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Behavioral Baselines and Modeling in a Changing Climate: Relating Temperature to the Summertime Behavior of the American Pika (Ochotona princeps) in the southern Rocky Mountains of Colorado

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Behavioral Baselines and Modeling in a Changing Climate:

Relating Temperature to the Summertime Behavior of the American Pika (*Ochotona princeps*) in the southern Rocky Mountains of Colorado

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Abstract:

Small mammals that make use of sub-surface microclimates may be able to adapt quickly to a warming climate by altering the level and timing of certain surface activities. For example, energy-intensive territorial defense or foraging activities might be shifted to cooler times of day. This hypothesis was explored using data on the American pika (*Ochotona princeps*), a small, diurnal lagomorph closely related to rabbits that uses rocky microhabitats for shedding heat between bouts of surface activity. Over three consecutive summers (mid-June to mid-August, 2012-2014), 94 observations (45 minutes each) were conducted involving N = 61 unique pikas, using a standardized protocol to record behaviors during continuous focal-animal sampling. During observations, data loggers were used to record shade temperatures in surface and sub-surface microhabitats available to the focal pika. Most observations were conducted at the Niwot Ridge Long Term Ecological Research (NWT LTER) site in Boulder County, Colorado (USA), with the goal of comparing historical data from this site with contemporary and future data. Here, I report a contemporary, temperature-indexed activity budget for pikas in this area of the southern Rocky Mountains. Surface temperatures averaged 5-10°C higher than sub-surface temperatures during diurnal observations, and pikas spent two-thirds of their time below the surface. Modeling surface activity as a function of microclimate and microhabitat variables, sub-surface temperature was found to be able to serve as the basis of a significant predictor model. The average surface-sub-surface temperature differential was also found to a significant non-linear model, surface temperature (values ≤ 15°C). This suggests that a strong temperature gradient is more important when the surface temperature is greater than 15°C. This study provides a current baseline for studying any future shifts in pika behavior, by providing data on behavior and temperature variation within currently available microhabitats, and by characterizing how pikas respond to temperature at this point in time.

Key words: microhabitat, microclimate, climate change, behavioral thermoregulation, small mammal

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Introduction

Modification of behavior can be an avenue of adaptation for mammals and other species challenged by climatic changes in ecosystems. Contemporary climatic changes, including warming temperatures and changes in precipitation patterns, are altering ecosystem processes and function globally. Documenting species' responses to these changes will be important for predicting the structure of future ecosystems. However, in order to identify possible behavioral adaptations, behavioral baselines need to be established for comparison with future data. Additionally, modeling how current microclimate conditions affect behavior across individuals of a species could help predict how changes in climate conditions will alter behavior. Establishing a baseline of behavioral information and behavior-influencing microclimate variables can help predict whether a species will be able to adapt to environmental changes.

Certain ecosystems are thought to be especially susceptible to climate change and alpine tundra ecosystems are particularly vulnerable as warming temperatures, declining snowfall and seasonal alterations can transform these ecosystems (Pepin 2000; Ray et al. 2008). Alpine ecosystems can thus be monitored as early warning signals of impending change in other ecosystems, because the effects of slight changes in inputs (energy, chemicals and water) can be magnified in alpine environments relative to lower elevation systems (Williams et al. 2002). Similarly, alpine mammals can constitute an early warning indicator of species response to changing environmental conditions, because alpine mammals are often persisting near the limits of physiological tolerance (Wilson 2011; Wilkening et al. 2013; Wilkening et al. 2015). Monitoring the behavior of an appropriate indicator species might be the easiest way to detect change in complex and remote ecosystems such as alpine landscapes. An indicator species, or bioindicator, is one whose presence, absence, or density reflects environmental conditions and that can therefore be a measure for the health of a specific system.

The American pika (*Ochotona princeps*) (hereafter referred to as the pika) could be considered a valuable indicator species for climate changes in alpine tundra systems because of the pika's physiology and narrow niche space. Pikas are small, temperature-constrained mammals that live in rocky debris or "talus" most commonly found at high elevations (Smith 1974; Wilkening et al.

2011). Presence or absence of individuals of this species is easy to determine because individuals are highly territorial, remaining on and defending their territories by calling to and chasing other pikas off. As natal dispersers, once they leave their "nursery" as a juvenile, they will remain in the first territory they colonize (Smith and Weston 1990). Therefore, sites and individuals can be monitored over years for presence and absence.

These saxicolous (living within or among rocks) organisms are highly specialized to persist in high-elevation areas, being adapted to cold climates by having a high metabolic rate and spherical body shape. As pikas do not hibernate or migrate, at high elevations they are heavily dependent on snowpack for insulation throughout the winter (Beever et al. 2011; Ray et al. 2012). Although pikas generate and maintain heat well for their size in order to survive cold alpine winters (MacArthur and Wang 1974), these adaptations make it difficult for them to inhabit warmer regions during the summer (Smith 1974). For this reason, pikas are found only at high elevations in the more southern, warmer portions of their range (Hafner 1994). As summer temperatures warm and winter snow packs decrease, one possible adaptation for many cold-tolerant species would be an upslope range shift, allowing species to escape to higher, colder elevations (Beever et al. 2003). However, as a mountaintop species, pikas do not have this option. Another possible response of pikas to warming temperatures is to modify their behavior by spending more time under the cover of talus (Ivins and Smith 1983). American pikas are uniquely dependent on talus and do not occur far from rocky debris, which provides a relatively cool and thermally stable microhabitat during summer days in the alpine (Millar and Westfall 2010).

Predicting pika occupancy and persistence using data on surface conditions has been successful in several western North American sites (Rodhouse et al. 2010; Beever et al. 2010, 2011; Wilkening et al. 2011; Erb et al. 2011; Jeffress et al. 2013). Population persistence has been linked to surface temperature and snowpack (Beever et al. 2010, 2011; Wilkening et al. 2011; Erb et al. 2011). Temperature is an important factor to consider because pikas can die after short exposures to ambient temperatures above 25°C (MacArthur and Wang 1973, 1974; Smith 1974; Smith and Weston 1990). Local extirpations can be related to warmer temperatures, which can cause chronic heat stress in individuals (Smith 1978; Hafner 1993; Beever et al., 2003; Ray et al. 2012). Pika survival rates in an area can also decrease in relation to decreases in snowpack cover (Ray et al. 2012), because snowpack provides vital insulation from extreme minimum temperatures during winter (Smith 1978, and Beever et al. 2010). The climatic changes in precipitation and temperature patterns can also affect the forage available to pikas, influencing the amount and quality of vegetation in patches near talus (Smith and Erb 2013). This change in vegetation can decrease the quality of vegetation in pikas' haypiles, on which they depend for food for overwintering (Huntly et al., 1986, Dearing 1997).

Temperature, wind and weather conditions can have a strong influence of pikas' surface activity levels. Pikas have difficultly shedding heat, as they maintain a relatively high body temperature (40°C), and are well-insulated for the cold climate. This causes their resting body temperature to be only a few degrees below their lethal body temperature maximum, and exposures to ambient temperatures of 28°C and above can cause hyperthermia and death (Smith 1974; MacArthur and Wang 1974). In order to stay active during high surface temperatures, pikas adjust their behavior on the surface, reducing amount of time and frequency on the surface. Pikas are active in bursts (less than 3.5 min) using the cooler, sub-surface microclimate to shed heat (MacArthur and Wang 1974). Pika surface activity can also be affected by wind and weather. High winds cause pikas to be less active on the surface, especially with energetic activities such as haying and running. Wind reduces the effectiveness of alarm calls from other pikas about predators which is predicted to outweigh the winds cooling advantage (Hayes and Huntly 2005). Pikas might also be less active in stormy weather conditions (Hayes and Huntly 2005), but overcast conditions can be related to beneficial cooler temperatures (MacArthur and Wang 1974).

Conditions in sub-surface microclimates could be a factor in determining pika survival (MacArthur and Wang 1973, 1974), yet this hypothesis is an understudied aspect of pika dynamics (Ray et al. 2012). Individual pikas need to amass and defend sufficient hay to survive the winter (Dearing 1996). These highly energetic activities must be undertaken during the (hot) summer when 1) high-quality forage is available for harvest and 2) territory boundaries must be defended against dispersing juveniles. Access to relatively cool, sub-surface microclimates allow the pika to shed heat (MacArthur and Wang 1974; Smith 1974). Therefore, the quality of sub-surface microclimates available within a pika's territory may be an important determinant of pika survival (Millar and Westfall 2010; Ray et al. 2012). Projections of future pika range retraction (e.g., Galbreath et al. 2009; Calkins et al. 2012) have not considered the quality of sub-surface microclimates as a factor in the pika's response to climate change. Little data are available on the sub-surface microclimates within talus habitats (but see Millar and Westfall 2010; Varner and Dearing 2014), and projections into the future are not available for these microclimates. This research project advances our understanding of sub-surface microclimates in taluses that might harbor important water resources (e.g., permafrost), and provides baseline data and models relating pika behavior to the combined effects of sub-surface temperature and surface conditions.

The present study provides a current baseline for studying any future shifts in pika behavior, by providing data on behavior and temperature variation within currently available microhabitats, and by characterizing how pikas respond to temperature at this point in time. Understanding how temperature can affect pika behavior can help in understanding the implications of climate change for this species. This project also provides data on sub-surface microclimates used by several other talus-dwelling species. Some taluses in the study area also harbor an important water resource: rock glaciers (ice covered by rocky debris) release meltwater late in the summer season when other water sources have dwindled (Millar and Westfall 2008). My data on near-surface and sub-surface temperatures may allow others to infer the existence or health of rock glaciers in these study sites. Ultimately, as an indicator species, the pikas themselves (or shifts in their behavior) could potentially help monitor the alpine tundra system and its potential climate thresholds (Wilkening et al. 2015).

Research Objectives

This project addresses how pika behaviors relate to ambient conditions and temperatures within the microhabitats used by pikas in the Rocky Mountains of Colorado, with the goal of establishing a behavioral baseline for future climate change studies. This project used behavioral data collected over several consecutive summers (2012-2014) from study sites associated with the Niwot Ridge Long Term Ecological Research site and comparison sites within the Indian Peaks Wilderness and at Loveland Pass. The observed surface activities of each pika were related to observed microhabitat conditions including surface and sub-surface temperatures in different portions of the pika's territory, categories of wind and weather, and relative site elevation and slope aspect. My goal was to model behavior as a function of microhabitat and microclimate conditions.

Temperature and behavior data from 94 such observations was analyzed for pika activity patterns from the past three summers. For this project, the data were compiled, standardized and analyzed to understand the correlation between temperature and pika behavior. The analysis examined surface and sub-surface temperatures in the talus as predictors of pika activity on the surface of the talus. The project summarizes comparisons between surface and sub-surface temperatures and establishes an indexed activity budget for pikas for a physiological stressor threshold. These analyses will allow future studies to assess behavioral and site changes.

This study models pika surface activity as a response to environmental variables (surface, sub-surface, wind, skies), and proxies for environmental conditions (relative elevation, aspect, time of day). Linear regression models, including mixed-effects modeling, were used to identify important variables and conditions related to pika behavior. Models were designed to address the following hypotheses:

1. After controlling for time of day, pikas will be less active on the surface when surface temperatures are higher.
2. The nature of surface activities will vary with temperature, with more energetic activities occurring during periods of cooler near-surface temperatures
3. There may be an effect of the gradient in temperature between warmer near-surface and cooler sub-surface microhabitats; the stronger the gradient, the more quickly pikas can shed heat in sub-surface locations and resume surface activities.

Methods

Study Site

This study was conducted in the high elevation alpine areas and lower elevation subalpine systems in Colorado, USA, during the summers of 2012-2014. A majority of the behavioral observations were recorded at Niwot Ridge, a Long Term Ecological Research site, and in the adjacent Brainard Lake Recreation Area in Boulder County. At Niwot Ridge, the observations (n=48) were taken on the West Knoll (WK), an alpine tundra site with northern and southern aspects, at an elevation of approximately 3,725 m. At the Brainard Lake area, Long Lake (LL) (n=15) and Mitchell Lake (ML) (n=20) sites are in forested subalpine areas, at approximately 3,200 m. LL study site is a north-facing, and ML is south-facing. A small number of observations (n = 11) were conducted at Loveland Pass (LP), CO, at an elevation of about 3,660 m. These sites were chosen to represent the range of elevations and aspects occupied by pikas in this area. Three of the sites (WK, LL and ML) were occupied by pika populations under long-term study.

The only historical study on pika response to sub-surface conditions was conducted at the LL site. LL lies within the Indian Peaks Wilderness, on a north-facing slope above Long Lake along the southern tributary to Brainard Lake (details below). The historical study (ca. 1965) includes a year-long characterization of temperatures above and below the surface of this talus patch, and a multi-year characterization of pika survival in the same patch. The current study leverages these historical data to determine whether or not the climate and sub-talus microclimate have changed over the past 50 years, as well as any trends in pika survival. In addition to the relatively low elevation, north-facing site with historical data, data were gathered at three additional sites: one at a comparably low elevation on a south-facing slope, and two at a higher elevation (one on a south- and one on a north-facing slope). Because the historical study site is at one of the lowest elevations at which pikas occur in this region, there are few other locations from which to choose a south-facing talus slope at a comparable elevation. The only suitable site lies within the Indian Peaks Wilderness on a south-facing slope above Mitchell Lake along the northern tributary to Brainard Lake (details below). Higher elevation sites suitable for comparison are located just outside the wilderness boundary within the Niwot Ridge Biosphere Reserve, making the historical study site (and its paired site near Mitchell Lake) even more useful as part of a comparative study. The additional high-elevation site at Loveland Pass was added as an appropriate comparison for the high-elevation site on the West Knoll.

Study Species

The focal animal of this study is the American pika (*Ochotona princeps*) due to its dependence on sub-surface dwelling to modify and maintain its internal temperature. The pikas' dependence on the insulated, below-talus spaces and its small territorial range makes the species an ideal choice for a microhabitat study. Long-term studies at the Niwot and Brainard sites have shown that pikas have been present continuously since at least the early 1960s.

Data Collection

Paired observational and temperature data were recorded at these sites in consecutive summers from 2012 through 2014. Specific observation sites were usually chosen based on historical records of the presence of an active pika territory, indicated by the construction of an overwinter food cache or "haypile". Each 45 minute observation was recorded by an individual observer, using the same methods and behavior recording sheet (See Appendix A). At the beginning of each observation, observers recorded their name, beginning time, location (including aspect), UTM coordinates (if GPS was available), ambient temperature, skies (e.g., sunny, cloudy, overcast), and wind (low, medium, high). At the end of observation, skies, wind, and the temperature were recorded again. IDs and locations were also recorded for each of the 3 temperature sensors positioned within the focal pika's territory during observations. Ambient temperature was recorded using a handheld thermometer, or estimated within 10 degrees Fahrenheit. "Skies" (a classification of current weather) were determined by the percentage of cloud coverage at the site: sunny less than 25% coverage, cloudy 25% cloud coverage to 75%, and overcast greater than 75%. Wind was similarly rated on a qualitative scale: low= only leaves or grass move, no motion in trees, medium= some gusts, branches sway, and high= trees bend.

Temperature Data

Before each observation, HOBO® Pendant Temperature Data Loggers (accuracy +/- 0.2 degrees; Onset Computer Corp., www.onsetcomp.com) were placed in the talus around and in the focal pikas' territory. One sensor was placed in the top strata of the talus (hereafter referred to as the surface sensor), one sensor was placed approximately 1 meter down into the talus (sub-surface), and one in a vegetation patch adjacent to the talus (meadow). All sensors were shaded by medium-sized rocks to insure the sensors were not exposed to sunlight. Sensors were positioned just prior to each observation, and recorded temperatures every 5 minutes during the observation. After the observation, the sensors were pulled and the sensors' ID was recorded by location in which it was placed (surface, sub-surface, or meadow).

Behavioral Observations

Each observation was 45 minutes long, and focused on a single "focal" pika using binoculars to track individuals. Observers chose specific site locations based on previously identified pika haypiles. Recorded observations included life stage (adult or juvenile) and identification tags (available at the WK, LL, and ML sites only). Tagged individuals had colored tags in the front and back of both ears. Activities included moving, resting, scanning, preening, feeding, haying (collecting and transporting vegetation back to haypile), and calling. For a full description of activities, refer to Appendix B. Activities were recorded by minute, and each minute could include multiple activities, so these minutes are labeled as activity-minutes. Full minutes in which the focal pika was not seen were also recorded as unseen. To obtain number of minutes the pikas were seen on the surface, the number unseen was subtracted from the length of the observation, henceforth called surface-active minutes or SA.

Data Entry & Organization

The majority of data entry was done by individual observers. Each observer entered data both from his/her own pika observations and correlated data from his/her own temperature records, and conducted data quality checks sufficient to support the construction and interpretation of a temperature-indexed activity budget for the group of pikas that he or she observed. Temperature data from the HOBO sensors was downloaded using a proprietary computer program, and then was converted into comma delimited files for import to an Excel spreadsheet. Additional data organization and compilation for this project was done chiefly by myself, and involved combining data sets on pika observations and temperature for a coordinated analysis. Observations were aligned with the corresponding temperatures using date, time, and observer, and each observation suitable for the combined analysis (i.e., with no missing data) was coded with a unique observation number (1-93, including 53.1). For detailed information on data entry and organization, refer to Appendix D.

Data Analysis

Temperature Data

To produce a baseline for microhabitat temperatures, the sensors' temperatures during the 45-minute observation were recorded. Since sensors took approximately 15 minutes to equilibrate to the talus temperatures, the average from the last 30 minutes of the observation was used to summarize sub-surface, surface and meadow temperatures at each site. As talus-surface and meadow placements both recorded shaded surface temperatures, these temperatures were averaged to represent surface temperature in some analyses. Surface and sub-surface temperatures were then analyzed by relative site elevation, slope aspect (North or South), and by site (LP, WK, ML and LL). A paired t-test was conducted to compare surface and sub-surface temperatures by all observations, by elevation and by aspect. An ANOVA test was conducted for average surface and sub-surface temperatures between the four sites. Air temperature measured or estimated by the observer was also used in some analyses, as was the relative site elevation and aspect. Elevation could also be a proxy for habitat, as the high elevation sites (LP, WK) is a high alpine system, and the low elevation sites (ML, LL) are below treeline, subalpine systems. For analyses based on aspect, LP data were omitted because aspect was not recorded for this site.

Behavioral Observations

Indexed behavior activity budgets were created for the main activities observed: short call, scan, move, rest, preen, feed, hay (collect hay), and unseen. Each activity (except for unseen) could be observed more than once every minute, and multiple activities could be observed within a minute.

Therefore, the fraction of time spent on a given activity could not be calculated as the raw number of times the activity was observed over the total observation time. Instead, "activity minutes" were calculated, in which one activity-minute was a minute in which the activity was observed at least once, and the total number of activity-minutes for a 45-minute observation was 45-U, where U was the number of minute in which the pika was unseen. Separate activity budgets were produced for observations recorded at surface temperatures >21°C and ≤21 °C. The 21°C cutoff was based on a threshold for pika heat stress: Macarthur and Wang (1974) observed that pikas switched from predominantly surface-active to predominantly hidden beneath the talus at air temperatures between 16 and 21°C. The surface temperature used to separate records between these two activity budgets was the average of mean talus-surface temperature and mean ambient temperature recorded by the observer during each observation. Paired t-tests were conducted to compare the activity levels of the different activities at >21°C and ≤21 °C surface temperature. The t-test compared the mean of the activity minutes within each surface activity.

Predictor Variables

Table 1 lists predictor variables used in this study. For predictor variables mean surface temperature, mean sub-surface temperature, and mean (air) temperature, values were used directly. A binary classification was used for high-elevation (1) vs. low-elevation (0) sites, and for north-facing (0) and south-facing (1) aspects. Time of day was also given a binary classification, with observations recorded between 05:00 and 11:00 coded as 1, and other times coded as 0. This classification system was adopted based on camera-trapping data which indicated that on WK activity peaked during the morning and dropped off significantly in the afternoon. Values for mean wind and mean skies were calculated as the average conditions (e.g., low = 0, medium = 1, high = 2) recorded at the start and end of the observation.

Temperature differentials were calculated to measure the potential behavioral thermoregulatory capacities of the talus. DiffSurfSub is the difference between the average surface and average sub-surface temperatures per observation. Similarly DiffMdwSub is the difference between average meadow and average sub-surface temperatures. There were two observations (69 and 72), in which the meadow temperature was twice as high as the talus-surface temperature, possibly due to placement of the surface sensor too deep in the talus. To address this problem, DiffBothSub was calculated as the difference between a) the mean of talus-surface and meadow temperatures and b) the average sub-surface temperature.

Table 1. Predictor variables used in modeling pika behavior and random effects variables.

Predictor	**Definition**
Predictors potentially affecting pika behavior	
Elevation	Elevation of sites; coded as 1 for high alpine, 0 for low subalpine
Time	Time of observation; coded as 1 5am-11am, 0 for all other times
MeanSurfC	Average surface sensor reading for last 30 min. of observation (°C)
MeanSubC	Average sub-surface sensor reading for last 30 min. of observation (°C)
MeanMdwC	Average meadow sensor reading for last 30 min. of observation (°C)
DiffSurfSub	Average surface minus average sub-surface temperature (MeanSurfC – MeanSubC)
DiffMdwSub	Average meadow minus average sub-surface temperature (MeanSurfC – MeanSubC)
DiffBothSub	Average of (avg. surface and avg. meadow) minus average sub-surface ((MeanSurfC*MeanSubC)/2) – MeanSubC
Aspect	Slope of sites; coded as 1 for South, 0 for North
MeanTemp	Average of start and end ambient temperature for each observation (°C)
MeanWind	Average of start and end wind conditions for each observation
MeanSkies	Average of start and end sky conditions for each observation
Random effects variables	
Elevation	Elevation of sites; coded as 1 for high alpine, 0 for low subalpine
Year	Year of the observation
Month	Month of the observation (June-August)
Location	Location of observation; LL, LP, WK or ML
Time	Time of observation; coded as 1 5am-11am, 0 for all other times

Modeling

To model how sub-surface microclimates affect pika surface activity, the number of minutes a pika was seen on the surface and movement activity-minutes were modeled as a linear function of one or more predictor variables. Up to 3 predictors were considered within each model, to avoid over-fitting the data and to facilitate interpretation of model results. Before building models, a correlation matrix was examined to determine whether predictors were too highly correlated to be used in the same model (See Table 2). A Pearson's r value above 0.7 was considered too high to allow both predictors to enter the same model. The candidate set of linear regression models included various potential interaction effects and random effects. The significance of each predictor or interaction within a model, and overall model significance, was interpreted using p=s and an alpha level 0.05. The relative support for each model within a set of candidate models was interpreted using Akaike's information criterion (AIC), which balances model fit against the number of parameters (mainly predictors) used to attain that fit (Burnham and Anderson 2002).

For mixed-effects models, AIC was based on fits obtained using maximum likelihood (rather than restricted maximum likelihood), to ensure results were comparable with AIC values obtained for fixed-effect models in the same candidate set. The null, or no model, was included in each candidate set. Model AIC values that were at least two units lower than the AIC of the null model were considered to have better support than the null, while models with AIC values within two units of the null were considered to have equal support as the null (Burnham and Anderson 2002). Similarly, any two models being compared were considered to have similar support only if their AIC values were within 2 units of each other. All models were fit using functions lm() or lmer() in R 3.1.0 (R Core Team 2014).

Table 2: Correlation matrix of predictor variables. This table shows the relatedness of predictor variables, reported as Pearson's r. Pairs of variables with r closer to -1 are negatively correlated, while 0 represents no correlation, and 1 represents total positive correlation. Where absolute values are higher than 0.7 (denoted with **) the two variables were not used in the same model. All of the highly correlated values came from two different temperature variables. Semi-correlated variables (>0.5) are denoted with an *.

Variables	Elevation	Time	Mean SurfC	Mean SubC	Mean MdwC	DiffSurfSub	DiffMdwSub	DiffBothSub	Aspect	Mean Temp	Mean Wind	Mean Skies
Elevation												
Time	-0.073											
MeanSurfC	0.168	-0.317										
MeanSubC	-0.178	-0.306	*0.528									
MeanMdwC	0.158	-0.496	**0.748	0.477								
DiffSurfSub	0.316	-0.168	**0.823	-0.048	*0.561							
DiffMdwSub	0.300	-0.345	0.477	-0.154	**0.795	*0.664						
DiffBothSub	0.338	-0.280	**0.716	-0.110	**0.741	**0.915	**0.909					
Aspect	-0.349	-0.009	0.048	0.075	0.092	0.0029	0.048	0.026				
MeanTemp	-0.170	-0.344	*0.612	0.480	*0.650	0.399	0.400	0.438	0.147			
MeanWind	0.179	-0.011	-0.205	-0.013	-0.220	-0.232	-0.238	-0.258	-0.149	-0.136		
MeanSkies	-0.198	-0.252	-0.1036	-0.027	-0.033	-0.106	-0.022	-0.071	0.084	-0.098	-0.247	

Results

A total of 94 behavior observations with associated microhabitat temperature data were used for analyses; other records were missing data targeted for this analysis. Of the 94 focal animals, 40 were unique individuals, meaning that they were observed only once for this analysis, and no focal pika was observed more than 5 times (see Figure A in Appendix C). The majority of the observations were conducted during the morning 06:00- 11:59 hours, with 61% of all the observations taking place between 09:00 to 11:59 (see Figure B in Appendix C). There were 59 observations conducted at the high-elevation sites (48 WK, 11 LP) and 35 at the low-elevation sites (20 ML, 15 LL). Aspect was not available at the LP site, so out of the remaining 83 observations conducted, 52 were at north-facing locations, and 31 were at south-facing locations. The observations were fairly evenly split between years; there were 37 in 2012, and 28 in both 2013 and 2014.

Baseline Temperature and Behavior Data

Temperature sensors recorded temperatures in 3 locations: talus surface, talus sub-surface and meadow. Across all observation sites, average talus surface and average meadow temperatures (15.11°C, 15.56°C respectively) were significantly (p= 2.89 E-24) warmer than average sub-surface temperatures (9.57°C) by over 5.5°C (Figure 1). Additionally, the maximum and minimum temperatures for surface and meadow sensors were similar (minima = 7.56°C, 7.08 °C and maxima = 26.37°C, 27.19°C for talus surface, meadow, respectively), while sub-surface temperature exhibited about half the temperature range with a minimum of 3.45°C and maximum of 11.84°C. As talus surface and meadow temperatures appeared similar, most of the analyses for this project focused on comparing talus surface and sub-surface temperature. Average surface temperature (Figure 2a) was not significantly different between low- and high-elevation sites (p= 0.05467; average 14.12°C, 15.701°C respectively) nor was average sub-surface temperature (p= 0.96985, average 10.15°C, 9.19°C respectively) (Figure 2b). Additionally, surface temperature was not significantly different between sites with north-facing versus south-facing aspects (p= 0.6842) and very similar averages (3a). Sub-surface temperature was also not significant between north-facing and south-facing sites, also with similar averages (p= 0.4858) (Figure3b). Lastly, the comparison of surface and sub-surface temperatures by sites, through ANOVA tests, showed that a) there was significant difference between average surface temperatures (p= 0.0087) and b) there was not a significant difference between sites in terms of average sub-surface temperature (p= 0.31) (Figures 4a and 4b).

Figure 1: Talus surface, sub-surface, and meadow temperature for all sites

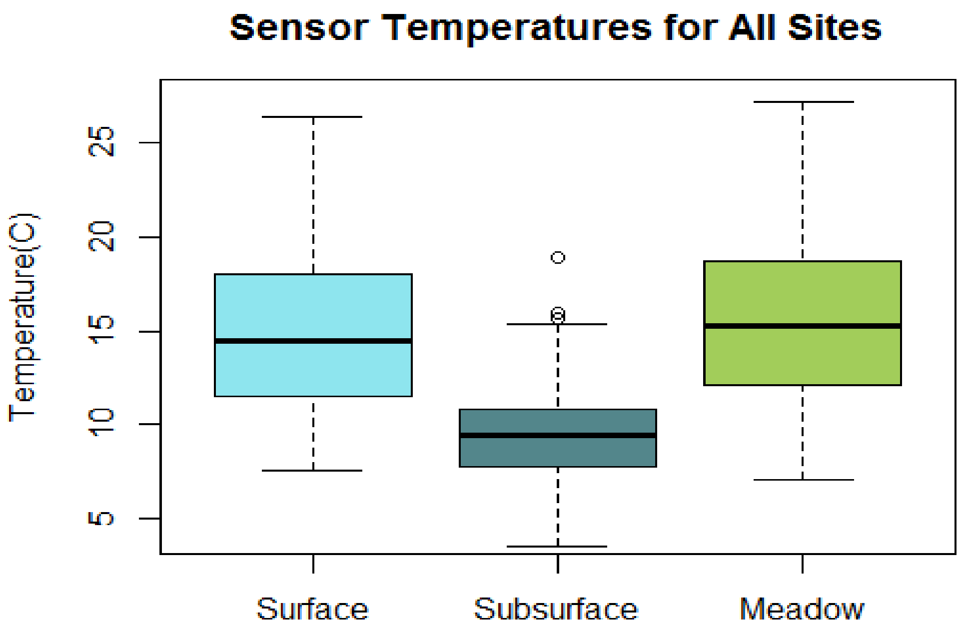
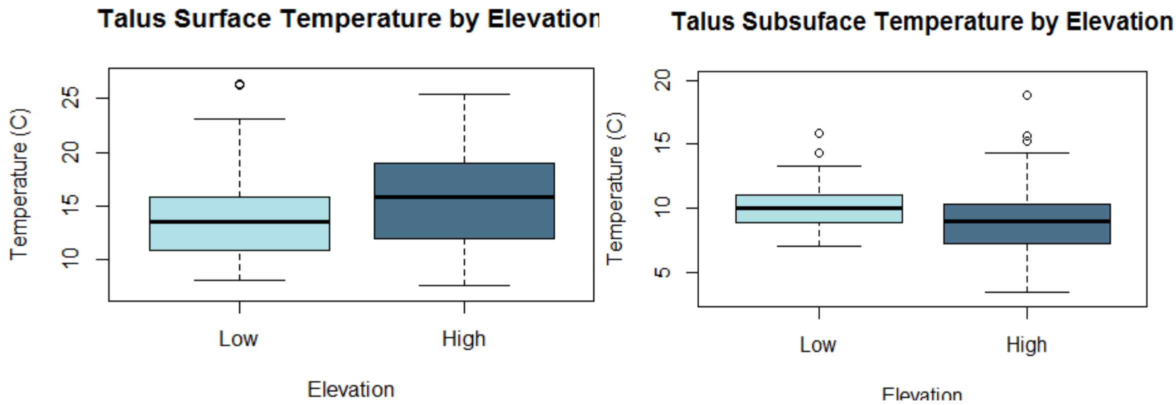


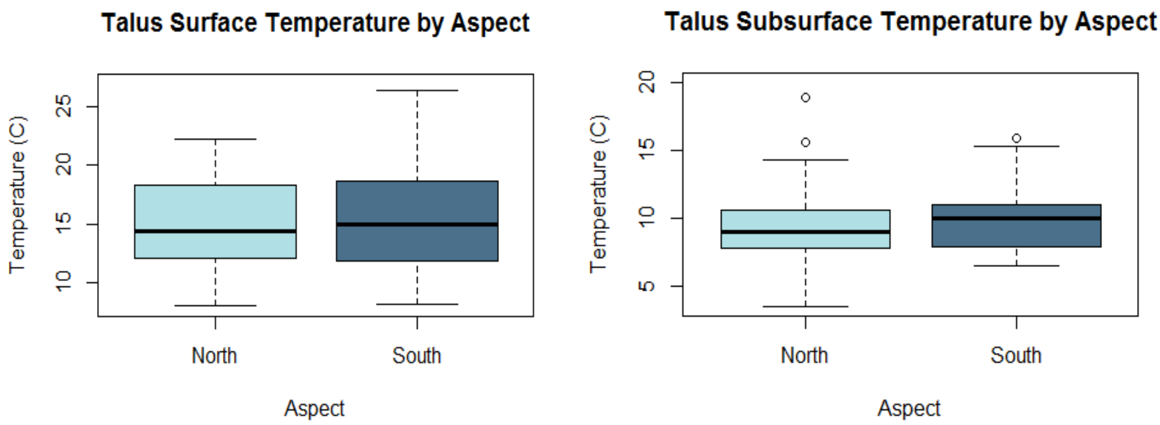
Figure 1: A summary of microhabitat temperatures is shown above. Surface and meadow locations showed a larger range of temperatures, with medians around 15°C. Sub-surface locations showed a narrower range of temperature with a lower median around 9°C. There are 3 outliers for sub-surface temperatures, all above 15°C.

Figures 2a and 2b: Talus sub-surface and surface temperature by elevation.



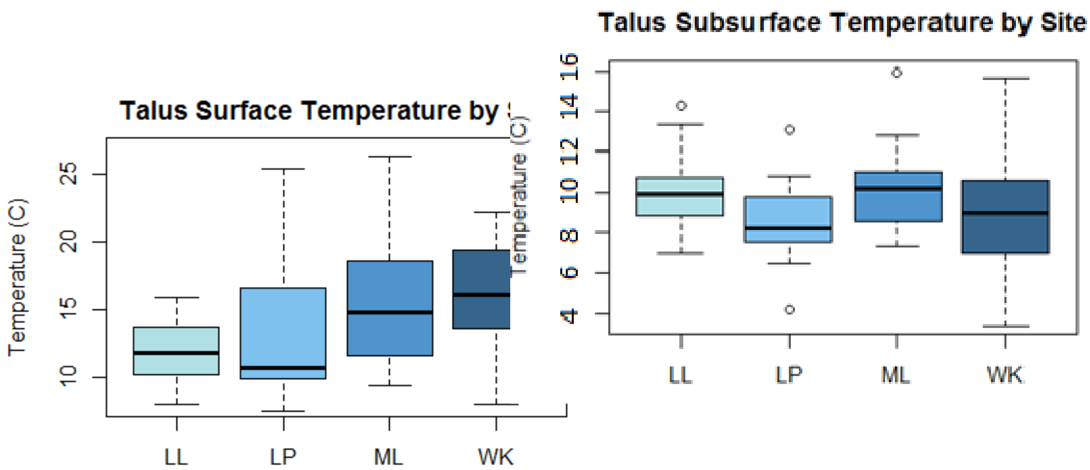
Figures 2a and 2b show baseline temperature data across all sites, by elevational (low being subalpine sites surrounded by trees, and high being alpine sites). Lower elevations had slightly higher median sub-surface temperature, with narrower range, but a lower median surface temperature than higher elevation sites.

Figures 3a and 3b: Talus surface and sub-surface temperature by aspect.



Figures 3a and 3b show baseline temperature data across all sites, by aspect. Surface and sub-surface temperatures were similar among aspects.

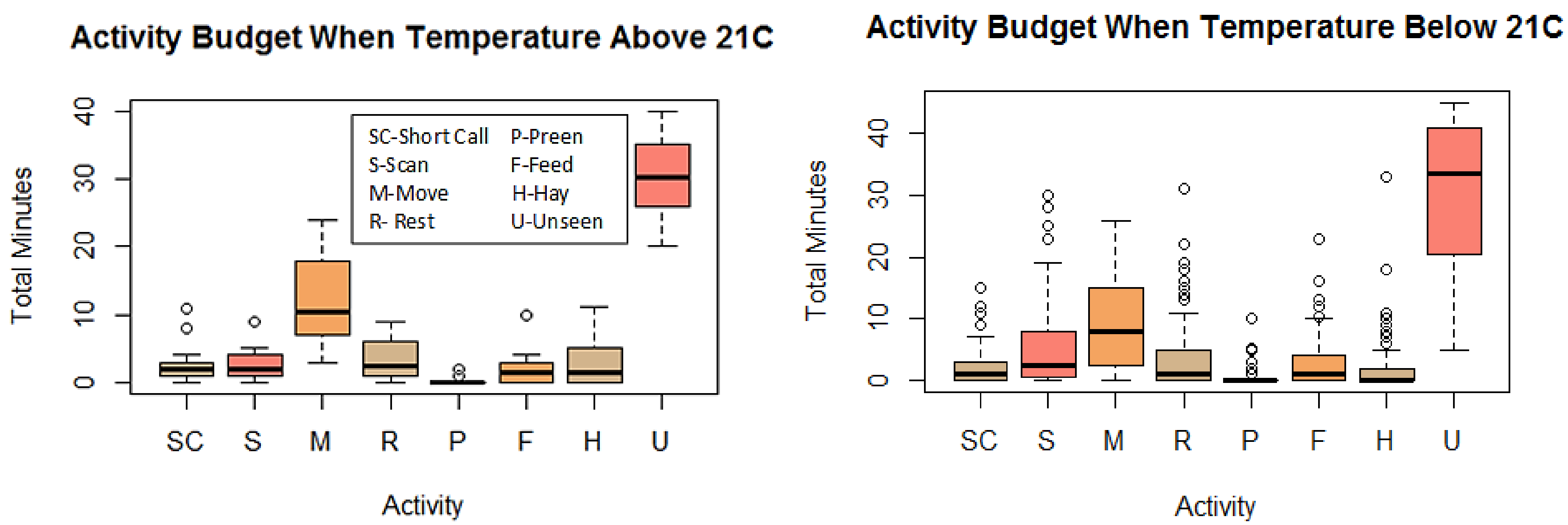
Figures 4a and 4b: Talus surface and sub-surface temperature by site.



Figures 4a and 4b compare surface and subsurface temperature data by site location (LL= Long Lake, LP= Loveland Pass, ML=Mitchell Lake, WK=West Knoll). There is a significant difference between the surface temperature of the sites, but not a significant difference of sub-surface temperatures between sites. There is larger variation in site surface temperatures in LP, ML, and WK than LL. Additionally, WK has the largest variation in subsurface temperatures.

Temperature indexed activity budgets were established using an assumed heat-stressor threshold of 21°C average surface temperature (See Figure 5a and 5b). A total of 14 observations were conducted at average surface temperatures at and above 21°C, and 80 observations were conducted below this threshold. The majority of the time, pikas were unseen within the high and low temperature observations (average of 30.116, 30.484 minutes respectively). The time spent in each of the activities was similar in both budgets, with pika movement (typically running) being the most frequent surface activity in both cases (average of 11.571, 9.132 activity-minutes for high and low observations respectively). The majority of activities did not significantly differ between budgets, with the exception of the activity of scanning. Scanning was significantly different (p== 0.00219), with high temperature observations averaging 2.65 activity-minutes and lower temperature observations averaging 5.61. Additionally, there were more outliers above the range of activity-minutes in the budget based on observations conducted during lower-temperature days. This indicates more variation in activity levels with cooler temperatures.

Figure 5a and 5b: Temperature indexed activity budgets of the American pika in the Southern Rockies

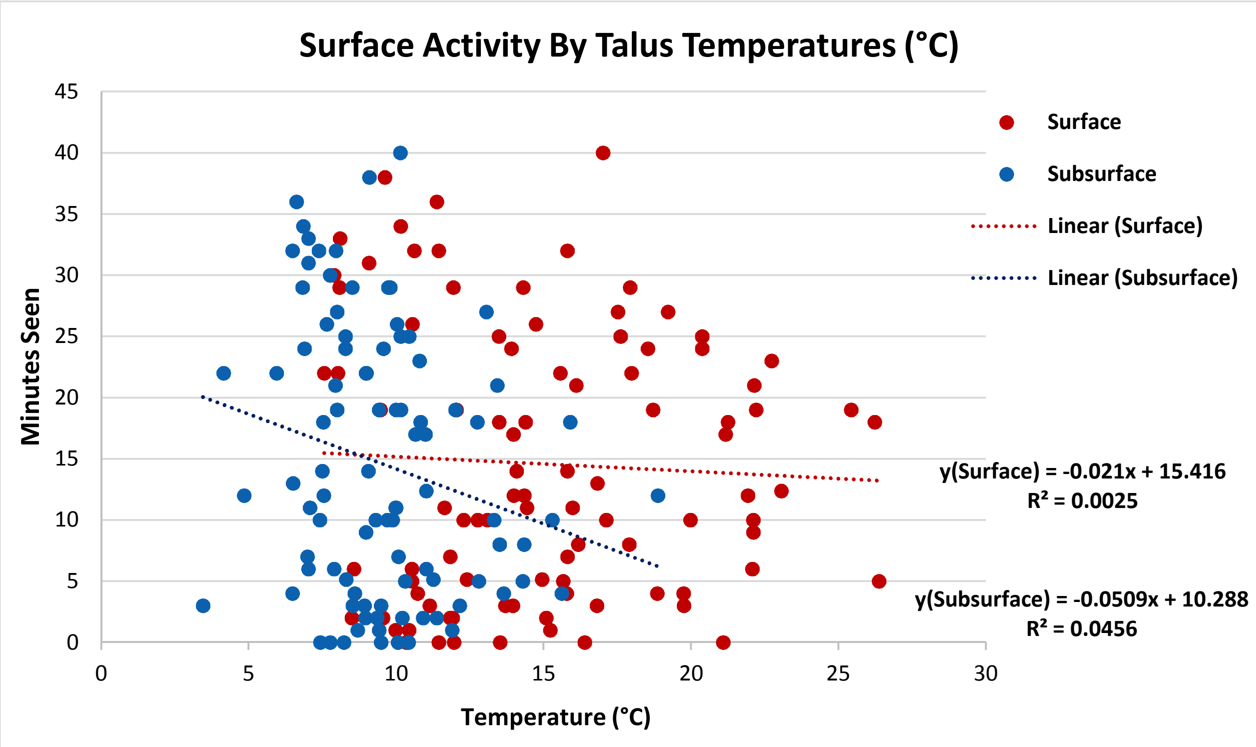


Figures 5a and 5b show the median and range of minutes during which pikas were seen performing each activity (short calling, scanning, moving, resting, preening, feeding, haying and minutes unseen). The budgets are indexed by temperature, using a threshold of 21°C. Since multiple activities could be observed in one observation minute, the total minutes of all activities is greater than the observation time of 45 minutes. The majority of the time, in both budgets, pikas were unseen, and the next most commonly seen activities were moving and scanning and resting.

Modeling Pika Behavior

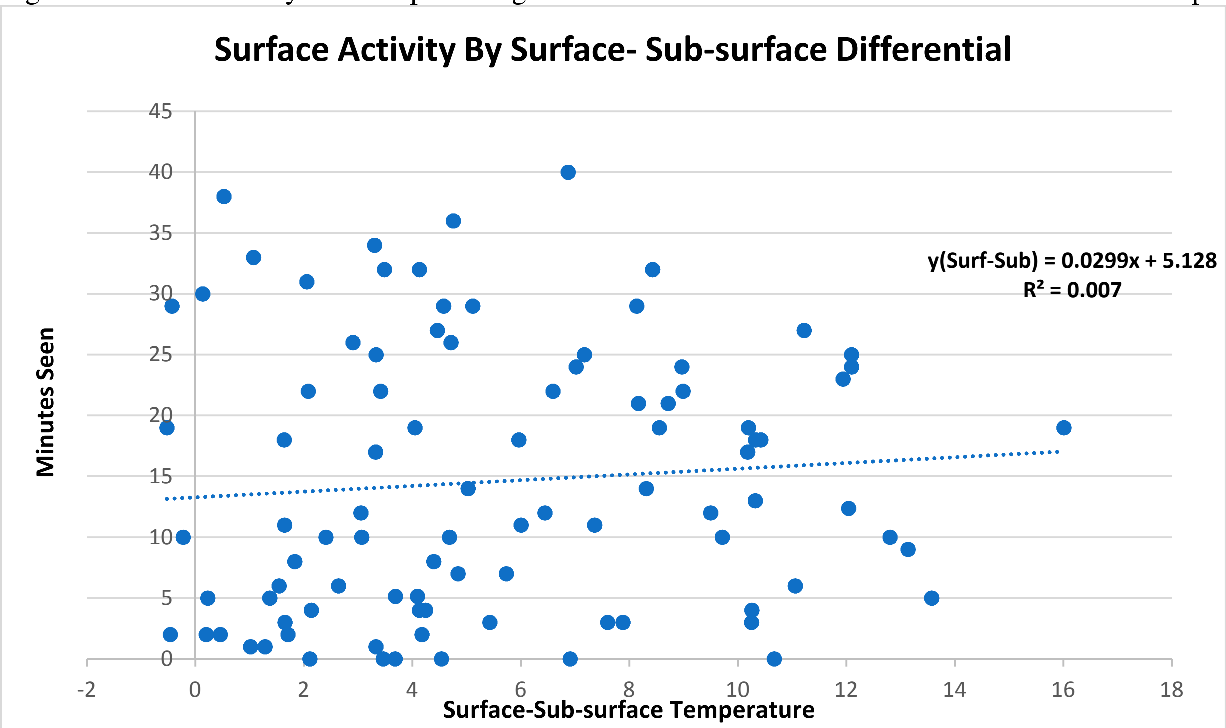
The first analysis examined how surface and sub-surface talus temperature might affect surface activity of pikas. Surface-activity minutes were graphed as a function of surface temperature of the talus and sub-surface temperature (Figure 6) and as a function of surface-sub-surface differential. Scatterplots of surface activity related to talus surface and talus sub-surface temperatures (See Figure 6) as well as the surface-sub-surface differential are shown (See Figure 7).

Figure 6: Surface activity minutes by surface and sub-surface temperature.



This figure shows, for all 94 observations for how many minutes pika were seen active on the surface, in relation to talus surface (blue) and sub-surface (red) temperatures. Trendlines for surface and sub-surface data have low R^2 values (0.0025, 0.0456 respectively), meaning these simple single linear regressions have a low ability to explain the variance in the data. The surface trendline is near horizontal with a very slight negative correlation. The sub-surface trendline has a more pronounced negative correlation.

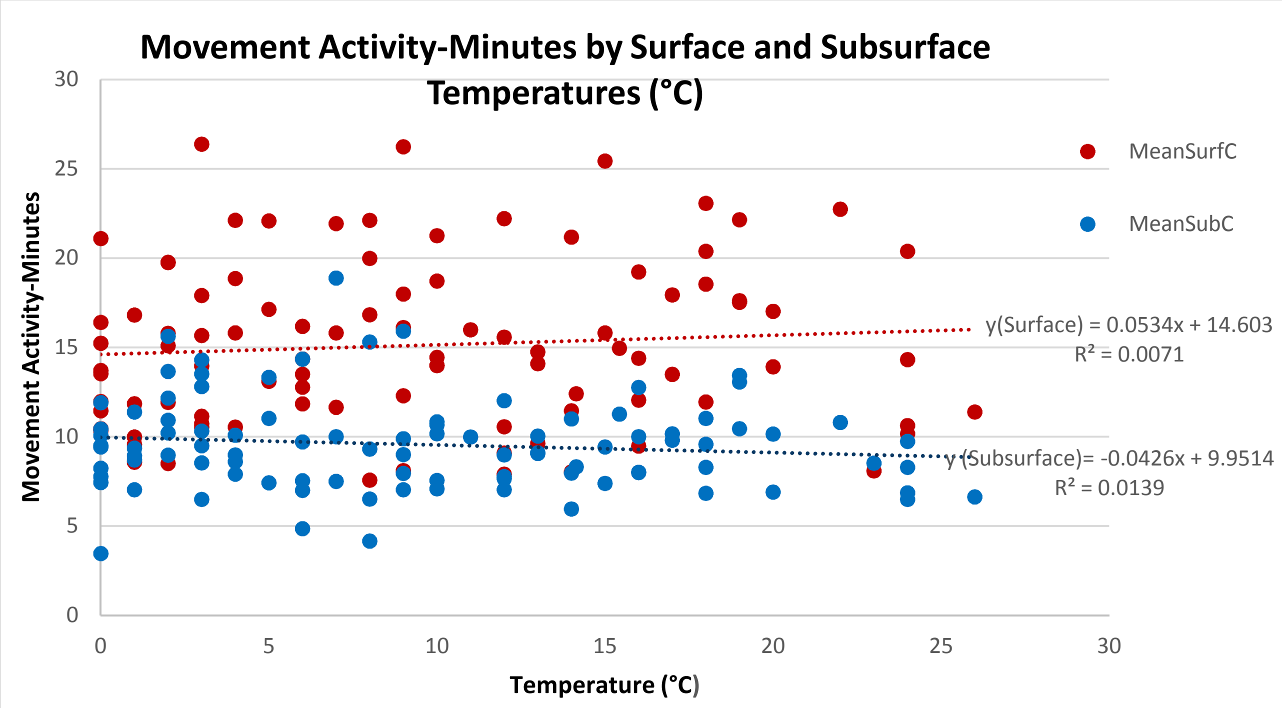
Figure 7: Surface activity-minutes plotted against the difference between surface and sub-surface temperatures.



This graph shows all 94 observations on for how many minutes pika were seen as a function of the difference between talus surface temperature and talus sub-surface temperature. The trendline shows a slightly positive correlation between minutes seen and the temperature differential.

In relating pika behavior to surface temperature, the frequency of pika movement during observations was also examined. The number of activity-minutes was charted by surface and sub-surface temperature for all observations (Figure 8). To determine whether there was an effect of temperature class (above vs. below 21C) on the number of movement activity-minutes t-test was used from the previous activity budget. The resulting p= (0.1244) was not less than 0.05, meaning that there was not a significant difference between the mean number of movement activity-minutes at higher vs. lower temperatures.

Figure 8: Movement activity-minutes plotted against surface and sub-surface talus temperatures.



The amount of time during which pikas were active on the talus surface (minutes seen) was modeled using microclimate variables. The only significant single-predictor model was based on sub-surface temperature. Sub-surface temperature had a statistically significant negative effect on surface activity ($p = 0.0388$), with an AIC value more than two units below the null model (See Table 3). To test for effects of aspect on activity, a separate analysis was required because aspect was not available for the data from LP. After excluding LP, all models were compared again, but aspect was not supported as a univariate predictor of pika surface activity. Interaction effects were modeled by considering a few variables based on a prior knowledge of ecological interactions and effects. In these models, only one interaction garnered more support than the null: MeanSubC*MeanTemp (sub-surface temperature by mean surface temperature recorded by the observer).

Table 3: Linear regression modeling of pika surface activity-minutes. The table shows the AIC (relative support) and p= (statistical significance) for each model defined by the list of predictor variables and (in some cases) interaction effects. Models with good support relative to the null are marked * and statistically significant (α = 0.05) models are marked **.

Linear Regression Models for Surface Activity-Minutes

Single Variable Predictors	**AIC**	**P=**
Null	719.6774	------
MeanSubC	*717.2925	**0.03883
Elevation	718.5541	0.08122
MeanTemp	719.5375	0.1489
MeanWind	720.1085	0.2165
Time	720.8483	0.369
DiffSurfSub	721.0135	0.4215
MeanSkies	721.1739	0.4839
MeanSurfC	721.4423	0.6324
DiffBothSub	721.5178	0.6935
DiffMdwSub	721.6674	0.9213
Multi-Variable Predictors	**AIC**	**P=**
MeanSubC*MeanTemp	*716.6065	**0.03307
MeanSubC+Elevation	*717.1956	**0.04339
MeanTemp+MeanWind	*717.2216	0.1223
MeanTemp*MeanSubC+Elevation	718.0746	**0.04027
MeanSurfC*MeanSubC	718.5359	0.07598
MeanSurfC+MeanSubC	718.7555	0.09233
MeanSubC+MeanTemp	719.0025	0.1041
MeanSubC+Time	719.153	0.1119
MeanSubC*Time	719.3359	**0.0466
MeanSubC*Time+Elevation	719.6774	0.05646

Additionally, activity movement and short calling were modeled using the same microclimate variables as surface activity-minutes (See Table 4). The purpose of this analysis was to test whether other high-energy activities (such as movement), and territorial defense (short-calling) could be related to microclimate factors. Here, the models for both activities were reported simultaneously because there were no models in either category that significantly predicted either activity based on AIC values.

Table 4: Linear regression models for movement activity-minutes, and for short call activity-minutes

Linear Regression Models for Movement			**Linear Regression Models for Short Call**		
Single Variable Predictors	**AIC**	**P=**	**Single Variable Predictors**	**AIC**	**P=**
Null	641.2828	-----	Null	471.2627	-----
DiffBothSub	640.6393	0.1087	DiffBothSub	473.2627	0.9956
DiffMdwSub	641.7931	0.2285	DiffMdwSub	473.2533	0.9253
DiffSurfSub	640.2732	0.08697	DiffSurfSub	473.2519	0.9181
Elevation	641.6411	0.2062	Elevation	471.9937	0.2664
MeanSkies	643.2827	0.996	MeanSkies	472.0266	0.2727
MeanSubC	641.9685	0.258	MeanSubC	473.0799	0.6731
MeanSurfC	642.617	0.4208	MeanSurfC	473.239	0.879
MeanTemp	643.252	0.8627	MeanTemp	472.4794	0.3825
MeanWind	641.9588	0.2563	MeanWind	471.7265	0.2214
Time	642.6608	0.4365	Time	472.9773	0.5981
Multi-Variable Predictors	**AIC**	**P=**	**Multi-Variable Predictors**	**AIC**	**P=**
MeanSubC*MeanTemp	643.1335	0.262	MeanSubC*MeanTemp	475.5067	0.639
MeanSubC*Time	643.1719	0.2661	MeanSubC*Time	471.7112	0.1482
MeanSubC*Time+Elevation	644.4953	0.6562	MeanSubC*Time+Elevation	472.4728	0.1648
MeanSubC+Elevation	642.7563	0.2944	MeanSubC+Elevation	473.581	0.4431
MeanSubC+MeanTemp	643.2762	0.3786	MeanSubC+MeanTemp	473.5251	0.4312
MeanSubC+Time	643.9386	0.5217	MeanSubC+Time	472.4306	0.2539
MeanSurfC*MeanSubC	642.9912	0.2476	MeanSurfC*MeanSubC	476.8795	0.9466
MeanSurfC+MeanSubC	641.1033	0.1323	MeanSurfC+MeanSubC	475.0728	0.9122
MeanTemp* MeanSubC+Elevation	644.0745	0.2887	MeanTemp* MeanSubC+Elevation	476.2802	0.5823
MeanTemp+MeanWind	643.9584	0.5267	MeanTemp+MeanWind	473.1947	0.3675

The next analysis considered the effect of the temperature differential between surface and sub-surface temperature as a variable presumably related to the potential for behavioral thermoregulation. The relationship between the surface-sub-surface differential and the average of surface and meadow minus the sub-surface temperature were considered and modeled (See Table 5).

Table 5: Linear models of temperature differential with and without low surface temperature observations

	Temperature Differential Modeling					
	All Observations		**Surface Temp. >10C**		**Surface Temp. >15C**	
	AIC	**p=**	**AIC**	**p=**	**AIC**	**p=**
Predictors						
Null	719.6774	----	620.0773	-----	328.4382	-----
DiffBothSub	721.5178	0.6935	620.4182	0.2047	*326.2954	**0.04805
DiffSurfSub	721.0135	0.4215	618.5803	0.06557	327.5113	0.09659
MeanSurfC	721.4423	0.6324	621.6649	0.5271	330.3412	0.7624
MeanSubC	*717.2925	**0.0352	619.5233	0.1156	326.9817	0.07096
MeanSurfC*MeanSubC	718.5359	0.07598	620.2491	0.134	329.1702	0.1833

Linear regression models were compared to mixed-effects models with random effects to determine whether random aspects of site location, time of day, seasonality (month) or elevations caused a change in fixed effects of temperature, etc. Mixed-effects models were used to consider fixed effects of sub-surface temperature and temperature differentials. The only supported model included a random effect of location and fixed effect of sub-surface temperature (Table 6).

Table 6: Mixed effects models. Models that were supported better than the null are marked *.

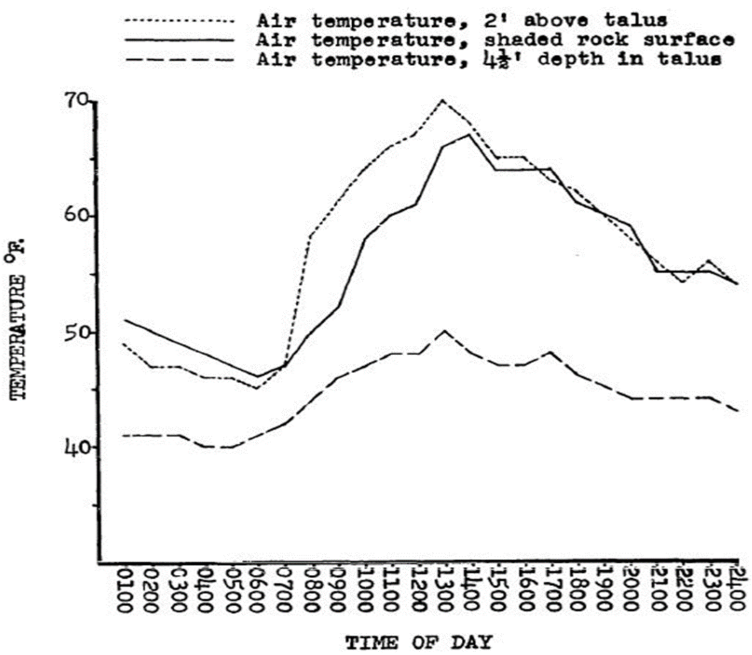
Mixed Effects Models	
Mixed Effects Models	**AIC**
Null	719.6774
MeanSubC+(1|Location)	*717.6732
MeanSubC+(1|Month)	718.5571
MeanSubC+(1|Elevation)	719.2925
MeanSubC+(1|Year)	719.2925
1+(MeanSubC|Location)	719.3723
1+(MeanSubC|Month)	721.2890
DiffBothSub+(1|Location)	721.6333
1+(DiffSurfSub|Location)	722.7723
DiffBothSub+(1|Elevation)	723.4460
DiffBothSub+(1|Month)	723.5178
DiffBothSub+(1|Year)	723.5178
1+(MeanSubC|Elevation)	723.9382
1+(MeanSubC|Year)	725.3103
1+(DiffSurfSub|Elevation)	725.4458
1+(DiffSurfSub|Month)	725.5886
1+(DiffSurfSub|Year)	725.6772

Discussion

The American pika has been considered an important species to monitor as a signal for alpine ecosystem change. The goal of this project was to provide behavioral and temperature baseline data, as well as model pika behavior as a function of microhabitat and microclimate conditions. The results indicate the importance of sub-surface temperatures as a factor in behavioral temperature regulation. The temperature data show a significant difference between talus surface and sub-surface temperatures, and the behavior models show important effects of sub-surface temperature and the temperature differential between the surface and sub-surface habitats.

Comparison of the surface, sub-surface, and meadow temperatures from all observations confirmed qualitative observations and past studies (Krear 1965, Philippe et al. 2012, Varner and Dearing 2014). Average sub-surface temperature was significantly lower than surface and meadow temperatures with a difference of about 5.5°C. Sub-surface spaces between rocks are insulated from direct solar heating and the trapped air heats slowly due to limited air exchange causing these spaces to be cooler (Philippe et al. 2012). Krear (1965) found that daily temperature deep below the surface (4.5 m down) were cooler than shaded surface temperatures at the Long Lake (LL) site in 1963 (See Figure 9) . The range of sub-surface temperatures was also significantly narrower indicating the climatic stability of these microhabitat spaces throughout the various sites.

Figure 9: Daily fluctuation of the air temperature, surface talus temperature, and below talus temperature from 1963.



Here Krear (1965) showed the difference between surface and sub-surface temperatures at LL over the course of a day.

Unfortunately, these patterns were not quantified in a way that would support monitoring of changes over time.

Surface and sub-surface temperatures were compared among elevations to understand the influence of these habitat characteristics on the talus microclimate. As generally accepted, elevation has an inverse relationship with temperature, thus making higher elevation locations cooler. However, in the present study the higher alpine sites averaged warmer surface temperatures than the lower sites, although statistically there was not a significant difference between these sites (p= 0.05467). One possibility for this difference could be the direct exposure of the high elevation sites to solar insolation, whereas the lower elevation sites were surrounded by tall trees. Vegetation could shade and trap cooler air currents in the talus spaces. Higher sites might have had lower sub-surface temperatures due to the presence of sub-surface ice, which may have been absent at lower sites. There were also more observations at higher elevations sites (59) than at the lower sites (35), which could underrepresent the temperature readings at the lower sites. Overall, this type of unexpected variance in the data is part of the motivation behind using random effects models, allowing the relationship between temperature and activity to vary with elevation.

Comparison of average surface and sub-surface temperature by aspect (North and South) revealed no significant differences. Although this study did not find significant differences in temperatures between aspects, aspect is still an important microclimate variable to in pika persistence (Ray et al. 2012). Aspect can influence snowpack distribution in the winter, a decrease of which can cause declines in survival rates and temperature by the direction of prevailing winds and solar insolation. In the northern hemisphere, the north-facing slopes tend to be cooler, drier and more heavily glaciated, sub-surface ice being a potentially important variable (Barbour et al. 1999).

Lastly, in the temperature comparisons, site was considered in establishing temperature baselines. Average surface temperature did appear to be significantly different between sites (p= 0.00857), although sub-surface temperatures were not significantly different (p= 0.31). WK and ML had the highest average surface temperatures (16.17°C, 15.75°C), higher than the overall surface average of 15.11°C. LP and LL had lower average surface temperatures (13.64°C, 11.93°C). These differences in site temperatures could be due to site characteristics including variables like aspect, and elevation, and wind conditions. This study suggests that there are at least temperature differences between sites, which could in turn affect pika behavior and survival.

The temperature-behavior response data was analyzed to determine how surface temperatures affected pikas' surface activity. Based on past studies, the present study projected that pikas would be less active on surfaces with higher surface temperatures (MacArthur and Wang 1974; Smith 1974). However, the surface activity-minutes were not significantly different (p= 0.433) between the above-21°C and the below-21°C temperature class. Examining the activity budgets the average majority of the observations were spent with the focal pika unseen (average approximately 30 minutes). The most commonly observed activities were moving and scanning and resting. There was a higher number of outliers, points more than 2/3 outside the range of the median, in the below-temperature-threshold budget, indicating more variation in activity levels with cooler temperatures. This increased fluctuation could indicate that pikas at lower temperature have more options in activity when temperatures are cooler. However, there were also many more observations that occurred below 21C, which could be the cause of the increased variation in these data. It will be important to observe pika activities during warmer parts of the day (e.g., in the afternoon, which is poorly represented among the samples analyzed here), but this will be difficult at these study sites, which are prone to lightning during summer afternoons. Camera studies may be warranted in this situation.

Based on the pikas' need to thermoregulate their internal body temperature, more energy-intensive activity was predicted to occur more often during cooler temperatures. However, there were not significant differences in behavior across the temperature threshold selected here, with exception of activity of scanning (p= 0.00219). Scanning averaged 2.65 activity-minutes for the higher temperature observations, but significantly more during lower temperature observations with an average of 5.61 activity-minutes. Scanning is a territorial monitoring behavior, as pikas usually scan near their haypile, and the activity is usually a response to noises nearby, including calls of other pikas or other species. This low-energy intensive activity occurred more frequently in cooler temperatures. Future studies could compare the number of scanning activity-minutes with the number of other pika short calls for each observation, as scanning is a component of territorial and predictor response. Additionally, a high-energy-intensive activity, "movement" was graphed by surface temperature and a standard t-Test revealed no significant difference between the amount of movement when surface temperatures averaged above vs. below 21 C. The average amount of movement was also not significantly different between morning and afternoon observations, in keeping with the bimodal (morning and evening) activity periods observed by other researchers (Krear 1965, Smith 1974).

Modeling surface activity of pikas is important in advancing the study of how microclimate characteristics could affect the survival of pikas. Sub-surface talus temperature was the only statistically significant model of pika surface activity-minutes with a single variable. Both the p= (0.03883) and relative AIC value supported the model as better than the null. The relative importance of sub-surface temperature is expected, because pikas use the cooler sub-surface cavities to shed accumulated heat after being active on the surface (MacArthur and Wang 1974). Although patterns of pika occupancy and persistence have been explained in part by sub-surface temperature in other studies, projections of pika persistence in a warming climate have not addressed this variable. The present study shows how pikas alter their daily behavior patterns based on sub-surface temperatures, a strategy that might allow for adaptation to climate change. However, the present study also reiterates that pikas require access to sub-surface spaces that are cool in an absolute rather than a relative sense. Surface activity was related directly to sub-surface temperature in this study, rather than being related to the difference between surface and sub-surface temperature. Therefore, there may be limits to how well pikas can adapt to warming temperatures if sub-surface temperatures are also warming. Sub-surface talus temperature has been poorly studied and future studies could further assess microhabitat conditions such as sub-surface ice features. Furthermore, the effects of climate change on sub-surface temperatures is unknown, but possible warming and melting of these ice features might result in a warming of these talus cavities.

On the other hand, when examining the effect of temperature differentials on surface activity, the data showed a non-linear relationship, and the model of surface activity based on DiffBothSub became significant after removing the low to moderate values of surface temperature (values ≤ 15°C). This suggests that a strong temperature gradient is more important when the surface temperature is greater than 15°C. The temperature differential between surface and sub-surface could provide pikas with a mechanism to shed heat during warmer days. If the ambient temperature is warmer, a pika might be able to rely heavily on cool sub-surface cavities in order to continue on with surface activities. Surface and sub-surface temperatures might be more similar at certain times of day, for example at night if the sub-surface temperature lags behind the daytime surface temperature. With a similar temperatures, pikas might be seen less on the surface in energetic activities as a method for conserving energy.

The other models (surface temperature, elevation, aspect, ambient temperature, wind, skies, time of day, all three temperature differentials) were not significant for surface activity, and none of the models were significant for the activities “movement” or “short call”. It may not be surprising that surface activity did not vary with these variables, because pikas in every habitat must accomplish surface activities like feeding, haying and territorial defense. However, it has been suggested that pikas shift surface activities to early morning and late evening hours at locations with higher diurnal temperatures (Smith 1974). If so, it might be possible to see an effect of elevation or aspect on behavior, especially if observations were mainly conducted in mid-morning, as in the current study. The temporal limitation of the present study may be why no effect of time of day was detected, because observations peaked when surface activity would be expected to peak. Similarly, the variance in wind or skies might not have been sufficient to reveal effects of these variables. Most observations in this study occurred on sunny days with low wind.

Random effects of elevation, year, seasonality (month), and location were also assessed to determine whether some of the variance in the data could be better explained by mixed-effect models. The only significant mixed-effect models in explaining surface activity-minutes was MeanSubC+(1|Location). This model indicates that location has a random effect on the intercept of the relationship between sub-surface temperature and surface activity. This information could be important in future monitoring of these specific sites, also considering the significant difference of surface temperature between sites. Random effects are important to consider because of variation in data, and when considering factors for which relationships might not be established.

Within this data set there are a couple of statistical issues that should be examined in the future. One statistical issue with using simple linear regressions of the response variable is that surface-active minutes is either a zero or a positive value, meaning that it is not normally distributed around its mean. The data might follow a Poisson or negative binomial distribution, both of which could be used in future analyses. Also, certain behaviors are not independent of one another. For example, moving is associated with the pika’s process of haying or feeding in vegetation patches off the talus, and pikas generally give a short call before leaving the haypile to feed or hay (Smith and Weston 1990).

While this study is a useful step in relating surface and sub-surface talus temperatures with pika behaviors, the study is limited in the variables considered. The study does not address biotic influences like predator-prey interactions such as predator effects on a pikas' behavioral response. The presence of predators, like pine martins and weasels, can cause pikas to conduct more short calls per minute, and call for a longer period of time (Ivins and Smith 1983). Also there are certain site/habitat characteristics that should affect pika behavior like distance to nearest vegetation patches, and population density. Allowing for random effects of site was one attempt to control for these factors.

There are also limitations with respect to the observations, and the process of standardizing observations across years, sites and observers can be difficult. Allowing for random effects of observer might become useful, especially as this data set grows and the set of observers is less defined by the set of years and sites. Another type of observer effect might also be important, as evidenced by examples of pikas attempting to hay the shoelaces and backpack straps of observers. Also, in a qualitative comparison of study methods, pikas were heard to long-call during observations much less frequently than long calls were recorded by automated audio equipment used at these sites when observers were not present (Chris Ray pers. comm.). Finally, when a pika was not seen on the talus the assumption here was that the pika was below the talus. However, the absence of the focal animal could be accounted for by the pika being outside the observable range. Alternatively, the pika might be surface-active but not visible due to the micro-topology of the site.

Future studies of pika surface activity using this or similar data sets could examine behavior in relation to life stage (adult or juvenile), sex or individual effect. For example, differences between sexes and stages in the timing (month) of initiation of haying behavior are well documented (Smith and Weston 1990). Individuals would have different activity budgets, these different activity levels could help explain individual characteristics that allow a pika to successful overwinter (i.e. increased haying). Future studies of pika behavior as a function of microclimate and microhabitat could use bootstrap data to further test the models. Further refined models could possibly to be able to project levels of pika activities related to general climate changes.

References

Barbour, M. G., J. H. Burk, and W. D. Pitts. *Terrestrial Plant Ecology, 3rd Ed.* Benjamin/Cummings. (1999) Chapter 14. pp. 390-391

Beever, E. A., P. F. Brussard, and J. Berger. "Patterns of Apparent Extirpation among Isolated Populations of Pikas (*Ochotona princeps)* in the Great Basin." *Journal of Mammalogy* (2003): 37–54. Web.

Burnham K. P., and D. R. Anderson 1st ed. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach.* Springer; (2002).

Calkins, M. T., E. A. Beever, K. G. Boykin, J. K. Frey, and M. C. Andersen. "Not-so-splendid isolation: Modeling climate-mediated range collapse of a montane mammal (Ochotona princeps) across numerous ecoregions". *Ecography* 35 (2012): 001–012.

Dearing M. D. "Disparate determinants of summer and winter diet selection in a generalist herbivore, *Ochotona princeps." Oecologia* 108 (1996): 467-478.

Dearing, M. D. "The Function of Haypiles of Pikas (Ochotona Princeps)." *Journal of Mammalogy* 78 (1997): 1156–1163.

Diaz, H. F., and J. K. Eischeid. "Disappearing "alpine Tundra" Köppen Climatic Type in the Western United States." *Geophysical Research Letters* 34.L18707 (2007): n. pag. Print.

Erb, L. P., C. Ray, and R. Guralnick. "On the Generality of a Climate-Mediated Shift in the Distribution of the American Pika (Ochotona Princeps)." *Ecology* 92.9 (2011): 1730-735.

Galbreath, K. E., D. J. Hafner, and K. R. Zamudio. "When cold is better: climate-driven elevation shifts yield complex patterns of diversification and demography in an alpine specialist (American pika, Ochotona princeps)". *Evolution* 63 (2009): 2848-63.

Hafner, D. J. "North American pika (Ochotona princeps) as a late Quaternary biogeographic indicator species." *Quaternary Research* 39 (1993): 373-380.

Hafner, D. J. "Pikas and permafrost: post-Wisconsin zoogeography of Ochotona in the southern Rocky Mountains, U.S.A." *Arctic and Alpine Research* 26 (1994): 375-382.

Ivins, B. L., and A. T. Smith. "Responses of Pikas (Ochotona Princeps, Lagomorpha) to Naturally Occurring Terrestrial Predators." *Behavioral Ecology and Sociobiology* 13 (1983): 277–285.

Jeffress, M. R., T. J. Rodhouse, C. Ray, S. Wolff and C. W. Epps. "The idiosyncrasies of place: geographic variation in the climate-distribution relationships of the American pika." *Ecological Applications* 23 (2013):864–878.

MacArthur, R. A. and L. C. H. Wang. “Behavioral thermoregulation in the pika, Ochotona princeps: a field study using radiotelemetry.” *Canadian Journal of Zoology* 52 (1974): 353-358.

Millar, C. I., and R. D. Westfall. “Rock glaciers and periglacial rock-ice features in the Sierra Nevada; Classification, distribution, and climate relationships.” *Quaternary International* 188 (2008): 90-104.

Millar, C. I. and Westfall, R. D. “Distribution and climatic relationships of the American pika (Ochotona princeps) in the Sierra Nevada and western Great Basin, USA: periglacial landforms as refugia in warming climates.” *Arctic Antarctic and Alpine Research* 42 (2010): 76-88.

Pepin, Nick. "Twentieth-Century Change in the Climate Record for the Front Range, Colorado, U.S.A." *Arctic, Antarctic, and Alpine Research* May 32.2 (2000): 135-46.

R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, (2014) Vienna, Austria. http://www.r-project.org

Ray, A. J., J. J. Barsugli, and K. B. Averyt. *Climate Change in Colorado: A Synthesis to Support Water Resources Management and Adaptation*. Rep. N.p.: Western Water Assessment, (2008). Print.

Ray, C., E. Beever and S. Loarie. “Retreat of the American pika: up the mountain or into the void?” pp 245-270 in Brodie, J. F., E. Post and D. F. Doak (eds.) *Wildlife conservation in a changing climate*. University of Chicago Press (2012). pp 416.

Ray, Chris. Personal communication. (Spring 2015).

Rodhouse, T. J., E. A. Beever, L. K. Garrett, K. M. Irvine, M. R. Jeffress, M. Munts, and C. Ray. “Distribution of American pikas in a low-elevation lava landscape: conservation implications from the range periphery.” *Journal of Mammalogy* 91 (2010):1287–1299.

Smith, A.T., Weston, M.L. “Ochotona princeps.” *Mammal Species* 352 (1990). Print.

Smith, A. T. “The Distribution and Dispersal of Pikas□: Influences of Behavior and Climate.” *Ecology* 55 (1974): 1368–1376. Web.

Smith, J. A., & Erb, L. P. “Patterns of selective caching behavior of a generalist herbivore, the American pika (Ochotona princeps).” *Arctic, Antarctic, and Alpine Research*, 45(2013): 396-403.

Varner J. & Dearing M.D. (2014). “The importance of biologically relevant microclimates in habitat suitability assessments.” *PLoS ONE,* 9 (2014): e104648.

Wilkening, J. L., C. Ray and K. L. Sweazea. “Stress hormone concentration in Rocky Mountain populations of the American pika (*Ochotona princeps*).” *Conservation Physiology* 1 (2013): cot027 (13 pp.).

Wilkening, J., C. Ray and J. Varner. “Relating sub-surface ice features to physiological stress in a climate sensitive mammal, the American pika (*Ochotona princeps*).” *PLOS ONE*. (2015).

Wilkening, J. L., C. Ray, E. A. Beever, and P. F. Brussard. “Modeling Contemporary Range Retraction in Great Basin Pikas (Ochotona Princeps) Using Data on Microclimate and Microhabitat.” *Quaternary International* 235 (2011): 77–88. Web.

Williams, M. W., M. V. Losleben, and H. B. Hamann. "Alpine Areas in The Colorado Front Range As Monitors Of Climate Change And Ecosystem Response." *Geographical Review* 92.2 (2002): 180.

Wilson, J. A. "Life in a Shrinking World: Thermal Physiology and Activity of Diurnal Alpine Mammals in Relation to Climate Change," University of Wyoming National Park Service Research Center Annual Report 33 (2011): Article 25.

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Title Page: Sara McLaughlin 2012

Appendices

Appendix A: Behavioral Observation Recording Sheet

Begin Skies (Sunny, Cloudy, Overcast)											Begin Wind (Low, Medium, High)				
Minute (1 to 22. Page 1)	Focal Animal (tags, marks, Juvenile, Adult)	Activity (Unseen, Move, Rest, Scan, Preen, Feed [sp], Hay [sp], LongCall, ShortCall, OtherCall, Chase, Escape, Tolerate, CheekRubbing)	Distance from Haypile (m)	Stimulus Species (e.g., Pika J/A, Marmot J/A, Wx, Noise, Human, Raven, Bird…)		Stimulus Type (Arrival, ShortCall, LongCall, OtherCall, Chase, etc.)		Distance from Stimulus (m)		Response to Stimulus (None, Pause, Look, Scan, Run, Hide, ShortCall, LongCall, OtherCall, Approach, Chase)		Recording Counter	Map Check (on Rocks, Off)	Notes (Changes in wx, skies, wind; Definitions of abbreviations for stimulus species [e.g., P1=UA=unmarked adult pika, P2=UJ=unmarked juvenile pika]; Definitions of abbreviations for plants fed upon/hayed; Rationale for shift in focal animal; etc.)

Minute (23 to 45)	Focal Animal (tags, marks, Juvenile, Adult)	Activity (Unseen, Move, Rest, Scan, Preen, Feed [sp], Hay [sp], LongCall, ShortCall, OtherCall, Chase, Escape, Tolerate, CheekRubbing)	Distance from Haypile (m)	Stimulus Species (e.g., Pika J/A, Marmot J/A, Wx, Noise, Human, Raven, Bird…)		Stimulus Type (Arrival, ShortCall, LongCall, OtherCall, Chase, etc.)		Distance from Stimulus (m)		Response (None, Pause, Look, Scan, Run, Hide, ShortCall, LongCall, OtherCall, Approach, Chase)		Recording Counter	Map Check (on Rocks, Off)	Notes (Changes in wx, skies, wind; Definitions of abbreviations for stimulus species [e.g., P1=UA=unmarked adult pika, P2=UJ=unmarked juvenile pika]; Definitions of abbreviations for plants fed upon/hayed; Rationale for shift in focal animal; etc.)

<table>
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<tr><td colspan="10">End Skies (S, C, O, Drizzle, Rain, Lightning)</td><td colspan="5">End Wind (Low, Medium, High)</td></tr>
<tr><td colspan="10">Temperature Sensor IDs (meadow__________, above talus___________, below talus___________)</td><td colspan="5">End Temp (°C)</td></tr>
</table>

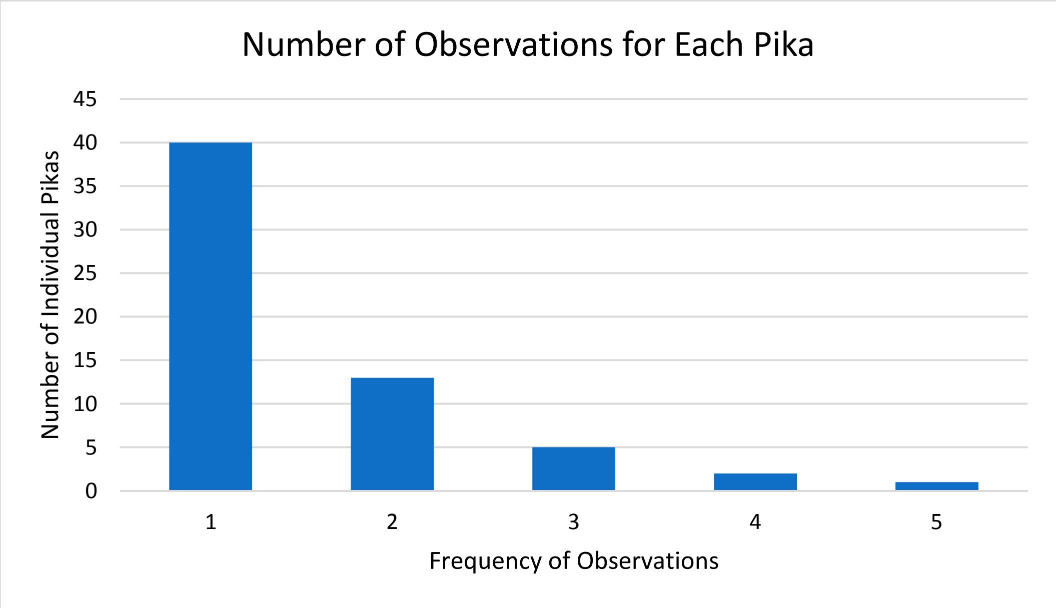
Appendix B: Index of Pika Activities

Activity	Description
Unseen	When the pika is not visible above surface; assumption that the pika is in the talus;
Move	Usually running or exploring on the talus rocks; often to get vegetation
Rest	When the pika is sitting on the rocks, sometimes sleeping
Preen	Cleaning itself with its paws and mouth
Feed	Eating vegetation; includes the species or category of plant if able
Hay	Collecting and bringing vegetation back to the haypile; includes the species or category of plant if able
Scan	Turning and looking out for other pikas, animals; also as a response to noises
Short Call	Short chirps; territorial response, or to warn of a predator
Long Call *	Long series of chirps; usually conducted by males
Other Call*	Any call from another animal
Scan from Haypile*	When the pika is scanning from its own haypile
Chase*	Focal pika runs after another pika as a territorial defence
Escape*	Focal pika is chased by another pika
Tolerate*	Focal pika coexists with another pika in its territory
Touch*	Focal pika and another pika touch
Cheek Rub*	Pika rubs cheeks against rock; way of marking area with its scent
Lick Rocks*	Pika licks or bites rocks; thought to be a way to obtain certain elements

(*)- These activities were not analyzed in this study although they were recorded during the observations. These activities were relatively rare compared to the other activities listed. Additionally, not all observers recorded these activities with the exception of long call and chase.

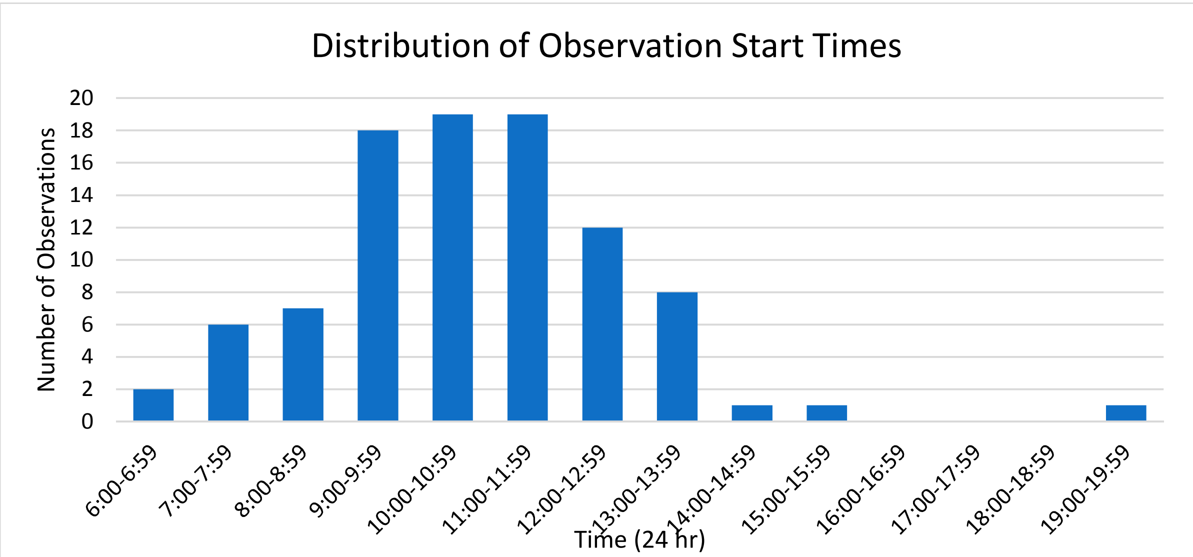
Appendix C: Supplementary Figures

Figure A: Number of unique pikas observed



This figure shows the frequency of observations of individual pikas. The majority of pika observations were conducted on a unique individual, meaning that the individual pika was only observed once per summer. The most frequently an individual was observed was 5 times during a summer.

Figure B: Time of Day of observations.



This figure shows that distribution of the time of day that observations were started. The majority of observations were conducted in the morning, peak times between 9:00 am to 11:00 am. There is only one evening observation at starting between 7:00 pm – 7:59 pm.

Appendix D: Metadata for Files

METADATA for PikaThesis_MeghanWiebe_2015

Objective: The objective of this project was to examine the behavior of the American pikas (*Ochotona princeps*) in relation to microhabitat temperature data. Behavioral observations of individual pikas were conducted in consecutive summers from 2012-2014 in Colorado, with temperature sensors placed the focal animals' territory. The organization and analyze of this data was conducted as part of an undergraduate honors thesis. In the future, the hope is that this data and analyzes can be published as part of a journal article.

Experimental Design and Data Collection: Behavioral observations of individual pikas were conducted at two high alpine sites in Niwot Ridge, a Long-Term Ecological Research site, and Loveland Pass, and two subalpine sites in Brainard Lake Recreation Area (Mitchell Lake and Long Lake). Three HOBO® Pendant Temperature/Light Data Loggers sensors were placed before each 45 minute observation in a surface, subsurface and meadow location at the beginning of the 94 behavioral observations.

Index of Documents:
This document contains a list of all the other files in this folder and a brief description of the file.

File	Description
TemperatureData_Combined.xlsx	This Excel workbook contains temperature data from each observer with a master sheet of all the temperature data combined.
Temperature_Sensor_Avgs.accdb	This Access database has a query on the trimmed average temperatures for each observation, and the length of observations.
AllBehaviorSheets.xlsx	This Excel workbook contains the individual observations 12-93
MasterDataObservations.csv	This .csv file contains the auxiliary data (such as site, aspect, and wind conditions) for each observation.
MasterDataBehaviorMinutes.csv	This .csv file contains the auxiliary information of each observation to be used as predictor variables and all the activity minutes recorded for each observation.
MasterDataTemps.csv	Copy of master sheet of all the temperature data combined
Results_Graphs_MW15.xlsx	
Anolmaous_Observations.docx	Lists anolamous observations by number, the problems and how they were adjusted for use in the datasets

Data Entry and Organization: The majority of the data entry, for the pika observations, was done by the individual observers. This includes making the activity budget for the group of pikas that he or she observed. The temperature data from the HOBO sensors downloads through a computer program and then converted into .csv and .xlsx files. The data organization for this project was chiefly done by myself (Meghan Wiebe) and Dr. Chris Ray. The process involved compiling the two data sets, pika observations and temperature data, and then combining the set for analyzes. The process of lining up observations with the corresponding temperatures used date, time, and observer, and coding each observation with a unique observation number (1-93, including 53.1). This observation number is key in connecting the two sets of data. Below I have attempted to explain all the data files, what spreadsheets and/or queries they contain, and what formulas or processes were used.

Excel Workbooks (.xlsx):

TemperatureData_Combined.xlsx- This excel work book contains temperature data the 3 sensor placements, surface, subsurface, meadow, in degrees Celsius. The HOBO sensors used in the field recorded the temperature in 5 minute intervals. The book also contains a combined sheet of all the observations temperature data.

Spreadsheet: HeatherBatts2014_Temps (Similar format for MeghanWiebe2013_Temps, MaxPlichta2014_Temps, JessicaJohnson2012_Temps, SaraMcLaughlin2012_Temps)

- Observer: First and last name of observer, text
- ObsNumber: Unique observation number used to match the observations with the correct temperature data, number
- Date: Date of the recording, m/d/yyyy format
- Time: Time of the recording, military, hh:mm
  - Used Text to Columns → Fixed Width to split date from temperature from the raw HOBO sensor readouts
- SurfaceC, SubsurfaceC, MeadowC- the temperatures in Celsius for each of the sensor placement locations

MaxPlichta2014_Temps and SaraMcLaughin2012_Temps also includes raw temperatures from the sensors.

Spreadsheet: MasterDataTemps All temperature data for each observer and observation combined.

- Observer, ObsNumber, Date, Time, SurfaceC, SubsurfaceC, MeadowC all same as columns in each observers' spreadsheet (see HeatherBatt2014_Temps above)
- IntervalNumber- corresponds to the time interval, where the start time equals 1, start time equals plus 5 minutes, ect. Up to 10 or 11. Most are 10 as the observations were 45 minutes, however the ones that are 11 the sensors were left in for another 5 minutes to allow for the lag effect. The two short observations are 38 and 48.
- SurfaceF, SubsurfaceF, MeadowF- uses the temperature data converted to Fahrenheit for reference. Uses =CONVERT(SensorC, "C", "F") for each location. Pasted as values

AllBehaviorSheets.xlsx- Contains each individual observation sheet for observations 12-93. Each sheet is labeled by the observation number. Each observation has associated auxiliary data that was later used for modeling analyzes. See MasterDataObservations.csv below for details on the auxiliary data.
For the pika activity recording the columns were as follows:

- Minute: listed 1-45, one row per minute
- Focal Animal: included whether animal was an adult or juvenile, and whether it was tagged or not. If tags were seen they were recorded in order of right front ear, right back ear/ left front ear, left back ear. Y=yellow, B=blue, R=red, G=green, W=white, X=unknown or missing.
- Activity: included Unseen, Move, Rest, Scan, Preen, Feed, Hay, LongCall(LC), ShortCall(SC), OtherCall, Chase, Escape, Tolerate, CheekRubbing, most often recorded as the first letter of the activity or an abbreviation
- Distance from Haypile (m)- the estimated distance the pika was from the haypile in meters, if the haypile's location was known
- Stimulus Species- other animals, including other pikas in the area, and humans
- Stimulus Type- included calls and other activities of the stimulus
- Distance from Stimulus- the estimated distance in meters from the focal animal to the stimulus
- Response to Stimulus-the response of the pika to the stimulus; includes lack of response
- Map Check- this was whether or not the pika was on the rocks
- Notes- details about pika activity, the observation, or anything related

Access Database (.accdb):

Temperature_Sensor_Avgs.accdb- This data base uses the spreadsheet MasterDataTemps from TemperatureData_Combined.xlsx for the table.

Query: AverageSensorTemps Uses MasterDataTemps table. The purpose of this query was to create find the averages for each observation for each sensor placement. Averages were found because each temperature readings are not independent of one another. (Temperature of one interval affects the temperature of the next interval). See screenshot below for the format.

- GroupBy: Observer, ObservationNumber, Date,
- Avg: SurfaceC, SubsurfaceC, MeadowC
- Where: IntervalNumber; Criteria ">4"

Grouping IntervalNumber by everything greater than 4, means that only temperatures from intervals 5 to 10 or 11 were averaged. This was to account for the lag effect of the sensors. It about 15 minutes for the sensors to adjust from ambient temperature to actual placement temperatures.

Field:	Observer	ObservationNumber	Date	SurfaceC	SubsurfaceC	MeadowC	IntervalNumber
Table:	MasterDataTemps	MasterDataTemps	MasterDataTemps	MasterDataTemps	MasterDataTemps	MasterDataTemps	MasterDataTemps
Total:	Group By	Group By	Group By	Avg	Avg	Avg	Where
Sort:							
Show:	☑	☑	☑	☑	☑	☑	☐
Criteria:							>4
or:							

Query: LengthofObservations Uses MasterDataTemps table. This query was done as a quick way to have both the start and finish time of each observation. See screenshot below for the format.

- GroupBy: Observer, ObservationNumber, Date
- First and Last: Time

Field:	Observer	ObservationNumber	Date	Time	Time
Table:	MasterDataTemps	MasterDataTemps	MasterDataTemps	MasterDataTemps	MasterDataTemps
Total:	Group By	Group By	Group By	First	Last
Sort:					
Show:	☑	☑	☑	☑	☑
Criteria:					
or:					

Comma Delimited (.csv)

MasterDataObservations.csv- Contains the auxiliary data from each observation connected with the observation number. The auxiliary data was taken from the top of each individual observation sheet.

ObsNum	Unique observation number
Date	m/dd/yyyy
Observer(s)	Observers name; sometimes includes additional observers
Location	LP= Loveland Pass, WK= West Knoll, ML=Mitchell Lake, LL= Long Lake; sometimes included other notes,
Aspect	Aspect of the slope, South or North
UTMEasting	GPS UTM Easting coordinates of the observer's location
UTMNorthing	GPS UTM Northing coordinates of the observer's location
Begin time	Observation start time
Begin temperature (C)	Beginning ambient temperature from handheld thermometer, sometimes estimated
Begin skies	Beginning Sky conditions; S=Sunny, C=cloudy, O=Overcast
Begin wind	Beginning Wind conditions; L= low, M=medium, H=high
End temperature (C)	Similar to Begin Temp but after observation
End skies	Ending sky conditions
End wind	Ending wind conditions
NOTES	Notes from the observation
Talus surface	Code on the sensor; used to track placement
Below talus surface	Code on the sensor; used to track placement (Subsurface)
Meadow	Code on the sensor; used to track placement

meanTemp	Average of the beginning and ending temperature
meanWind	Average of wind conditions; see scale below
meanSkies	Average of sky conditions

Note on the meanWind and meanSkies: Since these were qualitative assessments of conditions a scale (number on the left) was developed for wind and skies by Dr. Chris Ray.

Wind scale: (L=low, M=medium, H=high)	
1	L+L
2	L+M, M+L
3	M+M, L+H, H+L
4	M+H, H+M
5	H+H
Skies scale (Precip means light snow or drizzle):	
1	Sunny+Sunny
2	Sunny+Cloudy, Cloudy+Sunny
3	Cloudy+Cloudy
4	Cloudy+Overcast, Overcast+Cloudy, Sunny+Overcast, Overcast+Sunny, Sunny+Precip, Precip+Sunny
5	Overcast+Overcast
6	Overcast+Precip, Precip+Overcast
7	Precip+Precip

MasterDataBehaviorMinutes.csv- This file contains the culmination of the auxiliary data from MasterDataObservations.csv and the query AverageSensorTemps from Temperature_Sensor_Avgs.accdb and the activity minutes

- From MasterDataObservations.csv: ObsNumber, Date, the beginning time (TimeBegin), Location, UTMeasting, UTMnorthing, the sensor codes, meanTemp, meanWind, meanSkies,
    - Aspect was coded 0=North, 1=South; NA used in Loveland Pass were aspect was unknown
- Added was FocalPika from the individual behavior sheets
    - Note on zeros vs. NA: With some years or observers

MasterDataTemps.csv- Copy of MastaDataTemps spreadsheet from TemperatureData_Combined.xlsx