community was dominated by Ericaceous dwarf shrubs, graminoids, and tall shrubs (*Salix sp*.). This study area contained three distinct groups of study sites, or clusters of talus slopes occupied by pikas. Each of the 3 groups of sites were about 25 km apart and sites within each group were separated by 1 to 4 km, with assumed negligible rates of exchange among sites. The first group of sites was located along the Denali Highway, primarily in gently sloping talus patches near the road. The second group was located 6 – 8 km from the main road, and the sites in this group were entirely within steep boulder-filled drainages rather than gentle slopes. The third area was located along the Richardson Highway, and it contained a single study site on a south facing slope with the tallest and most abundant shrubs surrounding it. This site was occupied by a small number of individuals (<6 pikas) during the study.

The third study area was located on the military base, Joint-Base Elmendorf Richardson (JBER), in Anchorage. Situated only 17 km from the coast but at 1040-1130 m of elevation and at 61.1°N, this study area had a maritime subarctic climate with cool summers, cold winters moderated by proximity to the ocean, and consistent cloud cover and fog. Annual summer temperatures over the last decade (2010 – 2020) indexed as the average monthly means during the warmest months (June-August) ranged from 12°C to 17°C across years. Annual winter temperatures index as the average monthly means during the coldest months (December – February) varied widely across years from -16°C to -1°C (ACIS 2023). Annual precipitation was 35 – 58 cm during 2010-2020. However, snow depth was highly variable across years, averaging 25 – 38 cm from December through April 1990 – 2021, but ranging from a maximum of 91 cm in 1990 and 2006 to lows of 0 – 5 cm during mid-winter in other years (Alaska-Pacific RFC 2023). During our study, snow depth during mid-winter was relatively high, ranging from 48 cm to 107cm at a nearby SNOTEL site (Eagle River 7.8 SE) at a similar elevation (Alaska-Pacific RFC 2023). The vegetation community at JBER was sparse, primarily consisting of Ericaceous dwarf shrubs such as mountain heather (*Cassiope mertensiana*), graminoids, lichens and mosses. There were no tall shrubs and few forbs within or near these pika territories. We monitored one pika population in this study area over a large area of connected talus.

Behavior Surveys - To evaluate the influence of temperature, weather conditions, and time of day on foraging activity by collared pikas, we conducted behavioral surveys in all 3 study areas during August of 2020 and July and August of 2021. Prior to our surveys, we visited pika territories that were marked and monitored each year for occupancy by ADF&G. We selected focal individuals opportunistically for observation when we were within an occupied pika territory and initiated observations on the hour (i.e., 12:00, 13:00, etc. + 5-10 min) to avoid a potential bias by focusing on currently active pikas. Before beginning each survey, we waited 5-10 min to allow the pikas to recover from the disturbance to their routine caused by our presence. We observed pikas between 06:00 – 01:00 during a variety of weather conditions to capture the full gradient of conditions that pikas experience. We observed individuals for 30-min intervals and recorded the time they spent haying, grazing, traveling, and resting in sight. We recorded the furthest distance that we observed the pika traveling and foraging from its den, and also recorded the distance of the observer to the pika's haypile (or central location of their territory) with a rangefinder. We recorded the number of minutes spent on each activity as well as the amount of time that the focal individual was not in view, and we continued observations for the full 30 minutes whether the pika was visible or not. We also recorded the den ID and age (juvenile or adult) of the focal pika. As part of a concurrent study, pika dens were identified by observing individuals cache most of their forage beneath one boulder, or a small cluster of boulders. Dens were marked with a GPS point and wooden stake to facilitate finding them each subsequent season. We recorded ambient temperature and wind speed at the observer's location (Kestrel 2000 Wind and Temperature Meter), visual estimates of cloud cover in 5% increments, and occurrence of precipitation during the observation interval.

We also set one ambient temperature logger (Thermachron iButton and Onset® HOBO) housed within a protective PVC pipe container attached to a large boulder that stood above the expected snowpack at each site (N=10 out of 13 total sites) (Sakiyama et al. 2021, Varner and Dearing 2014). These ambient loggers recorded one temperature reading every hour for 1-3 years. Temperature data used for this study spanned July 2018 to August 2022.

Statistical Analysis - We tested 4 non-exclusive mechanistic hypotheses to determine how collared pikas made foraging decisions based on temperature and weather conditions (Table 2.1). We tested the effects of temperature and weather variables on the amount of haying and grazing activity observed during behavioral surveys with linear mixed-effects models with maximum likelihood estimation. We used a Poisson distribution with minutes spent grazing and haying as response variables (2 model sets). We detected overdispersion, so we corrected the standard errors using quasi-GLMM models (Zuur et al. 2009). *Den ID* was included as a random effect to account for non-independence of multiple observations collected from a single individual and differences in foraging behavior among those individuals.

Within our models, we included fixed effects for weather covariates as univariate and additive models, ambient temperature thresholds, and daily maximum and minimum temperature thresholds (obtained from temperature loggers or local weather station data) with an interaction with time of day (6-hr categories) (Table 2.3). We scored each activity into four 6-hr time categories of “morning” (6:00 to 11:59), “day” (12:00 to 17:59), “evening” (18:00 to 23:59), and “night” (0:00 to 5:59) as our time-of-day covariate (Miller and Hickman 2021). We tested temperature thresholds as a binary variable, determining whether the temperature exceeded each threshold at 2°C intervals for observations up to 26°C. We eliminated 15 surveys without records of cloud cover during that day. For all other surveys missing cloud cover data, we estimated cloud cover based on observations within 4 hours (mean <1 hr) for 19 surveys (6% of all surveys). When there were cloud cover estimates within 1 hr before and after a survey, we averaged the 2 observations to estimate cloud cover during that survey. Finally, distance from the observer to the pika’s haypile (den; center of their territory) was a significant confounding factor in amount of time the pika was visible during surveys. Therefore, we removed all surveys in which the observer was <15 m from the haypile. We also excluded all surveys of juvenile pikas due to the high variability in haying behavior of juveniles compared to adults. Finally, we tested continuous variables for correlation with Pearson’s correlation test and did not include correlated variables together in our models (r-value > 0.5).

Results

We completed a total of 306 30-min direct observations of focal individuals in the field totaling 153 hours of observation time during July of 2020 and July-August of 2021 (Table 2.4). These included 33 observations of juvenile pikas, which were excluded from the final analysis due to the difference in foraging behavior between adults and juveniles, specifically in the low frequency of caching (“haying”) behavior exhibited by juveniles. In total, we analyzed the behaviors of pikas associated with 124 dens from 261 observations across all 12 sites within our 3 study areas. Adults were observed during 218 observations and spent >1 min grazing or haying in 213 and 209 surveys, respectively, while they remained out of sight during 43 observations. Adults spent 28% of their time resting, 26% actively haying, 24% traveling (excluding travel time to forage or hay), and 22% grazing. Although focal individuals were not seen observed during 43 observations they were heard vocalizing in 20 of those observations, and we only spent time observing within known active pika territories. Most observations were conducted during 9:00 – 18:00, however, we conducted 27 observations in the early morning (6:00 – 8:00) and later evening (18:00 – 21:00), and 4 observations at night (21:00 – 1:00). Due to the high latitude of our study areas and mid-summer sampling season, it was light enough to observe pikas at all hours of the observation periods.

Temperature, weather conditions, and time of day all influenced haying and grazing activity of collared pikas during the primary foraging season of July and August. Our *summer heat*, *weather*, and *temperature*time-of-day hypotheses* were equally supported by models predicting haying activity, while our *time-of-day hypothesis* was not supported (Table 2.5a). Minutes of haying per observation were negatively influenced by both temperature ($\beta = -0.21$, $p < 0.05$) and wind ($\beta = -0.49$, $p < 0.0001$) (Figure 2.3), which aligned with the expectations of our *weather conditions hypothesis*. Pikas appeared to decrease haying activity above a threshold of 12°C such that minutes spent haying declined when ambient temperatures exceeded 12°C at the time of the survey (above 12°C $\beta = -0.80$; $p < 0.0001$) (Figure 2.4), which aligned with the expectations of our *summer heat hypothesis*. Finally, haying activity was also influenced by an interaction between daily minimum temperature and time of day (Figure 2.5), in accordance with our *time-of-day * temperature hypothesis*. As minimum daily temperature increased, pikas hayed for less time in the mornings (β = -

0.60, $p < 0.001$) and afternoons ($\beta = -1.5$, $p < 0.001$), but this effect was not significant in the evenings (Figure 2.5).

Pikas also altered their grazing activity schedules depending on temperature, although this change occurred at higher temperatures than documented for haying activity. Our *time-of-day * temperature hypothesis* was supported by the data, while our other 3 hypotheses were not (Table 2.5b). The model with time of day as an interaction with the maximum daily threshold of 22°C (thresholds of 10 – 26°C were tested) was the most parsimonious for predicting grazing activity. On days that exceeded 22°C, minutes spent grazing increased in the mornings ($\beta = 1.58$, $p < 0.0001$) and decreased in the afternoons ($\beta = -1.2$, $p <0.001$), but the interaction was not significant in the evenings (Figure 2.6). Finally, our *time-of-day hypothesis*, tested by a univariate model of the categorical 6-hr time-of-day covariate, was not strongly supported by the data in predicting either haying or grazing activity.

Across all our observations over two summers, pika haying activity varied by hour (Figure 2.7) with the most activity observed during mornings (6:00 – 11:59) and evenings (18:00 – 23:59), and least during afternoons (12:00 – 17:59), although there was the most variability in haying behavior during the afternoon (Figure 2.8). They grazed most in the morning and least in the afternoon and evening (Figure 2.8). Across all study areas, the hottest time of day was between 12:00 – 17:00 (Figure 2.9). While the univariate model with ambient temperature as the covariate was not the most parsimonious model of haying or grazing activity, it did show a significant negative linear effect on haying activity ($\beta = -0.25$, $p < 0.01$) (Figure 2.10), and a significant negative quadratic effect on grazing activity with a peak between 14°C and 16°C (Temp^2 $\beta = -0.38$, $p < 0.0001$) (Figure 1.10b). Within all our models, we tested the fixed effects of Julian day and study area, but neither had a significant effect on pika behavior. All of the top models were better supported than the null models, and almost all of the models evaluated had stronger support than the null models. We did not detect a significant effect of ambient temperature on the distance that pikas were observed traveling from their territories through a linear mixed model with *den ID* as a random effect (Pr(>|t|) = 0.44).

Discussion

Summer foraging activity by collared pikas in Alaska varied with temperature, weather conditions, and time of day. Similar to a report on foraging activity of American pikas (Smith and Ivans 1983), collared pikas spent about half of their time grazing or haying when active above ground and in view of an observer (Table 2.4). Our models collectively show that pikas hayed more on cool mornings and during cool temperatures with little wind (Figures 2.3-5). Although collared pikas were consistently active during the morning, which was typically the coolest time of day, the amount of time they spent on each activity during mornings differed as a function of temperature. As daily minimum temperatures increased, pikas reduced their time haying, particularly in the mornings and evenings (Figure 2.5). In contrast, grazing activity did not appear to be as sensitive to heat (Figure 2.6). Pikas decreased haying activity at a lower temperature threshold (12°C) compared to grazing (22°C) (Figures 2.4, 2.6, 2.10a&b) likely because haying is more energetically demanding. This shift in behavior during warm temperatures could affect overwinter survival of collared pikas if they do not spend sufficient time building up haypiles during periods of peak forage growth (Morrison et al. 2009, Yandow et al. 2015, Camp et al. 2020).

As predicted by our weather conditions hypothesis, both temperature and wind had a negative impact on the time that collared pikas allocated to haying (Figure 2.3). This finding is consistent with previous research that reported negative effects of temperature and wind on pika activity (Hayes and Huntly 2005, Zhou et al. 2023); however, our study is the first to establish a connection between climatic conditions and foraging behavior of collared pikas. Extensive research has focused on the heat tolerance of American pikas, close relatives of collared pikas, revealing that high temperatures restrict their activity (Smith 1974, Yandow et al. 2015, Otto et al. 2015, Moyer-Horner et al. 2015, Smith 2020, Benedict et al. 2020). Wind can reduce the ability of pikas to detect predators and hear warning vocalizations by conspecifics, and often precedes an incoming storm (Hayes and Huntly 2005, Moyer-Horner et al. 2015, Xianze et al. 2020). Climatologists have observed increased frequencies of extreme weather events including wind at high northern latitudes, which could restrict pika haying activity under the current expected climate trajectory (Screen 2014, Walsh et al. 2020). Although we expected collared pikas to hay less during hot periods, they decreased haying activity at a lower “heat threshold” than we expected (12°C) (Figure 2.4). As opposed to grazing, pikas often stray farther from the talus when haying and retreat quickly to their dens once they gathered vegetation, making it more energetically costly and likely increasing body temperature more than grazing (Huntly et al. 1986, Holmes 1991, personal observation 2020). Therefore, even slightly warmer conditions could narrow the window of time when conditions allow pika to hay and limit the amount of hay they gather for winter.

Similarly, pikas also spent more time haying on days with cooler minimum temperatures, and this effect was greatest in the morning (Figure 2.5). Whether driven by temperature alone or a combination of temperature and circadian rhythm, pikas in our study were most active during mornings (Figures 2.7, 2.8), which is consistent with literature on other pika species (Kawamichi 1969 (*O. hyperborea),* Smith 1990 (*O. himilayana)*, Morrison 2007 (*O. collaris)*, Bhattacharyya et al. 2014 (*O. roylei)*, Millar and Hickman 2021 (*O.*

princeps)). However, a study of collared pikas in 1965 did not report a lull in midday haying activity (Broadbooks 1965), but summer temperatures during that study conducted 60 years earlier may have been cooler than during ours, and this finding was based on observations of a single individual. Based on predictions from our data, haying activity in the morning decreased by nearly 50% when daily minimum temperature increased from 0°C to 10°C (Figure 2.5). In contrast, haying activity in the afternoon only marginally decreased with rising minimum temperatures, however, pikas were generally less active or not in view in the afternoons compared to the mornings, and minimum temperature may be a more influential factor during the cooler morning hours. Finally, we also expected that cold conditions would negatively influence time spent haying, but the temperature was infrequently below 10° C (< 20 surveys) and rarely below 5° C (1 survey) during our summer observations (Zhou 2023).

The grazing behavior of pikas also was negatively affected by warm temperatures. Beyond a daily maximum temperature threshold of 22°C, pikas grazed more frequently in the morning and reduced activity in the afternoon (Figure 2.6). This heat threshold is much higher than that documented for haying (12°C, Figure 2.4), suggesting that during warmer mornings, pikas may have switched from haying to grazing. On warmer mornings, there is a greater thermal cost to haying than grazing due to the energetic expenditure required for haying (Huntly et al. 1986, Holmes 1991, Roach et al. 2001).

Although the univariate ambient temperature model was not the best supported among all models, its significant effect is valuable for dissecting behavioral trends linked to temperature (Tables 2.5a&b). Ambient temperature measured at the time of surveys had a negative effect on both haying and grazing activity, but not to the same extent. The estimated amount of time spent haying decreased as temperature increased (Figure 2.10). Pikas predominantly stopped haying when ambient temperature was above 18°C and hayed more often when it was cool. The effect of temperature on grazing differed such that grazing increased from 4°C to 15°C where it reached a positive peak, and then decreased above 15°C (Figure 2.11). Overall, grazing activity was highest between 10°C-19°C while their haying activity was highest below 12°C. These differing trends provide additional evidence that haying requires cooler conditions than grazing, and pikas may switch from haying to grazing when temperatures are too warm to hay.

We made assumptions when using our field data in our models, although certain inherent constraints within the dataset may have influenced our results. Distance of observer to the pika's den was still a significant negative factor (linear model p-value < 0.05) in determining the amount of time pikas were observed during surveys even after eliminating surveys in which observers were <15m from the den; so some pikas may have changed their behavior in response to our presence during observations. Additionally, wind speed was measured at the start of observations and consequently, may not have represented wind conditions during periods with variable windspeeds. We conducted fewer observations during the "evening" time category (18:00-23:59) resulting in a small sample size (n=10) compared to "afternoon" and "morning" and had only 4 surveys during the nocturnal period (0:00-05:59), which limited our ability to infer behavioral patterns at this time of night. Finally, we assumed that during the 30-min observation periods, we did not miss haying events because we intentionally situated ourselves in clear view of the pika's primary haypile. We tested for variation in haying behavior across time and space by including Julian day and Study Area within our models, but neither were significant factors.

Limited research has explored the specific temperature thresholds at which pikas reduce essential activities like haying, rather than simply assessing their overall activity status; and none have investigated this question for collared pikas (Moyer-Horner et al. 2015, Ray et al. 2016, Smith et al. 2016, Camp et al. 2020). Collared pikas spent time haying under a narrower range of conditions than grazing, and pikas are known to travel farther from their territories while haying (Huntley et al. 1986, Holmes 1991, Roach et al. 2001). Haying is a more energetically demanding activity for pikas compared to grazing, and it becomes even more challenging in warm temperatures due to their high metabolic rate and low thermal conductance (MacAurthur and Wang 1973, Otto et al. 2015), as they are farther from their thermal refuges. Warmer springs and longer summers may increase the length of the haying season as well as plant productivity (Bhattacharyya and Ray 2015, Johnston et al. 2020), but this increased season length may not be enough to compensate for the decreased haying activity on summer days with temperatures exceeding 12°C. Haypiles enhance food security through winter in variable environmental conditions (i.e. melt-freeze events, longer or inconsistent periods of snow cover, unfavorable temperatures) that are increasing in frequency at high latitudes (Morrison et al. 2009, Overland 2020). Additionally, decreased haying activity could have broader implications for alpine plant communities (Morrison et al. 2009). Pika haying activity enhances nutrient cycling and contributes to plant diversity within highly sensitive alpine ecosystems (Aho et al. 1998, Huntly et al. 1986, Roach et al. 2001, Wesche et al. 2007, Bhattacharyya et al. 2014). Phenological mismatch may occur when the peak in plant quality does not coincide with peak haying activity (Huntly 1991, Yandow et al. 2015). Therefore, decreased haying activity under warm conditions during mid-summer could have broader implications for alpine plant communities in addition to a negative impact on winter survival of collared pikas.

Our work also identified avenues for future research to refine understanding about behavioral responses of collared pikas to climate and the community level effects of those changes over time. Targeted studies of alpine plant communities within current and historical collared pika habitat could help parse out the pathways and relative importance of pika grazing and haying behavior within these ecosystems. Likewise, such studies could determine length of the growing season for key forage species to assess the potential for phenological mismatches. Additionally, comprehensive monitoring of belowground activity using cameras across the entire foraging season would help construct a more comprehensive timeline of pika activity throughout the day. Those data would facilitate quantifying the frequency at which pikas returned to dens with or without hay under diverse seasonal conditions and would support a robust test of the influence of temperature and time of day on haying behavior.

Management Implications

Our observations of aboveground foraging activity provide important insights into the thermal limits of collared pikas and considerations for determining temperature constraints for foraging and haying behaviors. The temperatures at which pikas reduce activities that are critical to overwinter survival, rather than simply the lethal ambient temperature, may be important to consider for conservation (Vander Wall 1990, Morrison et al. 2009, Moyer-Horner et al. 2015). Closing knowledge gaps about behavioral thermoregulation by pikas is critical for assessing species vulnerability to climate change and, indeed, this lack of information was cited as one reason why a petition to list American pikas as threatened by climate change under the Endangered Species Act was not supported (Crist 2010, Moyer-

Horner et al. 2015). Although pikas display highly plastic behavior under adverse thermal conditions by retreating beneath the talus during the hottest hours of the day, consistently warmer conditions may diminish the quality or quantity of forage that they can cache throughout the summer season, and potentially decrease overwinter survival (Morrison et al. 2009, Yandow et al. 2015, Camp et al. 2020). Additionally, pikas are considered both a keystone species and indicator species for the effects of climate change on alpine ecosystems at northern latitudes worldwide (Hafner 1993, Moyer-Horner et al. 2012, Sumbh and Hof 2022). Observing shifts in pika behavior offers valuable insights into the underlying patterns and impacts of climate change, which could have far-reaching consequences for alpine ecosystems that are particularly sensitive to rapid change.

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Tables

Table 2.1. Hypotheses and predictions for the effects of temperature and weather conditions on the summer foraging behavior of collared pikas in Alaska, USA during the summers of 2020 and 2021.

Hypothesis	**Description**	**Predictions**
H1: Summer Heat	On warm days, pikas are less active aboveground and remain closer to their territories when it is hottest.	1) On warm days, foraging activity will decrease as ambient temperature increases. 2) On warm days, the maximum distance that pikas are observed from their den will be negatively correlated with ambient temperature.
H2: Weather Conditions	Pikas are less active during inclement weather.	Foraging activity will decrease during rain, high wind speeds, and low temperatures.
H3: Time of Day	Pikas have a circadian foraging pattern that is independent of weather or temperature.	Pikas will hay and graze most in the morning and late afternoon and rest during mid-day during all temperature and weather conditions.
H4: Temperature*Time of Day	Pikas modify daily foraging behavior in response to temperature	Pikas will hay and graze more frequently during the early morning, evening or night on days with high maximum temperatures.

Table 2.2. Description and habitat characteristics of each study area where we observed foraging behavior of collared pikas during the summers of 2020 and 2021 in Alaska, USA.

Study Area Name	**Hatcher Pass**	**Denali Hwy**	**JBER**
Location	Hatcher Pass State Recreation Area	Talus slopes along the Denali and Richardson Highways	Near Tanaina Lake and Snowhawk Valley within Training Area 427 and 431
# of Sites	4	8	1
Latitude (°N)	61.8	63.1-63.3	61.1
Elevation Range (m)	1120-1190	930-1370	1040-1130
Climate Type	Continental subarctic	Tundra	Maritime subarctic mountains
2010-2020 Dec-Feb Monthly Mean Temps (°C)	-17 to 0	-29 to -8	-16 to -1
2010-2020 June-Aug Monthly Mean Temps (°C)	12 to 17	12 to 17	12 to 17
2010-2020 Annual Rainfall (cm)	38 to 61	23-31	35-58
2010-2020 Dec-April Mean Snow Depth (cm)	69 to 163	50-100	25-38 (highly variable)
Vegetation Community	Diverse: Ericaceous dwarf shrubs, forbs, graminoids, lichens and mosses, and some tall shrubs *(salix sp.* and *alnus sp.*)	Dominated by ericaceous dwarf shrubs, graminoids, and tall shrubs (*salix sp.* and *alnus sp.*)	Ericaceous dwarf shrubs such as mountain heather (*Cassiope mertensiana*), graminoids, lichens and mosses. No tall shrubs within or near these pika sites and very few forbs.
Additional Information	Most abundant pika populations. Heavy recreation year-round	3 distinct groups of sites with different aspects and talus slope configurations	1 site spanning a large area of connected talus

Table 2.3. Descriptions of explanatory variables tested in linear models of collared pika foraging behavior measured by 30-minute focal animal observations during the summers of 2020 and 2021 in Alaska, USA.

	Covariate	**Description**
Temperature covariates	Temperature (°C)	Ambient temperature at time of survey
	Heat Threshold	Binary response of whether the temperature exceeded a threshold of 10°C to 26°C at 2°C intervals during survey and 24-hour period (12 variables)
	Cold Threshold	Binary response of whether the temperature was below a threshold of 8°C to 0°C at 2°C intervals during survey and 24-hour period (8 variables)
	Daily Min Temp	Minimum daily ambient temperature
	Daily Max Temp	Maximum daily ambient temperature
Temporal Covariates	Time Category	Morning (6:00-11:59), Day (12:00-17:59), Evening (18:00-23:59), Night (0:00-5:59)
Weather Covariates	Wind Speed (kmph)	Taken at start or end of survey
	Cloud Cover (%)	Visual estimation of % cloud cover during survey (5% increments)
	Precipitation (Y/N)	Record of any precipitation during survey period
	Furthest Distance Seen (m)	Furthest distance pika was seen from haypile

*Temperature covariates were obtained from handheld Kestrel weather meters or temperature loggers at each site, and averaged across study areas

Table 2.4. Total and proportional time pikas spent on each activity type during 30-minute direct observations in the field during the summers of 2020 and 2021 in Alaska, USA.

Behavior Class	**# of surveys observed** [a]	**Time Spent (mins)**	**Proportion of time surveyed**	**Proportion of time observed**
Foraging	213	453	0.05	0.22
Haying	209	523	0.06	0.26
Traveling	163	488	0.05	0.24
Resting/Observing	145	575	0.06	0.28
Pika Observed	218	2036	0.22	1.00
Calling [b]	187	416		
Total # Surveys	306	9180		

[a] number of surveys in which the focal individual was observed >1 min

[b] number of call events

Table 2.5. Results of quasi corrected Poisson mixed-effects regression models with minutes spent haying (a) and grazing (b) as by collared pikas as response variables during the summers of 2020 and 2021 in Alaska, USA. The top models for each response variable are displayed at the top of the table. Models are then separated by hypotheses (summer heat; weather; time of day and temperature*time of day) and displayed in order of lowest Akaike's Information Criterion (AIC) value and highest model weight (ωi). Other values reported are number of model parameters (k), log likelihood (log(L)) and delta AIC (ΔAIC).

Model Set (Hypotheses) ^{a}	**Model**	**k**	**log(L)**	**AIC**	**ΔAIC**	ω_i
All Models						
	Day T_{min}*Time Category	7	-481.83	978.10	0.00	0.34
	Temp + Wind	4	-485.62	979.40	1.30	0.18
	Ambient T_{max}12°C	3	-486.74	979.57	1.47	0.16
Summer Heat						
	Ambient T_{max}12°C	3	-486.74	979.57	1.47	0.96
	Ambient T_{max}18°C	4	-489.00	986.16	8.06	0.04
Weather						
	Temp + Wind	4	-485.62	979.40	1.30	0.62
	Temp + Wind + Precip	5	-485.56	981.35	3.25	0.23
	Wind	3	-488.62	983.34	5.24	0.09
	Wind + Precip	4	-488.46	985.08	6.98	0.04
Time of Day						
	Day T_{min}*Time Category	7	-481.83	978.10	0.00	0.62
	Day T_{min}8°C*Time Category	7	-483.18	980.80	2.70	0.16
	Day T_{min}10°C*Time Category	7	-484.82	981.97	3.87	0.09
Null	1	2	-499.60	1003.25	25.15	0.00

Model Set (Hypotheses) ^{b}	**Model**	**k**	**log(L)**	**AIC**	**ΔAIC**	ω_i
All Models						
	Day T_{max}22°C*Time Category	7	-386.35	787.13	0.00	0.34
Summer Heat						
	Temp^{2}	4	-398.26	804.67	17.54	0.79
	Ambient T_{max}20°C	3	-400.97	808.03	20.90	0.15
	Ambient T_{max}22°C	4	-401.89	809.87	22.74	0.06
Weather						
	Temp + Wind	4	-402.32	812.80	25.67	0.72
	Temp + Wind + Precip	5	-402.24	814.72	27.59	0.28
Time of Day						
	Day T_{max}22°C*Time Category	7	-386.35	787.13	0.00	0.34
Null	1	2	-423.38	850.81	63.68	0.00

Figures

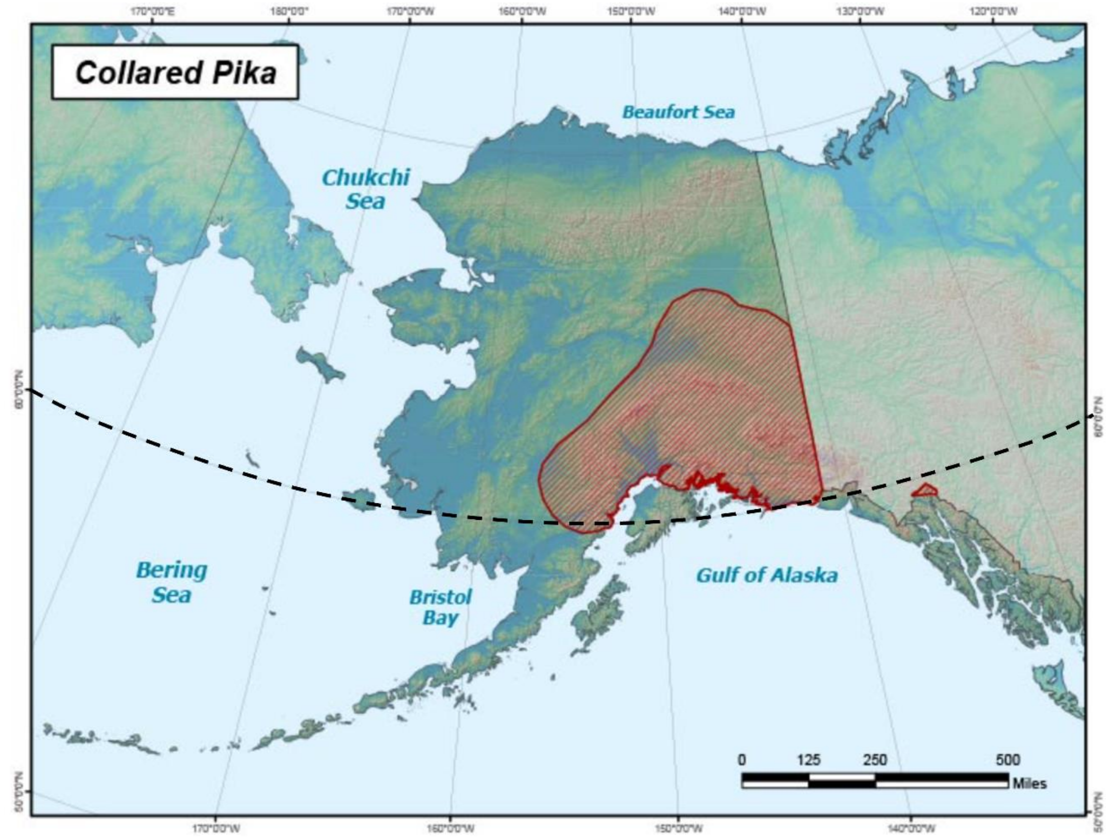

Figure 2.1. Collared pika distribution across Alaska, USA (©Alaska Department of Fish & Game). The dashed line represents 60°N latitude, above which climate scientists have observed *arctic amplification* resulting in more pronounced temperature increases compared to regions south of this latitude.

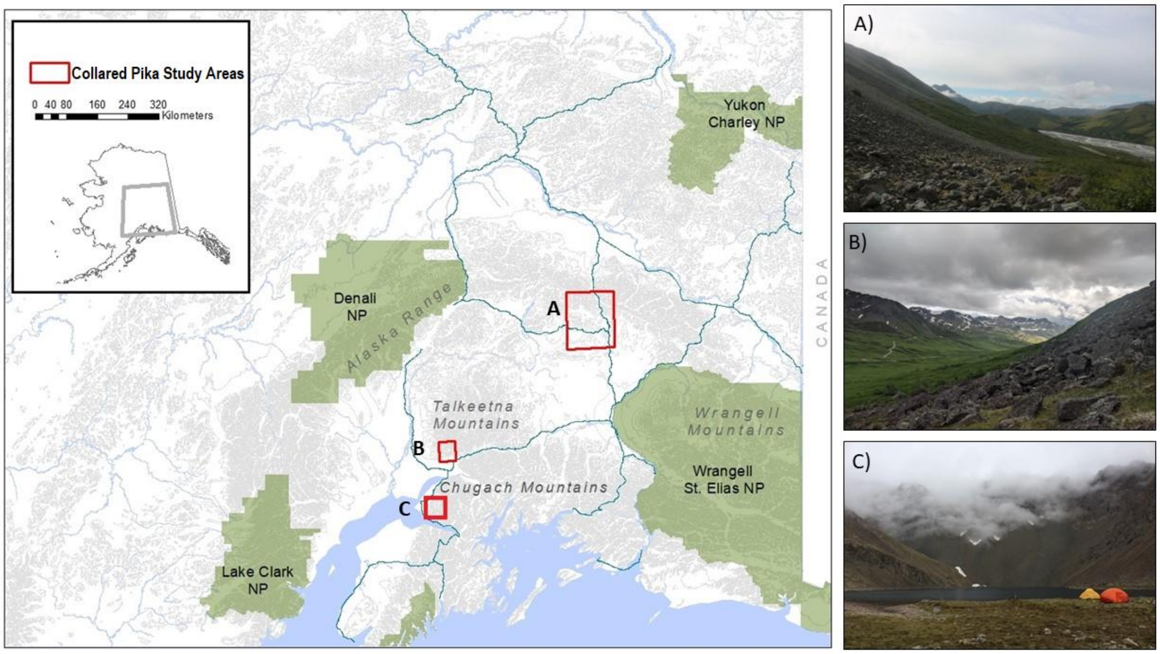

Figure 2.2. Study area locations in southcentral Alaska, USA, 2020-2021. A) Denali Highway, B) Hatcher Pass, C) Joint-base Elmendorf Richardson (JBER). The green areas are National Parks.

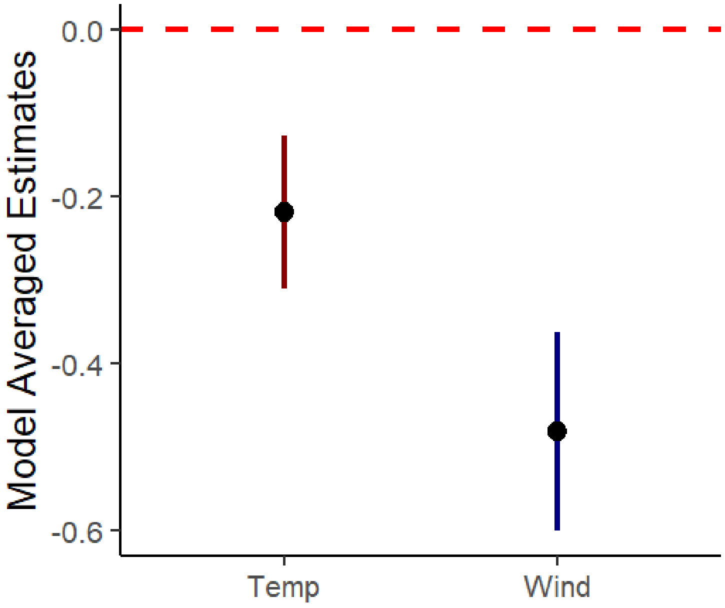

Figure 2.3. Beta estimates of temperature and wind speed (± 95% confidence interval) in the top *weather conditions* model predicting minutes spent haying by collared pikas during 30-min focal observations in July and August 2020-21 in Alaska, USA.

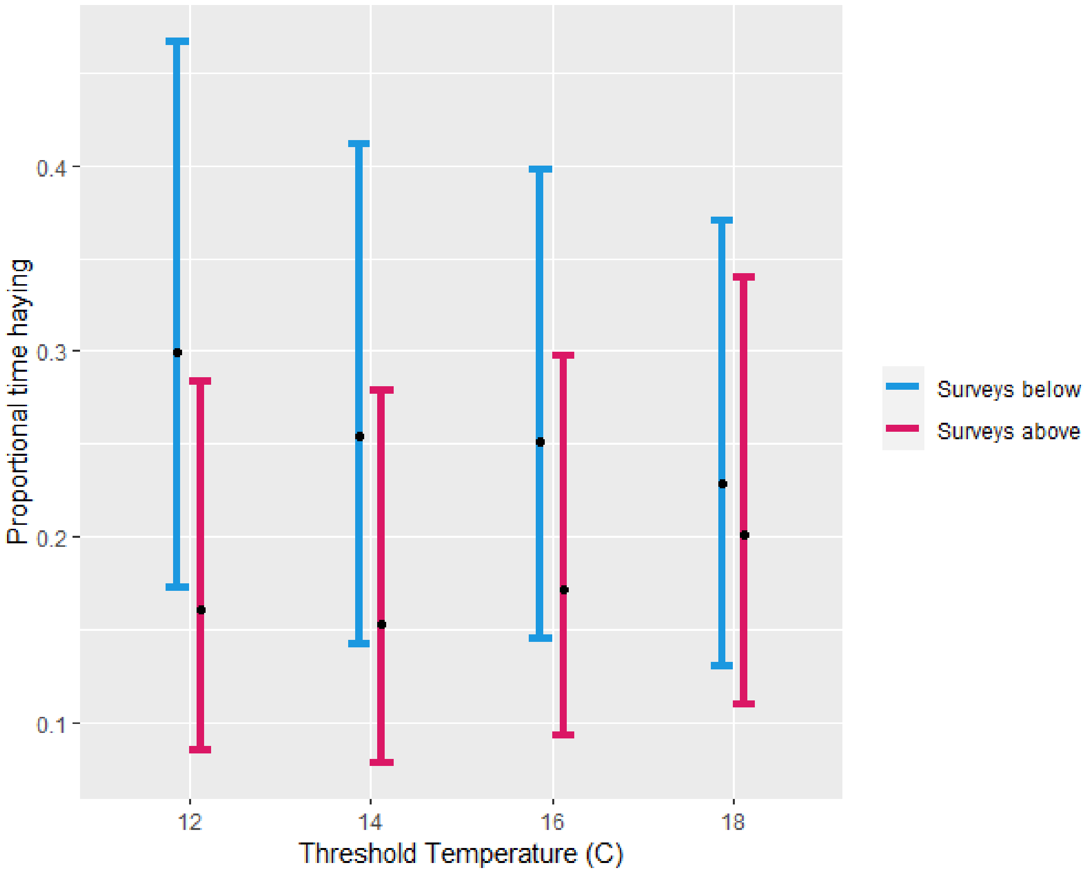

Figure 2.4. Influence of temperature on haying behavior by collared pikas observed during July-August 2020-21 in Alaska, USA. Predicted proportional time pikas spent haying and the associated prediction intervals during surveys that were above or below each temperature threshold during summers of 2020-2021 in Alaska, USA. The threshold 12°C was most informative of haying behavior in our models. These 4 thresholds were the only significant "heat thresholds" of those tested (10°C to 26°C, at 2°C intervals) in our models.

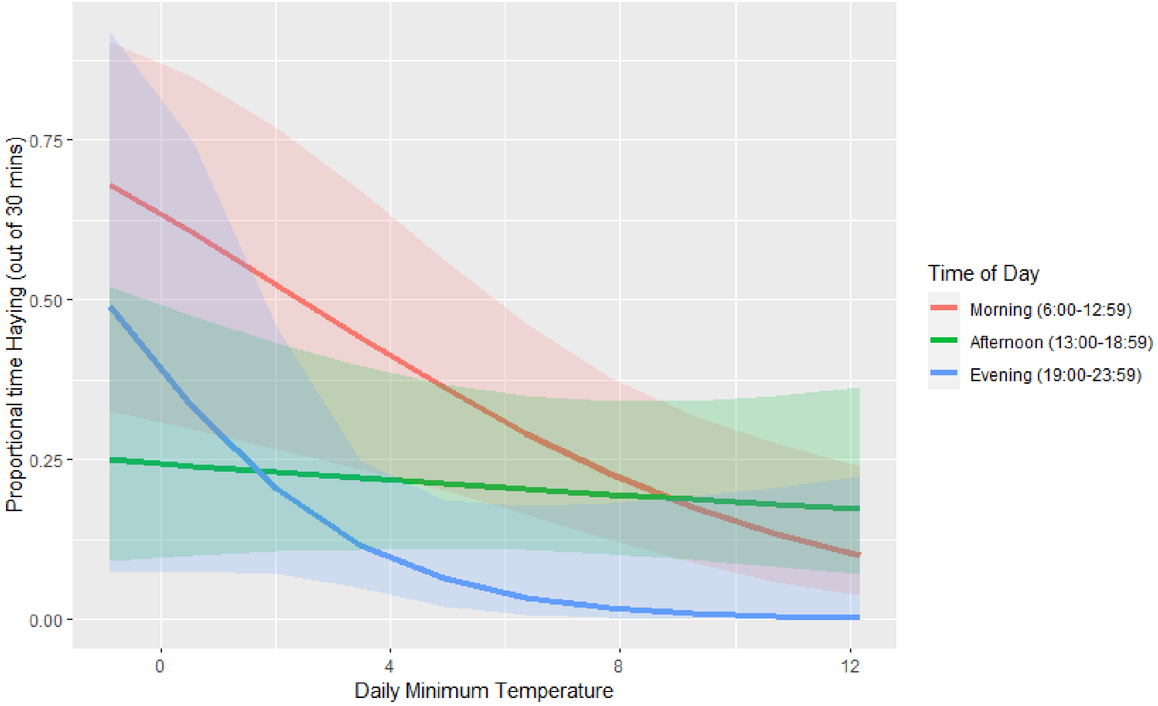

Figure 2.5. Predicted proportion of minutes spent haying across all observed minimum daily temperatures (-1 - 12°C) during each time of day during summers of 2020-2021 in Alaska, USA. Pikas hayed most during the morning and evening on cool days, but minimum temperature had little effect on haying during the afternoon.

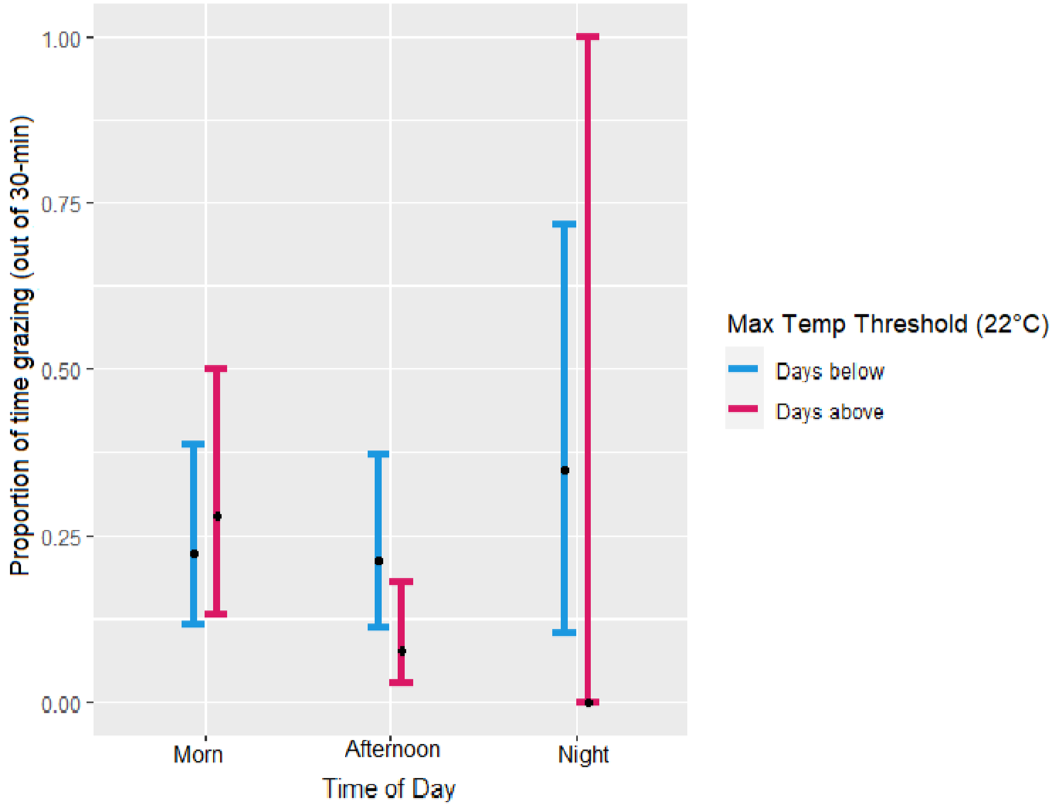

Figure 2.6. Predicted proportion of minutes spent grazing and the associated prediction intervals during each time of day during 30-minute direct observations on days that reached above and below 22°C during summers of 2020-2021 in Alaska, USA.

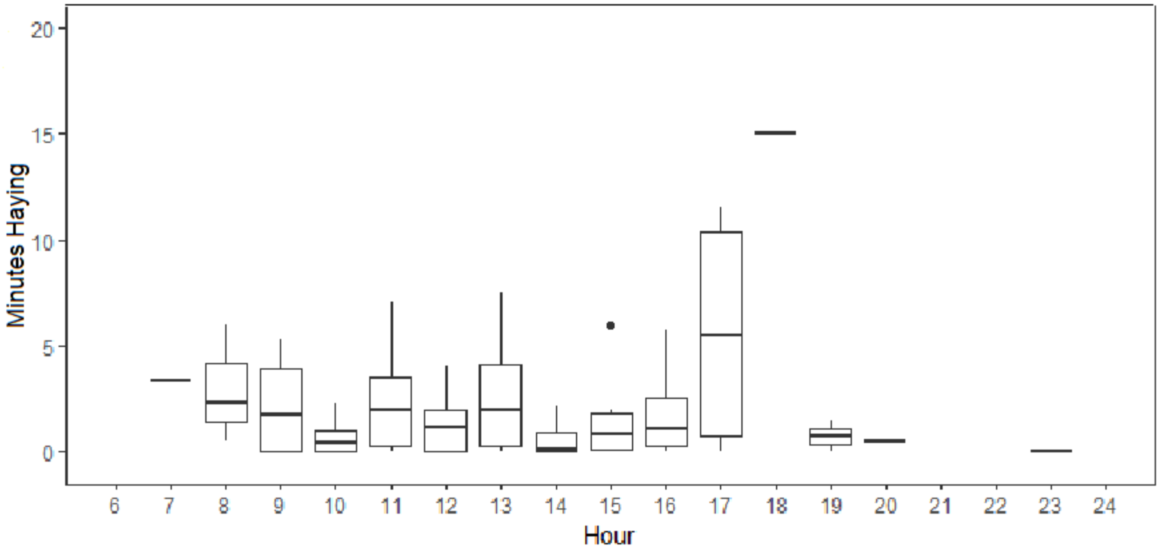

Figure 2.7. Boxplot of minutes per hour within a 24-hour day that collared pikas were observed haying averaged across 30-min observations of focal individuals conducted from July to August 2020-2021 in Alaska, USA.

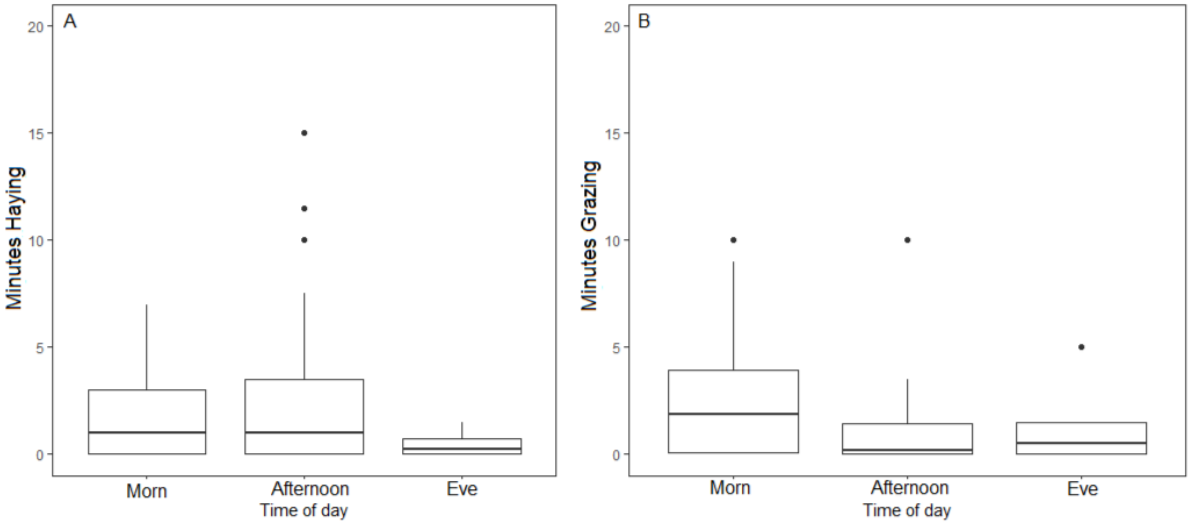

Figure 2.8. Average minutes collared pikas were observed haying (a) and grazing (b) during 30-min observations of focal individuals during each daily time category during summers of 2020-2021 in Alaska, USA.

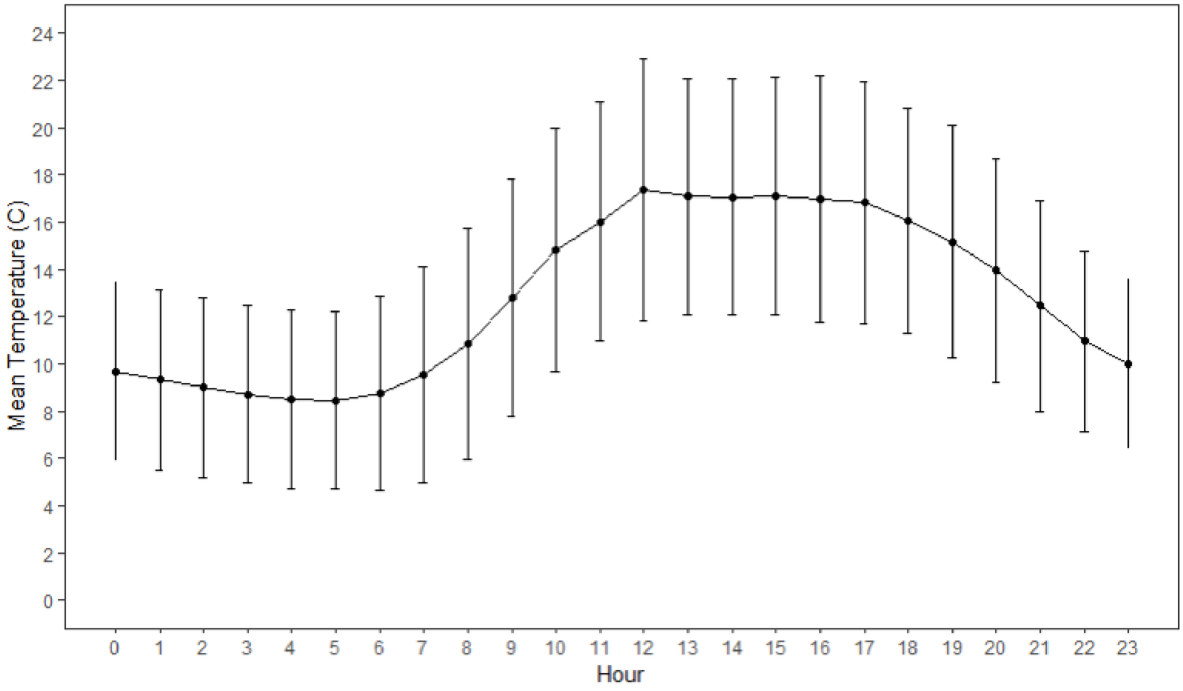

Figure 2.9. Average temperature per hour recorded by ambient temperature loggers at 12 sites across all study areas in Alaska, USA during July and August 2018-2021.

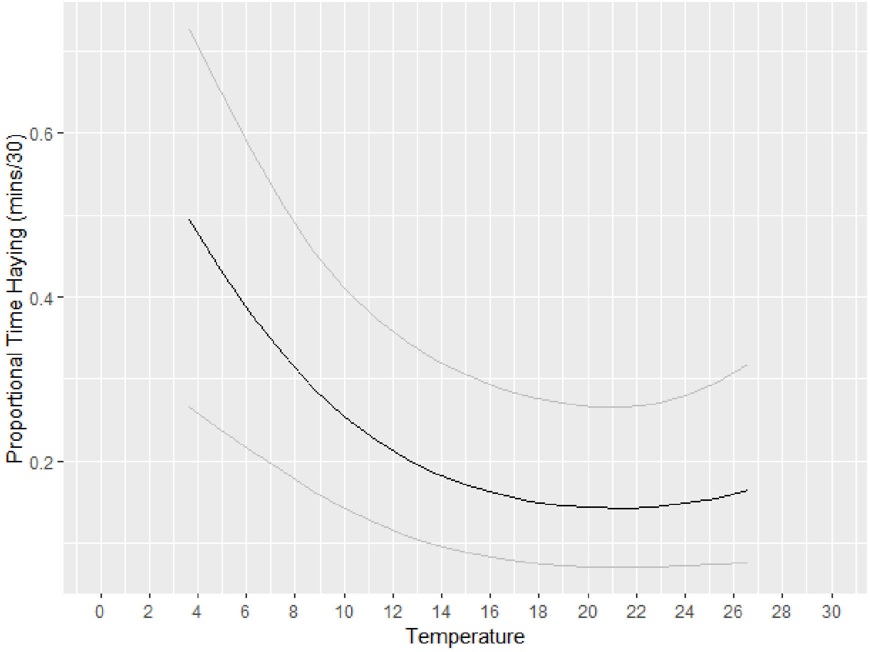

Figure 2.10. Predicted proportion of minutes that collared pikas spent haying (± 95% confidence interval) at all temperatures recorded (4 - 27℃) during 30-min observations of focal individual during July and August 2020-21 in Alaska, USA. Temperature had a negative effect on time spent haying. Pikas hayed the most at the coolest temperatures observed and least during the highest temperatures.

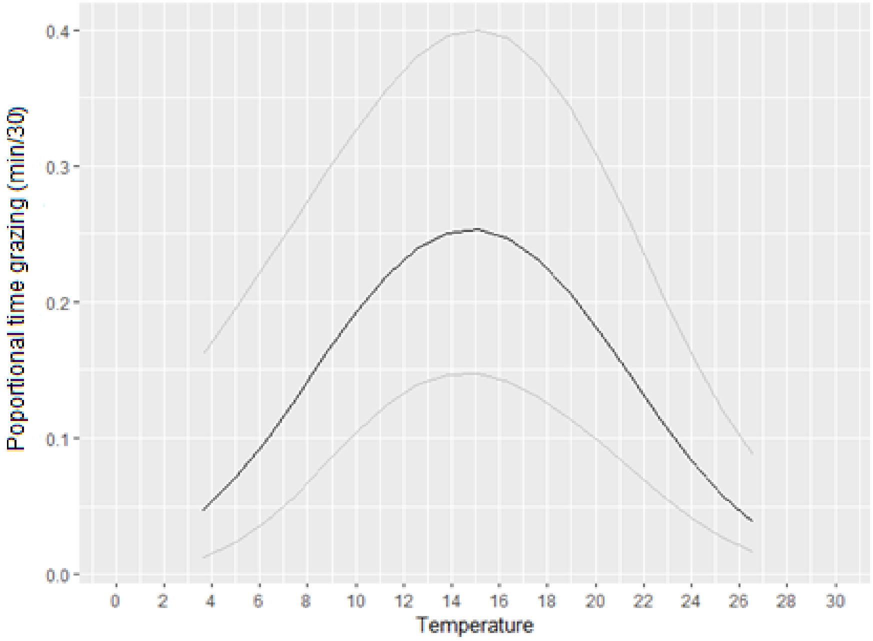

Figure 2.11. Predicted proportion of minutes that collared pikas spent foraging (± 95% confidence interval) at all temperatures recorded during 30-min observations of focal individuals during July and August 2020-21 in Alaska, USA. Temperature had a negative quadratic effect on time spent grazing. Pikas grazed most between 14°C and 16°C and least at the lowest and highest temperatures observed.

Appendix

Tables

Table A.1. Extended haying model results (Chapter 2). *Top models* displayed are all models tested that were < 2 ΔAIC from the top model. Additional model sets reported are separated by hypotheses and displayed in order of ascending AIC value and model weight adding up to a minimum of 0.9.

Response Var	Model Set	Model	Beta Est	Est.	2.50%	97.50%	z.val	p	AIC	Weight	Null AIC
Hay Mins	**Top models**	MinT*TimeCategory	(Intercept)	-1.47157	-2.2411	-0.70205	-3.74808	0.000178	978	0.34	1003
			MinT	-0.00384	-0.33335	0.325673	-0.02283	0.981782			
			Evening	-22.8159	-591.463	545.8315	-0.07864	0.937319			
			Morning	0.234288	-0.10777	0.576348	1.342447	0.179451			
			MinT:Evening	-19.5202	-531.102	492.0618	-0.07479	0.940385			
			MinT:Morning	-0.60262	-0.95105	-0.2542	-3.38986	0.000699			
		Temp + Wind	Temp	-0.20656	-0.37319	-0.03993	-2.42964	0.015114	979.4	0.18	
			Wind	-0.48697	-0.7182	-0.25574	-4.12777	3.66E-05			
		MaxT_12°C	MaxT_12°C	-0.80346	-1.11113	-0.4958	-5.11841	3.08E-07	979	0.16	
	Heat	MaxT_12°C	MaxT_12°C	-0.80346	-1.11113	-0.4958	-5.11841	3.08E-07	979	0.96	
		MaxT_18°C	MaxT_18°C	-0.16091	-0.47048	0.148653	-1.01879	0.308302	986	0.04	
	Weather	Temp + Wind	Temp	-0.20656	-0.37319	-0.03993	-2.42964	0.015114	979.4	0.62	
			Wind	-0.48697	-0.7182	-0.25574	-4.12777	3.66E-05			
		Temp + Wind + Precip	Temp	-0.21892	-0.39858	-0.03925	-2.38809	0.016936	981.3	0.23	
			Wind	-0.48113	-0.714	-0.24827	-4.04954	5.13E-05			
			Precip	-0.07639	-0.48854	0.335766	-0.36326	0.71641			
		Wind	Wind	-0.52509	-0.75749	-0.29269	-4.42833	9.50E-06	983.3	0.09	
		MinT*TimeCategory	(Intercept)	-1.47157	-2.2411	-0.70205	-3.74808	0.000178	978	0.63	
	Time		MinT	-0.00384	-0.33335	0.325673	-0.02283	0.981782			
			Evening	-22.8159	-591.463	545.8315	-0.07864	0.937319			
			Morning	0.234288	-0.10777	0.576348	1.342447	0.179451			
			MinT:Evening	-19.5202	-531.102	492.0618	-0.07479	0.940385			
			MinT:Morning	-0.60262	-0.95105	-0.2542	-3.38986	0.000699			
		MinT_8°C*TimeCategory	(Intercept)	-1.87448	-2.66308	-1.08588	-4.65879	3.18E-06	980.8	0.17	
			MinT_8°C	0.837806	-0.08242	1.758026	1.784429	0.074354			
			timecat6Eve	-15.7755	-4560.34	4528.786	-0.0068	0.994572			
			timecat6Morn	-0.17983	-0.53431	0.174645	-0.99432	0.320067			
			MinT_8°C:timecat6Eve	14.30841	-4530.25	4558.87	0.006171	0.995076			
			MinT_8°C:timecat6Morn	0.740681	0.065578	1.415784	2.15035	0.031528			
		MaxT_10°C*TimeCat	(Intercept)	-1.58937	-2.27536	-0.90338	-4.54106	5.60E-06	981.9	0.1	
			MaxT_10°C	0.54903	0.030549	1.067511	2.075446	0.037945			
			Evening	-2.08738	-3.16915	-1.00562	-3.78198	0.000156			
			Morning	-16.2871	-7481.5	7448.929	-0.00428	0.996588			
			MaxT_10°C:Evening	-1.05223	-2.40385	0.299388	-1.52583	0.127053			
			MaxT_10°C:Morning	16.20906	-7449.01	7481.425	0.004256	0.996605			

Table A.2. Extended grazing model results (Chapter 2). No other models tested were < 2 ΔAIC from the top model, which was the only model containing the *time of day* parameter that held significant weight. Additional model sets reported are separated by the two other hypotheses (without *time of day* covariates) and displayed in order of ascending AIC value and model weight adding up to 1.

Response Var	Model Set	Model	Beta Est	Est.	2.50%	97.50%	z.val	p	AIC	Weight	Null AIC
Graze Mins	**Top Model**	MaxT_22°C*TimeCategory	MaxT_22°C:Afternoon (Intercept)	-1.23816	-1.95196	-0.52436	-3.39975	0.000674	787	0.7	850.8
			MaxT_22°C	-1.16084	-2.19186	-0.12982	-2.20676	0.027331			
			Evening	0.122828	-0.81133	1.056989	0.257706	0.796634			
			Morning	0.101962	-0.44937	0.653291	0.362473	0.716998			
			MaxT_22°C:Evening	-16.7154	-334.051	300.6197	-0.10324	0.917773			
			MaxT_22°C:Morning	1.575866	0.853832	2.297901	4.277692	1.89E-05			
	Heat Models	Temp^2	Temp^2	-0.40158	-0.57914	-0.22402	-4.43279	9.30E-06	804.7	0.79	
		MaxT_20°C	MaxT_20°C	-1.24154	-1.62697	-0.85612	-6.31353	2.73E-10	808	0.15	
		MaxT_22°C	MaxT_22°C	-1.38395	-1.84847	-0.91944	-5.83942	5.24E-09	808.9	0.06	
	Weather Models	Temp+Wind	Temp	-0.38294	-0.54638	-0.2195	-4.59217	4.39E-06	812.8	0.72	
			Wind	-0.52506	-0.8213	-0.22881	-3.47377	0.000513			
		Temp + Wind + Precip	Temp	-0.37821	-0.54321	-0.2132	-4.49242	7.04E-06	814.7	0.28	
			Wind	-0.53074	-0.82885	-0.23264	-3.48948	0.000484			
			Precip	0.09844	-0.39215	0.589034	0.393274	0.694117			

Figures

Figure A.1. Examples of haypiles cached out in the open without direct protection from rocks in arid mountain regions of A) Eastern California, USA (Millar and Hickman 2021), B) the Sierra Nevada Mountains along the Pacific Crest Trail, California, USA (Slichter 2020), and C) The Salmon River Mountains, Idaho, USA (personal observation 2023).

Figure A.2. Juvenile collared pika at Hatcher Pass, Alaska, USA (2020) with a tick embedded below it's right eye. An increase in ectoparasites, especially ticks, is another potential consequence of increasing temperatures in alpine ecosystems that may impose a cost to collared pikas in Alaska.

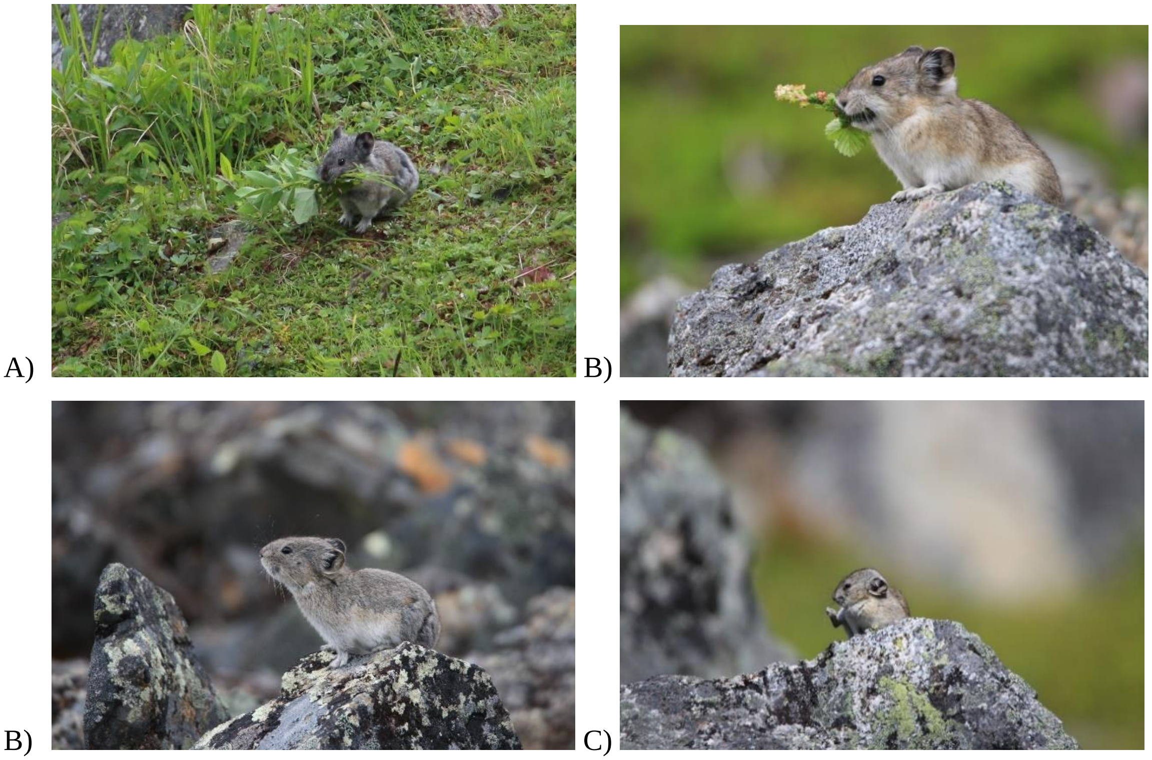

Figure A.3. Photos of collared pikas haying (A & B), displaying territoriality (B), and resting/grooming (C) in Alaska, USA, 2020.