Re-evaluating climate as the best predictor of pika (*Ochotona princeps*) surface activity

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Abstract

Alpine and subalpine ecosystems are expected to experience a disproportionate amount of warming in the coming decades. Rising temperatures in these ecosystems threatens biodiversity and water resources globally. The American pika (*Ochotona princeps*) is a small mammal restricted to talus and rocky slopes often found above treeline. *O. princeps* has an acute sensitivity to high temperatures and utilizes microhabitats present in the talus to regulate body temperature. These attributes make pikas a bioindicator candidate for warming in the alpine. Monitoring and predicting pika persistence represents a potentially powerful tool to asses the current and future health of alpine ecosystems. Here, I analyze paired temperature and observational data collected across several years at five separate locations in Colorado and Montana. I explore the relationship between surface activity and two sets of predictor variables; physiological predictors (new) and climatic predictors (historic). Males pika were found to be more surface active than females. Additionally, ectoparasite abundance was found to be the best physiological predictor of surface activity. Analysis of historic predictors found wind speed and aspect to be important predictors of surface activity. Based on these findings, I suggest that temperature alone is likely not the best predictor of pika surface activity. Instead, surface activity is likely influenced by both climatic and physiological variables. A better understanding of these relationships can aid future studies at predicting pika behavior and accounting for some of the complexity we see in pika persistence.

Acknowledgments

Content

Introduction

The rate of climate change threatens biodiversity in a way that habitat destruction and overexploitation have not approached (Thomas et al. 2004). The effects of climate change have no borders, and can impact the most secluded and well protected of habitats (Groom 2005, Primm et al. 2014). Conservative projections estimate that the warming of global air temperatures is likely to exceed 1.5°C by the year 2100 (Pachauri et al. 2015). Climate change is expected to have varying effects on different ecosystems and across many regions (Hulme et al. 1999, Scholze et al. 2006). In the case of alpine ecosystems, changes in snowfall, precipitation, and air temperatures could have a dramatic effect on the vegetation and in turn, the organisms living there (Pepin 2000). Monitoring climate change remains a top priority for conservation biologists and ecologists. Traditionally, direct weather and atmospheric measurements have been the primary tools for monitoring climate change. Alternatively, plants and animals can be monitored as a proxy for climate change, or to indicate the magnitude of its effects. Indicator species are organisms that vary in correlation with some quality of their environment and, in some sense, are among the most sensitive organisms in an ecosystem (McDonald & Brown 1992). This sensitivity allows them to act as an early warning sign to researchers (Wilkening 2015). Changes in the health, vital rates, or behavior of indicator species allow researchers to determine whether a system is being altered by climate change. A climate sensitive indicator species in the alpine would be a valuable tool for researchers to assess the current and future health of alpine ecosystems under climatic stress.

Background

The American pika (*Ochotona princeps*) is a small mammal commonly found at high elevations in the Western United States. A specialist, pikas are restricted to habitats consisting of talus and rocky slopes, commonly above tree line (Smith 1974). Unlike most alpine mammals, pikas do not hibernate or undergo torpor and therefore do not store fat and must remain active throughout winter. As a result, pikas are cold adapted. They have round bodies, small round ears, no visible tail, thick fur, and a high metabolic rate, all valuable traits to conserve and maintain body heat in the harsh alpine winters (Krear 1965). These traits are invaluable in the winter time, but can be problematic in the relatively hot summer months. During summer, alpine pikas must collect the food needed to sustain them through winter months when food is not readily available. Given the high levels of activity required to harvest an entire winter diet during the short alpine summer, the traits that keep pikas warm during the winter can cause them to overheat during the summer. A pika's metabolic rate is so high that its resting body temperature is just a few degrees below lethal maximum. It only takes a few hours of exposure to temperatures above 24°C to kill a pika (MacArthur and Wang 1973). Pikas have evolved to mitigate this disadvantage by utilizing microclimates that are present within their rocky habitats.

During summer, temperatures in the cracks and crevices of the talus are significantly lower than above ground temperatures (Varner and Dearing 2014). Pikas use these subsurface microclimates to shed heat during the summer (MacArthur and Wang 1973). These same subsurface microhabitats, when properly insulated with snow cover, can produce very stable temperatures in the winter (Krear 1965, Millar et al. 2016). Subsurface microclimates have allowed pikas to thrive in some of the most extreme habitats on the planet. However, changing temperatures and weather patterns threaten to alter the summer and winter microclimates used by pikas. Warming alpine temperatures may force pikas to reduce surface activity to avoid heat exposure. Staying below ground could mitigate the risk of hyperthermia, but at the expense of valuable foraging time. Additionally, changes in temperature and precipitation can alter vegetation (Pauli et al. 2014), which could impact the pika's food source year round (Bhattacharyya and Ray 2015). Declining snowpacks and an increase in mid-winter thawing events can also increase the overwinter mortality of pikas by exposing them to cold surface temperatures (Ray et al. 2012).

Sensitivity to climate makes the pika a key candidate as an indicator species of climate change in the alpine. Pikas are major consumers of native vegetation and are food sources themselves for other alpine species (Krear 1965, Aho et al. 1998). Understanding how climate change will affect pikas may give us insight into how climate change will affect other alpine organisms and the ecosystem as a whole. While the alpine supports a wide variety of unique plants and animals it also is the source of much of the water used in the American West. Glaciers, snow, and permafrost provide the western states with the majority of their water (Fountain et al. 2012). Identifying pikas as a sentinel of climate change in the alpine can be a valuable way to monitor the health of this unique and critically important ecosystem (Wilkening et al. 2015). Changes in behavior can be one of the most immediate effects of climate change and by monitoring these changes researchers can better assess the current and future state of these ecosystems. To understand how behavioral shifts might indicate changes in climate and alpine ecology, we must first identify the drivers of behavior and how they alter behavior at the individual level.

Goals and Predictions

To identify factors affecting pika behavior and to characterize current (baseline) patterns of behavior, observational studies were conducted in Colorado and Montana over several summers during 2008-2015 (C. Ray, unpublished data). Portions of this dataset have been analyzed to summarize pika activity budgets and to suggest relationships between behavior and temperature (Wiebe 2015). I have collected additional behavior and temperature data, and have expanded the list of candidate predictor variables to re-evaluate the importance of temperature as a determinant of pika surface activity. In addition to temperature, I have considered sex, life stage, and ectoparasite load to explain differences in behavior on an individual level. By identifying how climatic, habitat, and physiological variables affect a pika's behavior, researchers can better explain the variability we see on an individual and population level.

Understanding and controlling for this variability can make the pika a more valuable and reliable indicator species. Specific questions that I have addressed in this thesis are; can sex (1), life stage (2), ectoparasite load (3), or a combination of these factors explain differences in the activity budgets observed in *Ochotona princeps*, and can trends identified in previous analyses of this system generalize across data from additional years and study sites (4)? I hypothesize the following: females have greater physiological demands associated with gestation and weaning, and will be comparatively less surface active (1); juveniles require metabolic flexibility to grow and to disperse through areas often lacking in suitable microclimates, and will be comparatively more surface active (2); higher ectoparasite loads are often associated with reduced fitness or health, so individuals with high parasite loads will be comparatively less surface active (3); and, finally, a larger data set may reveal trends that were not supported in previous studies. I predict that analyzing an expanded data set will reveal that pika surface activity is related to wind speed, slope aspect, and the difference between surface and subsurface temperatures in talus habitats. Also, I expect that predictors identified in previous analyses (surface temperature and subsurface temperature) will remain significant predictors of surface activity (4).

Methods

Study Sites

Data for this study was collected at five sites located in alpine and subalpine environments. Four sites are located in the Front Range of Colorado, USA. The majority of observations were conducted on the West Knoll (WK) at the Niwot Ridge International Biosphere Reserve which is associated with the Niwot Ridge Long Term Ecological Research project (NWT LTER) and the University of Colorado. This site is at an elevation of approximately 3700 m and has taluses on both north- and south-facing slopes. The West Knoll is entirely above treeline and has ample vegetation and talus habitat. Many observations were also conducted at Long Lake (LL) and Mitchell Lake (ML), located in the Indian Peaks Wilderness, Roosevelt National Forest, Colorado. Both LL and ML are at approximately 3200 m in elevation, entirely below treeline, and each consists of a single large talus patch surrounded by subalpine forest. Long Lake is north-facing and Mitchell Lake is south-facing. A small number of observations were also conducted at Loveland Pass (LP) located in Arapahoe National Forest, Colorado, at approximately 3700 m in elevation. The fifth and final site is located at Emerald Lake (EL) in the Gallatin Range of south central Montana. Emerald lake is located in a box canyon which has ample talus habitat at the base of the canyon walls. This site is the northernmost site, and sits at approximately 2750 m in elevation.

Study Species

The focal animal for this study is *Ochotona princeps*, or the American pika. There are five recognized subspecies of the American pika, all located in the western United States and southwestern Canada (Hafner and Smith 2010). In their southernmost range individuals are generally found only in talus above treeline, although pikas can be found at much lower elevations in the northwestern portion of their range. The American pika belongs to the order Lagomorpha and, although often mistaken for a rodent, is more closely related to rabbits and hares. Within Ochotonidae, the American pika is medium in size. Adult individuals range 162-216 mm in length and 121-176 g in weight (Smith and Weston 1990). As referenced earlier, the American pika has a relatively high body temperature averaging 40.1°C and a relatively low maximum (lethal) temperature averaging 43.1°C (Smith and Weston 1990). The American pika disperses only once after birth, and this 'natal dispersal' event usually occurs before its first winter. Studies of pika surface activity are facilitated by their territorial behavior. Pikas are also highly visible during summer due to their caching activities. When 'haying' (collecting vegetation) for the 'haypile' (winter food cache), each WK pika makes about 13 trips per hour to harvest vegetation from sources adjacent to its talus habitat (Dearing 1997).

Data Collection

Behavioral Observations and Temperature

Each 45-minute behavioral observation was conducted by one primary observer using standardized observation and recording methods, as described here. Observations were conducted at sites currently or recently occupied by pikas (e.g., within territories where pikas were recently captured) that also included ample evidence of pika presence over the long term (e.g., having old hay, old fecal pellets, and urine stains). Most pikas targeted for observation were tagged uniquely with a set of colored ear tags, facilitating individual identification. Adult pikas that were not tagged could often be distinguished from neighboring pikas by unique patterns of molt or ear damage, or because neighboring pikas were uniquely tagged.

Prior to each observation, three HOBO® Pendant Temperature Data Loggers (accuracy +/-0.2°C; Onset Computer Corp., www.onsetcomp.com) were positioned to record the microclimate in three locations within the pika's territory, so that real-time temperature data could be correlated to behavioral observations. One logger was placed on the surface of the talus (surface), another was placed approximately 0.5 m below the surface of the talus (subsurface), and finally one was placed in a nearby patch of vegetation (meadow). All data loggers were placed within 10 meters of the central hay pile and were shaded with a rock to ensure that they were not in direct sunlight. Data loggers recorded temperatures every five minutes during the observation.

The primary observer recorded the time, date, location, aspect (north or south), observer's name, easting and northing (UTM), beginning wind (low, medium or high, defined as bending

grasses, branches or trees, respectively), beginning skies (sunny, cloudy, overcast, light rain or light snow), and the initial temperature (°C) measured by handheld thermometer.

In order to minimize observer influence on the behavior of the focal pika, observers placed themselves no less than 10 meters away from the focal pika's food cache at a comparable elevation to the territory. The 45 minute observation began once the observer was in position. Without the aid of binoculars, the primary observer would scan the territory looking for the focal pika. Once the focal pika was seen, the observer would record its life stage (adult or juvenile), ear tags (if applicable), the distance between the pika and its food cache, and any behaviors (Appendix A) that the focal pika exhibited during each minute, using binoculars to identify tags and behaviors if necessary. If the focal pika was unseen, then it was assumed that it was below the surface and it was recorded as unseen for that minute. Additionally, the observer recorded any potential stimuli (noise, call, intruder, etc.), the stimulus species (pika, human, raven, etc.), the distance to each stimulus, and any notes that were worth mentioning about a specific behavior, interaction, or stimulus. At the end of the 45-minute observation period, the observer recorded the end temperature, sky and wind metrics, and finally the data loggers were collected.

Marking and Sampling

According to University of Colorado-Boulder IACUC-approved protocols 1104.06 and 1405.03, pikas were captured during daylight hours using wire-mesh traps (Tomahawk model 201) placed near haypiles and provisioned with local vegetation. Traps were checked every two hours. Prior to handling, trapped pikas were allowed to self-transfer into an induction chamber containing inhalant anaesthetic (Isoflurane). Light anesthesia was maintained throughout the marking and sampling process (~20 minutes), using repeated induction as necessary. Stage and sex were determined by visual examination of molt status, proportions, and genitalia. Ectoparasites were collected from the induction chamber or as they arose from the fur (fleas), or were pulled from the skin of the outer ear (mites) using tweezers. For each pika, the sampling team recorded the number of fleas observed, the number of fleas collected, and the area covered by feeding ear mites (<4 mm^2, <16 mm^2, or >16 mm^2). Each pika was marked for identification at a distance using a unique combination of colored ear tags. Designed for rabbits, these permanent ear tags do not appear to interfere with a pika's behavior (Chris Ray, personal observation). Trapping and handling were relatively brief events: each animal was handled for less than half an hour and each site was subject to only 1 or 2 days of trapping. Observations generally were not conducted at trapping sites during trapping events, to avoid unknowingly conducting an observation on a trapped pika. No trapping occurred at Loveland Pass.

Data Analysis

Temperature

Temperature sensors required 15 minutes to calibrate, so the temperatures during an observation were estimated as the mean temperature during the last 30 minutes of the observation. ANOVA and the TukeyHSD were used to determine differences in mean

temperature among sensor locations (surface meadow, surface talus, and subsurface talus). Two additional temperature metrics were calculated as potential predictors of pika behavior: mean surface temperature (averaged across surface meadow and surface talus temperatures) and the talus temperature differential (mean difference between surface and subsurface temperature in the talus).

Behavior

At every minute during an observation, all observed behaviors were recorded. An activity budget was constructed by summing the frequencies of the most commonly observed behaviors. Less common behaviors and behaviors not universally identified by all observers were omitted. Because multiple behaviors could be observed within a given minute, the summed total of all activity-minutes for a 45-minute observation was generally greater than 45. Total minutes of surface activity or total "minutes seen" was therefore calculated by subtracting the total minutes unseen from total observation time (45 minutes). Minutes seen and mean distance from food cache were the two metrics of surface activity modeled in this analysis.

Predictor Variables

Two categories of predictor variables were used in this study: physiological predictors (Appendix B; new predictors), and climatic predictors (Appendix C; historical predictors). Integer flea counts and numeric temperature metrics were not coded. A binary classification system was used for life stage (1 = adult, 2 = juvenile), sex (1= male, 2 = female), and aspect (1 = north, 2 = south). The remaining predictor variables were coded using an ordered, numeric classification system; e.g., 1 = low, 2 = medium, 3 = high.

Models

Generalized linear models, assuming a binomial error distribution, were used to analyze the relationships between predictor variables and "minutes seen" (total minutes of surface activity). Linear models were used to analyze the relationship between predictor variables and average distance from food cache. Candidate models included from one to three predictor variables, and highly correlated predictors (Pearson's $r > 0.7$) were not included in the same model. Models were created using existing knowledge and logical relationships. I adopted an information-theoretic approach, using AIC (Akaike's information criterion) as a measure of relative support for each candidate model (Anderson & Burnham 2002, Burnham & Anderson 2004). The difference between AIC values (ΔAIC) for any pair of models reflects the relative support for each model. A ΔAIC of two or more indicates much stronger support for the model with the lower ΔAIC. For comparison, I also report P-values for each model, based on an alpha level of 0.05 as well as compare models to a null model. Models were fit using the lm() and glm() functions in R (R Core Team 2015)

Results

A total of 218 behavioral observations with correlated temperature data were used in this study. Each analysis only used a fraction of this data due to variations in the extent of the data collected. For example, not all individuals were tagged so data on sex and ectoparasite load were unavailable for many individuals. As a result, the data set for analyzing physiological predictors (n=100) was smaller than the data set looking at historical climatic predictors (n=135). Data were analyzed from 48 uniquely tagged pikas and 86 potentially unique but untagged pikas. All observations took place between 06:17 and 19:45, with 68.8% of all observations taking place before noon. The earliest ordinal date of observation was June 20th and the latest was October 19th. Data from 8 primary observers was used, although there were many more observers in this study.

Temperature

There were significant differences between surface and subsurface temperatures (Fig. 1; ANOVA, p-value < 0.001), verified by the Tukey HSD test, which identified differences between meadow and subsurface temperature as well as between talus surface and subsurface temperature (talus temperature differential). No significant difference was found between meadow and surface talus temperatures (ANOVA, p-value=0.65), verified by the Tukey HSD test. Mean (+/-SE) microhabitat temperatures were as follows, surface talus (14.76+/-0.4°C), subsurface talus (10.46+/-0.3°C), and meadow (15.21+/-0.4°C). The mean surface temperature, averaged over talus and meadow placements, was 14.98°C and the mean talus temperature differential was 5.19°C.

Behavior

The most common behaviors identified and the mean number of activity-minutes (mins) associated with each behavior across all observations were moving (mean = 9.83 mins), resting (mean = 5.73 mins), scanning (mean = 5.24 mins), haying (mean = 2.88 mins), short calling (mean = 2.75 mins), feeding (mean = 2.59 mins), and preening (mean = 0.54 mins) (Fig. 2). On average, pika were below ground (Unseen) 65.6% of the time. The remaining 34.4% (Seen) was spent above the surface doing some activity. Across all observations, pikas averaged 8.73 meters away from their food cache.
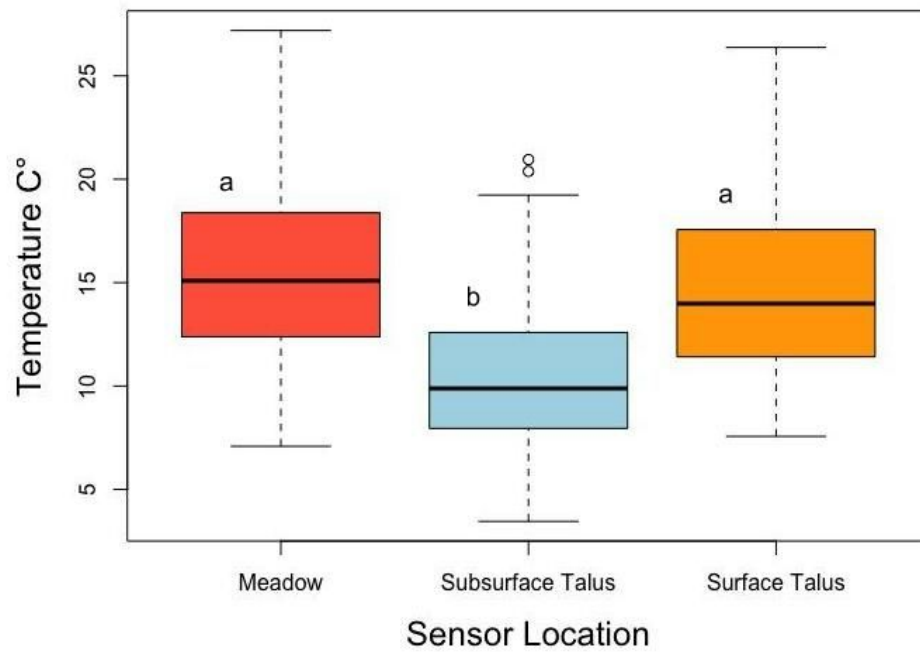
Figure 1. Comparison of microhabitat temperatures across all observations. Boxes depict medians and 25% and 75% quartiles. Letters (a and b) differentiate temperatures found to differ significantly in mean value using Tukey's HSD test.
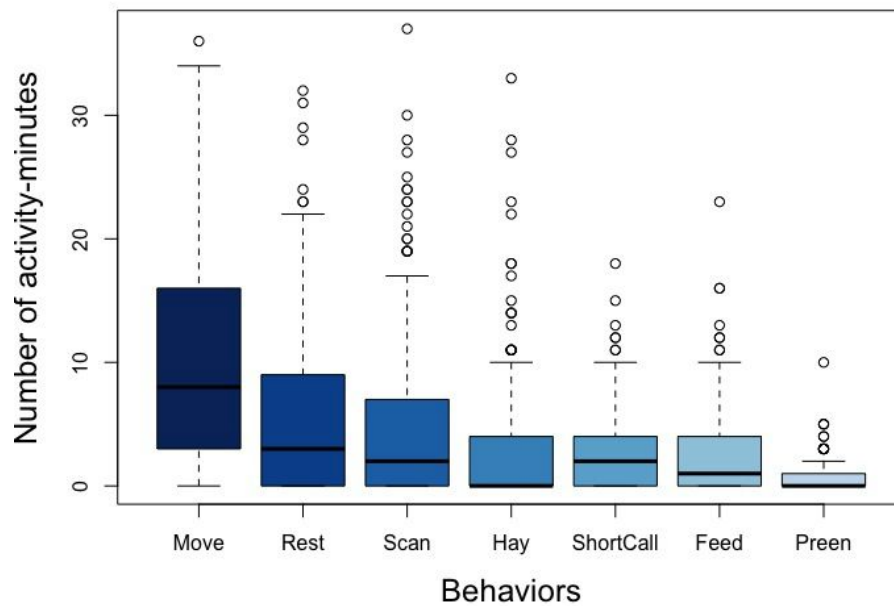
Figure 2. Pika activity budget averaged across all observations at all study sites (four sites in Colorado and one in Montana). Boxes depict medians and 25% and 75% quartiles.

Models based on (new) physiological predictors

Minutes seen

Generalized linear models revealed that total surface activity was related positively and significantly to both ear mite abundance and flea load (p-value<0.001), and males spent significantly more time above the surface than females (Fig. 3; p-value<0.001). No relationship was found between life stage and minutes seen (p-value=0.34). Univariate models based on ear mites, fleas, or sex were better supported than the null model (Table 1; ΔAIC>>2), although relative support for all univariate models was low. The model with best support included both mites and fleas, although it did little to explain the variance observed (Fig. 4). All other models had low relative support compared to the top model (ΔAIC>>2).

Mean Distance from Food Cache

Linear models showed a significant positive relationship between flea load and average distance from food cache (Fig. 5; p-value<0.001). Fleas were present in the three best supported models predicting distance from food cache (Table 2). No significant relationship was found between the other predictor variables and mean distance from food cache.
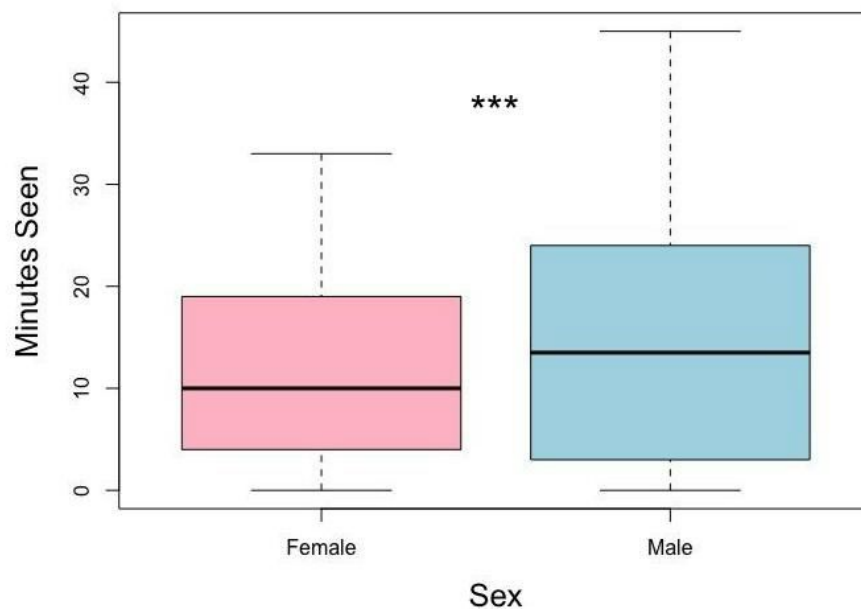
Figure 3. Males were seen above the surface significantly more often than females. Boxes depict medians and 25% and 75% quartiles.

Table 1. All generalized linear models of total surface activity based on new predictors (n = 100).

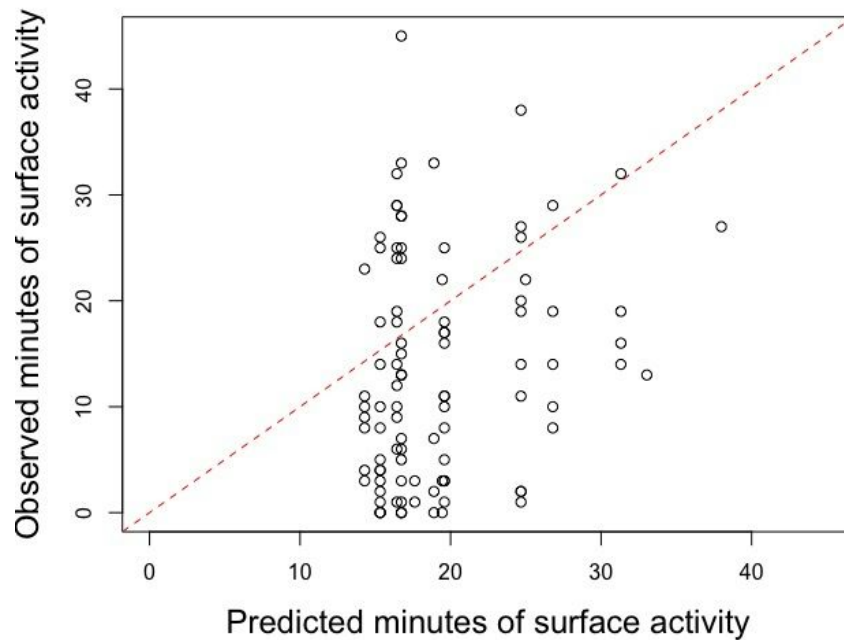| Model	ΔAIC	P-value
Mites*Fleas	0.00	0.002
Sex+Fleas	33.79	<0.001
Fleas	45.06	<0.001
Mites	49.44	<0.001
Sex	49.75	<0.001
Null	64.93	——
Stage	66.06	0.346

Figure. 4 The best supported model still fails to explain much of the observed variance.

Models based on (historical) climatic predictors

Minutes Seen

Generalized linear models showed that all historical predictor variables except subsurface talus temperature had significant effects on minutes seen in univariate models (Table 3; p-value<0.05) and ΔAIC showed that these same univariate models had better support than the null (ΔAIC>>2). When compared to the top model, all univariate models had considerably low relative support. The best supported model included the additive and interaction effects of mean wind and mean skies, with windspeed having a negative effect on minutes seen and cloud cover having a positive effect. Mean wind was present in the top 4 supported models.

Mean Distance from Food Cache

Aspect alone was the best predictor of mean distance from food cache (Table 4). Pika on south-facing slopes were observed further from their food cache than on north-facing slopes (Fig. 6; lm, p-value=0.001). The univariate model containing aspect had highest support and the three next-best models with similar support (ΔAIC<2) contained aspect.
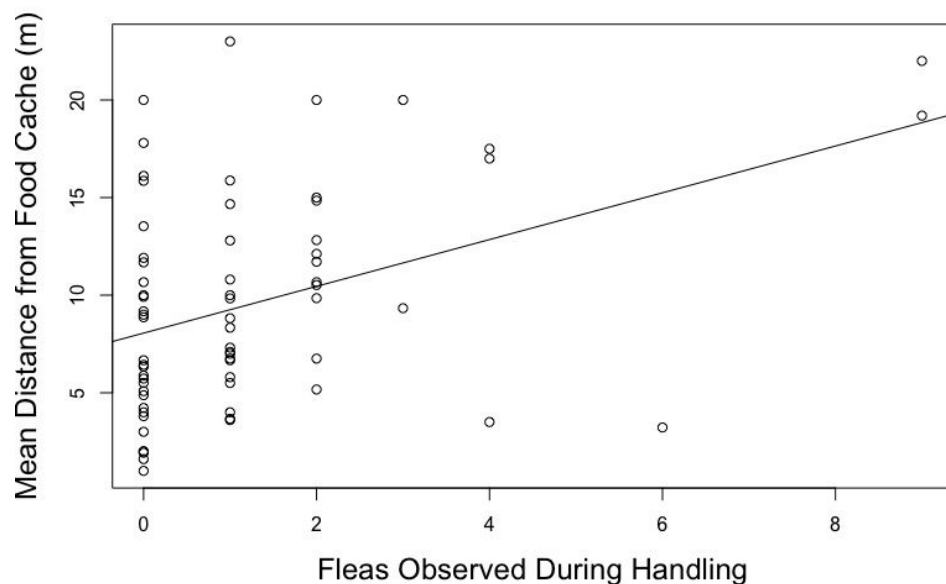
Figure 5. Positive relationship between the total number of fleas observed on a pika during handling and the mean distance between that pika and its food cache recorded during behavioral observations.

Table 2. All linear models of mean distance from food cache based on new predictors (n = 70)

Model	ΔAIC	P-value
Fleas+Sex	0	0.001
Fleas	0.33	<0.001
Fleas+Mites	2.33	0.004
Null	10.07	——
Sex	10.49	0.216
Stage	11.26	0.376
Mites	11.32	0.394

Table 3. Best supported generalized linear models of total surface activity based on historic predictors. (n = 135)

Models	ΔAIC	P-value
Skies*Wind	0	<0.001
Wind*Aspect*Surface	51.72	0.127
Wind*Aspect*TalusDifferential	102.78	<0.001
TalusDifferential*Wind	115.66	<0.001
Skies*Aspect	118.45	<0.001
Wind*Aspect	122.96	<0.001
Surface*Wind	125.58	0.077
Null	203.68	——

Table 4. Best supported linear models of mean distance from food cache based on historic predictors (n = 83)

Models	ΔAIC	P-value
Aspect	0.00	0.001
Surface+Aspect	0.93	0.004
Wind+Aspect	2.00	0.006
TalusDifferential+Aspect	2.00	0.006
Wind	7.19	0.075
Null	8.47	——
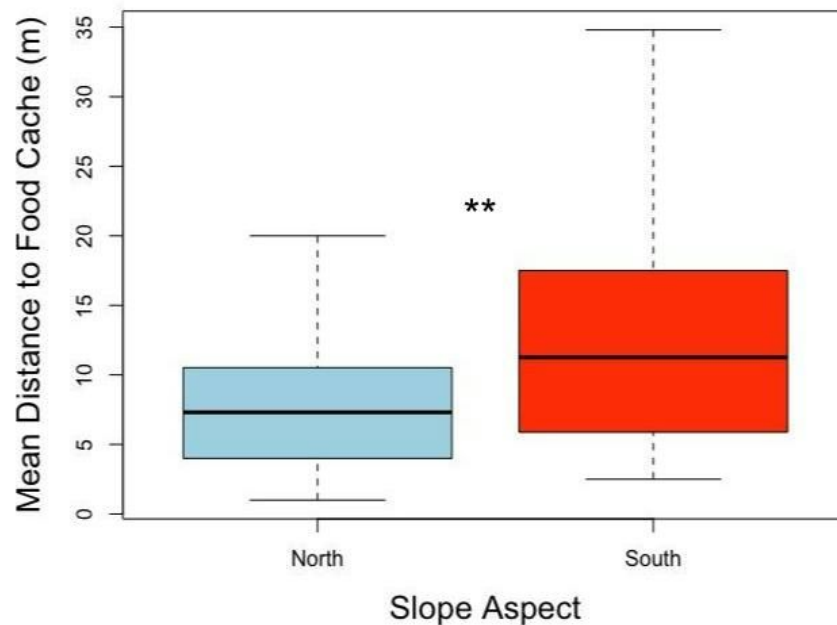
Figure 6. Pikas traveled farther from their food caches on south-facing slopes. Boxes depict medians and 25% and 75% quartiles.

Discussion

New Predictors

Previous studies have analyzed the relationship between pika surface activity and climatic metrics (Wiebe 2015, Huntly et al. 1986), but to date, few studies have discussed the relationships between physiological metrics and pika activity. Including physiological predictors in models is important if we are to understand their relationship to pika behavior and in turn their effect on pika persistence. I found support for models containing both sex and ectoparasite load when predicting pika surface activity. There was also considerable support for models containing flea abundance when predicting mean distance from the food cache.

Sex

As predicted, males were found to be more surface active than females (Fig. 2; p-value<0.001). Although relative support for the univariate model containing sex was relatively low, the model had greater support than the null model. These findings support my first hypothesis that females will be relatively less surface active than males. Given the difficulty of observing subsurface activity, it's hard to determine the nature of this below ground activity. Female nursing responsibilities are possible explanation. Pika are seasonally polyestrous and have two litters every summer. The gestation period is approximately 30 days and females were found to nurse for 10 minutes every two hours for at least 18 days after birth (Smith and Weston 1990). When nursing, female pika tend to favor foraging over haying to supply their immediate

higher caloric demands associated with gestation and nursing (Huntly et al. 1986) Although not significant, my results suggest a potentially similar trend. Mean minutes spent haying across all observations for females was 1.9 minutes and mean minutes spent foraging was 2.8 minutes (n = 44). These findings support the nursing explanation for why females are comparatively less surface active. Given the short nature of alpine summers, increased caloric demands coupled with lower haying frequency compared to males (t-test; p-value=0.026) could put females at a comparative disadvantage. As a result, it's possible that any effect of climate change may first be observed in females rather than males. This being said, a recent analysis of stress hormones in pika on the WK among other sites found that males had higher baseline stressor levels than females (Wilkening 2014). There has also been no evidence to suggest that male to female ratios have been changing in *O. princeps* within the last few decades (C. Ray, unpublished data), or in other pika species (Wang et al. 2004). Though there is no current evidence for a sex based selection pressure, my results show that sex does have an effect on both surface activity and behavior. Sex should be considered in future models aimed at predicting pika surface activity.

Ectoparasite load

Flea load and ear mite abundance were both found to have a positive correlation with surface activity (p-value<0.001). Of the models predicting surface activity the interaction and additive effect of ear mite abundance and flea load had the highest support. Also, flea abundance was present in the three best supported models predicting average distance from the food cache. Based on these findings, I would reject my third hypothesis that flea load and mite abundance would be correlated with low surface activity. These findings instead suggest that a high ectoparasite load is correlated with a higher level of surface activity. This correlation between surface activity and ectoparasite load is interesting because very little is known about pika host-parasite interactions. Many ectoparasites found on pika have not yet been described (Barrett & Worley 1970). Based on very limited literature, it is difficult at this time to speak about the nature of this interaction; specifically, if high surface activity facilitates increased ectoparasite loads or if an increased ectoparasite load facilitates higher surface activity. For now, my results suggest that ectoparasites are a good predictor of surface activity and if data is available should be included in future models aimed at predicting surface activity.

Life stage

Juveniles disperse from their mother's territory mid summer (Smith 1974), and as a result, juveniles must claim a territory, grow, and amass a hay pile for winter in half as much time as an adult pika. Based on this evidence I would expect juveniles to be considerably more surface active than adult pika, yet no relationship was found between life stage and either metric of surface activity. My data set suffered from a lack of juvenile observations resulting in only 11 observations conducted on confirmed juvenile pika in the final data set. Juveniles proved difficult to observe because they are small, elusive, and often had not yet established territories of their own (Krear 1965). Even if a juvenile was trapped in a specific location, upon returning to that location later in the season the juvenile was often not observed, presumably because the

trapping location was not the site of the juvenile's final claimed territory. Additionally, juveniles often lack fur discolorations and have no molt patterns from the previous winter, so identifying a juvenile without tags is very difficult. A more robust data set may have yielded different results, but based on these findings I must reject my second hypothesis that juveniles will be comparatively more surface active than adults.

Historical Predictors

The second component of this study was reanalyzing the historical predictors that had been tested in a previous study using an earlier version of this same data set (Wiebe 2015). By incorporating recent observations from 2015 as well as additional observations from the Montana site (EL) I have increased the data set from 94 observations to 135. It was decided to model the data using generalized linear models instead of linear models to more accurately fit the data. Wiebe 2015 found support for temperature, both surface and subsurface, as the best predictors of surface activity. In contrast to previous findings, my results showed no support for subsurface temperature. In fact, the univariate model containing subsurface temperature had the lowest support of any model and had worse support than the null model. Surface temperature was found to have a significant negative effect on surface activity, although the univariate model containing surface temperature had the second lowest support compared to all other models. My findings starkly contrast those in Wiebe 2015 despite very similar data sets. This difference is likely the result of both an expanded data set and the method of analysis. By using generalized linear models instead of linear models, I can more accurately fit the data by assuming a binomial distribution error. My results were surprising given the wealth of studies that cite rising temperatures as a major contributor to pika range contraction and population extirpation (Millar & Westfall 2010, Beever et al. 2011, Wilkening et al. 2011). Still, my results are important because they suggest that although rising temperatures may be driving population shifts, they are likely not the most important driver of behavior on an individual level.

Wind

Wind was found to be an important predictor of surface activity. Wind speed (mean wind) had a significant negative relationship to surface activity (p-value<0.001) and was present in the three best supported models of surface activity (Table 3). Wind has been found to distort and degrade pika short calls, which are used as predator warning signals (Hayes & Huntly 2005). These findings support my own, and offer a potential explanation for the relationship we see between wind and surface activity. This relationship is important, because wind could affect mortality rates by increasing predation and or by decreasing valuable foraging time which could influence overwinter mortality. The effect of wind should be included in future behavioral studies especially those that span multiple locations with diverse wind conditions.

Aspect

Lastly, I found an interesting relationship between average distance from food cache and aspect. Pika were found to have a higher mean distance from their food cache on south-facing

slopes (Fig. 6; p-value<0.001). More so, the univariate model containing aspect was the best supported model, and the three additional models with similar support all contained aspect as a predictor of mean distance from food cache (Table 4). One explanation for this observed relationship could be a higher frequency of haying in pika on south-facing slopes. It's well documented that pika travel greater distances when haying than compared to foraging (Huntly et al. 1986). An unpaired t-test between observed haying behavior on north- and south-facing slopes revealed that there was a higher instance of haying on south-facing slopes (Fig. 7; p-value=0.013). This difference in haying behavior could result in a higher mean distance from food cache. This contrast in haying behavior is interesting, because it could suggest that vegetation structures are different on north- and south-facing slopes. A thorough analysis of Niwot Ridge did find differences in vegetation structure between the north- and south-facing slopes (Komárková & Webber 1978), although there was no difference found in alpine avens (*Geum rossii*), the largest component of alpine pikas haypiles (Johnson 1967). This relationship could also be associated with site specific variables like population density and topography. Accounting for these variables will be key in future studies to test for a relationship between aspect and surface activity.
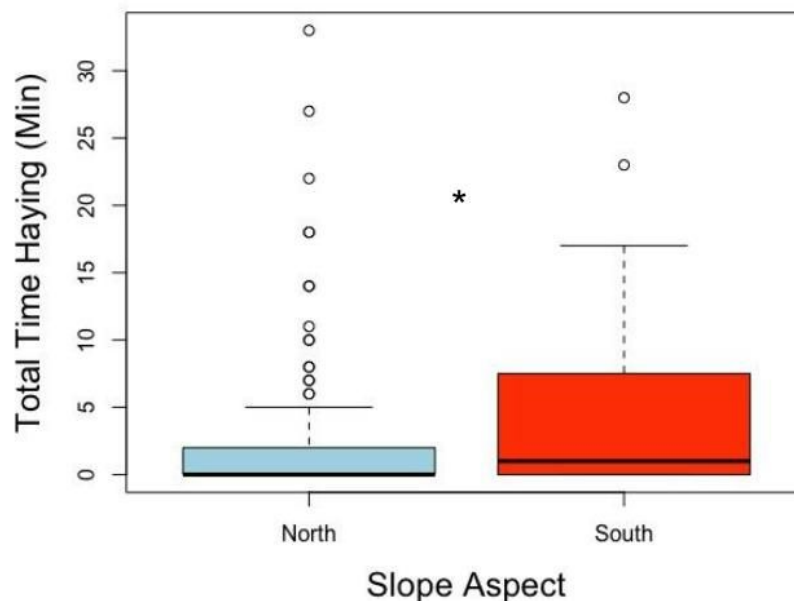
Figure 7. Pikas on south-facing slopes hayed more than pika on north-facing slopes. Boxes depict medians and 25% and 75% quartiles.

Limitations and Future Directions

This study suffers from some limitations with data collection. As mentioned earlier, observations were conducted immediately after temperature sensor placement, yet analysis revealed that 15 minutes were required for the sensors to adjust to ambient temperature. As a

result, the temperatures during an observation were estimated as the mean temperature during the last 30 minutes of the observation. I propose that future studies include a 15 minute delay before beginning the observation to allow for both the temperature sensors to adjust and to avoid bias in behavior related to the disturbance caused by the sensor placement event itself. Although precautions were taken to distance observers from focal pika, as to not influence their behaviors, instances of pika attempting to hay shoelaces and backpack straps confirm that an observer effect was still present. Observations with any noticeable instance of an observer caused influence were omitted from analysis, but a bias could remain.

This study uses data from many observers across multiple sites and years, as a result standardizing procedures can be difficult. Although all observers are trained under similar protocol, classifying behaviors and climate metrics like wind speed and cloud cover can vary from observer to observer. Also, when a pika was unseen it was assumed that the pika was below the surface, though it's possible that the focal pika was outside the pika's assumed territory. Due to the complexity of talus habitat it is also possible that a pika was surface active and not visible from the observer's vantage point.

This study was able to account for some climatic, habitat, and physiological variables, although there are many additional variables that could affect a pika's activity that were neglected. Site/habitat variables such as population density and distance to vegetation could have unknown effects on pika behavior. Also, stimuli (pika, human, raven, etc.) were not accounted for in this study, but likely had an effect on pika behavior. Lastly, by expanding this data set to include observations conducted in Montana another subspecies of *O. princeps* was included in analysis.

Due to missing data associated with untagged individuals, in order to compare models across new and historic predictors the data set would have had to have been reduced significantly. In order to preserve the size of the data set, it was decided to analyze the new and historic predictors separately. Unfortunately, this method did not allow me to look at the relative strength of the new predictors compared to historical predictors, nor was I able to look at models containing both new and historical predictors. In order to make these comparisons, additional observations with correlated trapping data must be collected to expand the data set so a more encompassing analysis can be done without jeopardizing the size and power of the analysis. Random effects were not considered for this study, yet their inclusion will be important in future studies to account for the effects of year, ordinal date, time, individuals, and location.

Importance

This study is unique, in that it identifies physiological variables as predictors of surface activity in *O. princeps*. Previous studies aimed at modeling pika behavior and activity have often neglected physiological variables for more pressing climatic variables like temperature and weather. Based on my findings, I suggest that temperature is likely not the best predictor of surface activity and instead surface activity is likely influenced greatly by both physiological

variables like sex and ectoparasite load as well as climatic variables like wind speed and aspect. A better understanding of these relationships may allow future studies to account for some the complexity we see in pika persistence and help conservation ecologists and biologists identify *O. princeps* populations that are at risk of extirpation by identifying patterns in behavior and monitoring changes in surface activity.

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Appendices

Appendix A. Indexed Behaviors

Behavior	Description
Unseen	Pika not seen and presumably underneath talus
Move	Pika relocating from point A to B, and so on
Rest	Pika being still and not vigilant
Scan	Pika being still and vigilant (actively looking around)
Hay	Pika collecting materials and depositing said materials in hay pile
Feed	Pika eating vegetation from meadow or from hay pile
Preen	Pika grooming itself with paws and mouth
Short Call	A short, high-pitched chirp, often emitted in succession
Long Call*	A long series of chirps, sometimes with varying pitch
Visit*	Pika within a known or suspected neighbor's territory
Tolerate*	Pika not chasing away a visiting neighbor or a juvenile
Chase*	Pika actively chasing away a visiting neighbor or a juvenile
Escape*	Pika avoiding conflict with neighbor by running away
Cheek Rub*	Pika rubbing cheeks on rocks to mark territory
Lick Rocks*	Pika licking rocks, possibly to obtain salts
Scan From Hay Pile*	Pika being still and vigilant while on or very near hay pile

*Behaviors were not analyzed either because they were extremely rare or they were not universally recorded by all observers.

Appendix B. New predictors indexing pika physiology.

Predictor	Description
Life Stage	Adult or juvenile
Sex	Female or male
Fleas	Number of fleas observed during handling
Ear Mites	Abundance (cover) of ear mites embedded in outer ear, classed by area

Appendix C. Historical predictors indexing climate.

Predictor	Description
Mean Surface Temperature	Temperature averaged across surface placements in talus and meadow
Mean Subsurface Temperature	Temperature averaged across subsurface readings in the talus
Talus Temperature Differential	Mean talus surface minus mean talus subsurface temperature
Mean Wind	Wind speed class, averaged across initial and final estimates
Mean Skies	Weather class, averaged across initial and final estimates as in Wiebe (2015)
Aspect	Main aspect of the observed pika territory (north or south)

Appendix D. All Generalized Linear Models for Historic Predictors and Minutes Seen

Models	∆AIC	P-value
Skies*Wind	0	<0.001
Wind*Aspect*Surface	51.72	0.127
Wind*Aspect*TalusDifferential	102.78	<0.001
TalusDifferential*Wind	115.66	<0.001
Skies*Aspect	118.45	<0.001
Wind*Aspect	122.96	<0.001
Surface*Wind	125.58	0.077
Surface*Aspect	128.23	<0.001
Wind	146.67	<0.001
Subsurface*Wind	147.73	0.109
Surface*TalusDifferential	153.66	<0.001
Subsurface*Surface	160.52	<0.001
Subsurface*Skies	176.85	<0.001
Surface*Skies	178.04	<0.001
TalusDifferential+Skies	184.78	<0.001
TalusDifferential+Aspect	187.94	0.003
Skies	189.98	<0.001
TalusDifferential	194.60	<0.001
Surface	195.15	0.001
Aspect	197.71	0.005
Null	203.68	――――
Subsurface	205.65	0.865

Appendix E. Linear Models for Historic Predictors and Mean Distance from Food Cache

Models	ΔAIC	P-value
Aspect	0.00	0.001
Surface+Aspect	0.93	0.004
Wind+Aspect	2.00	0.006
TalusDifferential+Aspect	2.00	0.006
Wind	7.19	0.075
Null	8.47	——
Surface+Wind	8.56	0.152
Wind+Subsurface	8.65	0.159
Wind+Skies	8.89	0.178
Wind+TalusDifferential	9.19	0.205
Surface	9.58	0.353
Subsurface	9.97	0.486
TalusDifferential	10.40	0.785
Wind+TalusDifferential+Surface	10.42	0.275
Sky	10.47	0.95
Surface+Subsurface	11.52	0.633
Surface+TalusDifferential	11.52	0.633
Surface+Skies	11.58	0.65
TalusDifferential+Skies	12.40	0.964