Pika Response to Microhabitats on Niwot Ridge

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Abstract

Biodiversity is integral to healthy ecosystems, but is decreasing globally as climate changes. Indicator species like the American pika, *Ochotona princeps*, serve as a measure of ecosystem health and can suggest how other organisms might be impacted in the future. Pikas regulate their body temperature through behavioral changes, such as resting in cool sub-surface spaces between rocks. The range of pika occurrence has retracted from many lower elevation sites as temperatures increase; however, pikas persist in favorable microclimates and high elevations. This study compared the features of several pika territories in close proximity to understand why some remain occupied more than others. The recency or frequency of occupancy was compared to land cover, sub-surface temperatures, and pika thermoregulatory behavior. Grass cover was negatively correlated with recent pika occupation. Thermoregulation potential was defined as the sum of absolute differences in summertime temperatures near the surface and deep under the rocks, representing the range of temperatures accessible for a pika to shed heat. Thermoregulation potential exhibited a positive relationship with recent occupancy, while temperatures at shallow or deep sub-surface positions were no different across territories. Differences in the potential to support pika thermoregulatory behavior may thus be more important than absolute temperature. Climate-dependent pika behaviors did not vary significantly across territories, though trends were in the direction expected for behavioral thermoregulation. This study enhances our understanding of how animals’ territories in close proximity can vary in important ways, which can have implications in guiding human interventions as more taxa experience climate-related stress.
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Thank you to Max Wasser, who collected the remnant haypile data this study is based on. Without those data, I could not have explored the topic of this study in the same way.

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Finally, thank you to my family and friends for their support, and putting up with me constantly talking about my research.
Introduction:

The global climate is changing with respect to temperature, precipitation, and seasonal weather events (Brodie et al. 2012). These changes, which are predicted to increase in coming decades, have a profound effect on the biodiversity of organisms living across the planet (Brodie et al. 2012). Many organisms respond to climatic changes by shifting their distribution, moving into newly expanded habitable areas from habitats where they can no longer persist (Parmesan and Yohe 2003; Doak and Morris 2010). By studying these shifts, we can better understand how species and ecosystems are affected by climate change, assess impacts to human activities, create plans to mitigate problems, and make predictions for the future. The potential response of many species can be predicted based on studies of an indicator species, or a species that currently experiences climate based limitations other species may be subject to in the future (Hafner 1993). The present study assesses a distributional shift in the American Pika, *Ochotona princeps*, which is widely regarded as an indicator species of climate change (Hafner 1993; Beever et al. 2010; Ray et al. 2012).

The American pika is a small herbivorous mammal from the order Lagomorpha, to which rabbits also belong. American pikas, henceforth called pikas, live throughout the mountainous American and Canadian West, most commonly in alpine talus slopes. The species has undergone many recent population shifts and extirpations, or localized extinction events, as climatic stressors have increased (Moritz et al. 2008; Beever et al. 2011; Ray et al. 2012; Yandow et al. 2015; Stewart et al. 2017). Pikas cope with extreme climatic conditions through behavioral modifications to maintain their body temperature, most utilizing the spaces between piles of broken rocks, or talus, as refuges (Millar and Westfall 2010; Beever et al. 2017).
Habitats can be understood on a fine scale in terms of microhabitats and microclimates, which are characteristics of a small section of habitat that may differ from the surrounding ambient conditions of the habitat as a whole, as well as from other surrounding sections of habitat (Varner and Dearing 2014a). Microclimates can shed light on why individuals occupy certain portions of a habitat and not others, and can guide our understanding of both the species and its environment. It has been argued that thermal refuges, such as the talus rocks used by pikas, must be defined using fine-scale, species specific data (Rodhouse et al. 2017), which the present study aimed to do.

The present study examined microclimates in relation to historical pika occupation on Niwot Ridge in Colorado, where pika occupancy appears to be declining (Max Wasser, unpublished data). The central study area was previously surveyed for signs of pika occupancy, and evidenced an apparent decline in recent pika signat lower elevation sites (Fig. 1; Max Wasser, unpublished data). Territories, synonymous with sites, were classified on the basis of apparent time since occupied, facilitating a comparison of changes in occupancy over time (Fig. 1; Max Wasser, unpublished data). The present study aimed to identify differences that may explain the apparent shifts present in these data (Fig. 1; Max Wasser, unpublished data). Site characteristics such as vegetation and rock cover, pika behavior in 2017, and temperature data were compared to historical occupation in order to explain the changes observed.

Figure 1. Data illustrating the shrinking distribution of occupied pika habitats on Niwot Ridge (courtesy of CU student Max Wasser and Dr. Chris Ray).
Hypotheses:

Designating pika territories as having been occupied historically, recently or through some intermediate time, as depicted in Figure 1, the following hypotheses were tested:

1. **Land Cover Hypotheses:**
   a. Territories with higher percent cover of alpine avens (*G. rossii*) and other forbs (flowering dicot plants that are not grasses) relative to graminoids (monocot grasses) will be associated with more recent signs of pika occupancy, because of the relative abundance of these plants in a pika’s diet (Dearing 1996).
   b. Higher rock cover will provide greater opportunity for behavioral thermoregulation, and will be positively correlated with more recent signs of pika occupancy (Millar and Westfall 2010; Hall et al. 2016).

2. **Summer temperature hypothesis:** Daily mean summer temperatures will be negatively correlated with the apparent recency of pika occupancy (Beever et al. 2010; Wilkening et al. 2011).

3. **Behavioral thermoregulation hypotheses:**
   a. Territories characterized by a high potential for behavioral thermoregulation will be positively correlated with signs of apparently recent pika occupancy.
   b. As observed in currently occupied territories, a low potential for behavioral thermoregulation will prevent pikas from spending as much time performing temperature dependent surface behaviors as pikas in territories with a high potential for behavioral thermoregulation (MacArthur and Wang 1973; 1974; Smith 1974).
Literature Review:

Biodiversity:

Plants and animals provide ecosystem services that have intrinsic and economic value to many aspects of human society. Historically, biodiversity has been understood in terms of species richness, and later in terms of redundant ecosystem services (Walker 1992). More recently, Gamfeldt et al. (2008) found that biodiversity must be understood in terms of the variety of services provided by a diversity of species in conjunction, rather than a single ecosystem function. This means that the connections among species are important, and the loss of one species may have a greater impact than previously thought. Globally, ecosystems are under increasing stress, and biodiversity is declining (Pereira et al. 2010; Brodie et al. 2013). Declines in biodiversity have been found to inhibit the efficiency of biological processes and decrease the stability of ecosystem functions (Cardinale et al. 2012). Impacts on ecosystems from biodiversity loss vary depending on relative species abundance, trophic levels, and functional traits of lost organisms (Cardinale et al. 2012). Biodiversity is positively associated with agriculture yields, fishery stability and yields, and wood production, among others; a loss of biodiversity would hinder these processes essential to human life (Cardinale et al. 2012). Diverse community assemblages have also been shown to decrease rates of disease transmission when compared to less species rich communities, highlighting the health implications of biodiversity (Johnson et al. 2013).

Across taxa, species are experiencing range shifts, expanding poleward and to higher elevations in response to stress from a changing climate (McDonald and Brown 1992; Parmesan and Yohe 2003; Moritz et al. 2008, Ray et al. 2012). In alpine ecosystems, climate has been predicted to be the greatest driver of biodiversity change by 2100, followed closely by nitrogen
deposition (Sala et al. 2000). Climate-mediated decline of biodiversity is expected to continue on a greater scale in coming decades, especially as conditions at a species lower distribution extremes exceed a biologic “tipping point,” and force range contractions (Doak and Morris 2010). The American pika is often seen as a sentinel or indicator species for climate change, providing clues to how other animals may be impacted by a changing climate in the future (Hafner 1993; Beever et al. 2010; Ray et al. 2012). As described below, the unique physiology and life history of a pika put the species at great risk for climate mediated decline, risks that may be assumed by other species as they approach their physiological limits.

The American Pika:

The American pika is considered an indicator species for the impacts of climate change on other animal species because of the pika’s unique behavioral thermoregulation needs and associated limitations leading to climate sensitivity (Hafner 1993; Beever et al., 2010; Ray et al. 2012; Yandow et al., 2015). Pikas cannot effectively cool their bodies using typical mechanisms for thermoregulation such as sweating, panting, or exposing bare skin; instead, they must engage in behavioral thermoregulation by seeking refuge in a cool place to rest (MacArthur and Wang, 1974; Smith and Weston, 1990). A pika’s high resting body temperature of 40.1°C, combined with its spherical body shape and extensive fur coat, allow it to stay warm and survive without hibernation in winter (MacArthur and Wang 1973). However, the pika’s upper lethal temperature is relatively low at 43.1°C, and pikas can die upon exposure to just a 3-4 hours of modestly warm ambient temperatures of 25.5-29.4°C if they cannot behaviorally thermoregulate by retreating to a cooler place (MacArthur and Wang 1973; 1974; Smith 1974). The crevices between rocks, such as those in talus fields, provide necessary refuge for the pika by trapping cool air and acting as a buffer from varying ambient temperatures (Millar and Westfall
Pikas are active on the surface in short bursts when ambient temperatures are high, increasing surface activity time in cooler temperatures (Smith 1974). As the climate warms, pikas must respond by spending more time under the rocks, or shifting their already high elevation range upslope to cooler territories, an option not possible for most mountain top populations (Beever 2003).

Pika populations are most likely to persist in areas dominated by forbs, or flowering plants (Wilkening et al. 2011, Ray et al. 2016). Additionally, pika occurrence has been found to be negatively correlated with graminoid cover (Rodhouse et al. 2010; Ray et al. 2016). Furthermore, pika abundance is also positively correlated with climatic conditions favorable for forb growth in high elevation systems (Yandow et al. 2015, Wilkening et al. 2015a), and has been shown to have a positive relationship with precipitation (Beever et al. 2011). Pikas select two different diet types, one for immediate consumption in the summer and the other to be stored for winter (Dearing 1996). Both diet types rely heavily on forbs, with the forb *G. rossii*, also known as alpine avens, composing the majority of the winter diet (Dearing 1996). Pikas store vegetation for winter consumption in caches known as haypiles, which they rely on for an average of 150 days each year (Dearing 1997). Pikas selectively forage, and cache vegetation of higher quality than the average of what is available (Smith and Erb 2013). On the West Knoll of Niwot Ridge in Colorado, where the present study took place, haypiles have been found to contain 263 days of food when accounting for decomposition (Dearing 1997). Haypiles on Niwot Ridge have also been found to be dominated by alpine avens (Bhattacharyya and Ray 2015). Abundant forage near a home territory allows pikas to be more energetically efficient in gathering vegetation, and minimizes time spent away from undefended haypiles (Yandow et al. 2015). A pika’s overwinter survival may be hindered by climatic changes affecting vegetation
available to cache, as well as by increased summer temperatures that could reduce their ability to effectively gather and cache enough forage due to thermoregulation demands. Bhattacharyya and Ray (2015) found that alpine avens abundance has decreased on Niwot Ridge, while summer temperatures increased, in comparison to historical measures at the site. These changes were accompanied by an increase in graminoid prevalence in haypiles, which the same authors noted may indicate a decline in available over-winter nutrition (Bhattacharyya and Ray 2015).

Pikas exhibit behavioral flexibility in habitat use, foraging, and thermoregulatory behaviors in response to varying climatic conditions (Varner and Dearing 2014b; Beever et al. 2017). Even though pikas are typically found in mountain talus slopes, populations have also been observed in atypical landscapes. Populations persist in lava beds, where ambient (above-surface) temperatures regularly exceed a pika’s physiological limits (Rodhouse et al. 2010; Ray et al. 2016). Pikas use the deep crevices and tunnels in the lava beds as thermal refuges, modifying their behavior to buffer the temperature extremes of the surface (Rodhouse et al. 2017). Pika populations have also been described in low elevation territories (121-255 m) in the Columbia River Gorge, Oregon, where individuals persist in moss-covered talus outside of the commonly assumed range of suitable habitat (Simpson 2009; but see pages 121-122 of Grinnell 1917). Microclimates can vary drastically within just a few meters, allowing behavioral thermoregulation unique to the microhabitat (Varner et al. 2016). Pikas in the Columbia River Gorge habitat specialize in foraging on mosses abundant year round, in contrast to their typical diet low in mosses and cushion plants, and do not construct large haypiles (Dearing 1996; Varner and Dearing 2014b, Varner et al. 2016). The differences observed in the Columbia River Gorge habitat suggest a great ability for behavioral and dietary plasticity in the face of new resources (Varner and Dearing 2014b; Varner et al. 2016). Such behavioral plasticity may help pikas to
cope to some extent with climate changes too rapid for evolutionary adaptations to manifest (Austin et al. 2012). An understanding of behavioral and dietary plasticity can aid assessments of future vulnerability to climatic shifts (Varner and Dearing 2014b). However, this mechanism might not allow the species to adjust sufficiently to current rates of climate change.

Past research has correlated changes in pika distribution and persistence with specific climatic variables to provide an understanding of how climate change affects pikas. Beever et al. (2003) found evidence of recent pika extirpations from historically occupied sites in the Great Basin to be best modeled by elevation, suggesting thermal stress. A study by Moritz et al. (2008) resampled the historic “Yosemite transect,” which was first surveyed in the early 1900’s, and found the low elevation limit of pika’s range to have risen over 150 meters. The authors concluded that the minimum average monthly temperature of 3.7°C in the past century explained upslope range retraction for pikas and other species (Moritz et al. 2008). Wilkening et al. (2015a) found pika stress to be positively correlated with loss of permafrost. Recently, extirpation of the American pika from a core habitat fragment has been attributed to climate change; pika populations in the northern area of Lake Tahoe, California were not detected in recent searches, despite suitable habitat and historical populations (Stewart et al. 2017). The extirpation is associated with a 1.9°C increase in temperature since 1910, as well as a decrease in snowpack recorded over the same period (Stewart et al. 2017).

A number of studies have found temperature, in the forms of both heat stress and cold stress, to limit pika persistence. Beever et al. (2010) found pika distribution to be strongly controlled by climate, and tested types of thermal stress through temperature measurements near historical territories; temperatures were measured by sub-surface loggers, and compared to data from the US Historical Climate Network. The study found that chronic heat stress and acute cold
stress were the best indicator of recent extirpations in the southern Great Basin (Beever et al. 2010). Extirpated sites experienced more days below -5°C and -10°C, and had warmer average summer temperatures than extant territories (Beever et al. 2010). Beever et al. (2011), as further described by Ray et al. (2012), used subsurface microclimate data and historical weather station data to show that long term average climate best explained observed extirpations. Further, it was found that cold stress, caused by a lack of snow cover during sub-freezing temperatures, best explained extirpations (Beever et al 2011), especially when days below -10°C was used as the threshold for cold stress, rather than days below -5°C or 0°C (Ray et al. 2012). In a temporal comparison of climatic and other predictors of pika extirpation originally proposed by Beever et al. (2003), summer heat stress became more predictive over time, indicating climatic drivers have become more important in recent extirpations (Beever et al. 2011). Wilkening et al. (2011) re-surveyed historically occupied territories for microclimate temperature and vegetation data to explain extirpations. The authors found that average summer temperature provided the best explanation for extirpations, with little support for cold stress as a predictor (Wilkening et al. 2011). Yandow et al. (2015) found that pika persistence in the Wind River Range, Wyoming, was limited by winter snowpack persistence and available forage within and around talus patches. The authors did not find support for summer heat as a limiting factor of pika abundance in the region (Yandow et al. 2015).

It is important to note that apparent drivers for pika persistence and extirpation may not be the same across their entire range. For example, climatic stressors in the Great Basin are likely different from those in Wyoming ranges (Yandow et al. 2015); both would likely be different from those experienced in Colorado. Heat stress has been found to be influential in dry areas, while an upper elevational limit based on precipitation and cold temperatures exists in other parts
of the species’ range (Jeffress et al. 2013). Understanding the breadth of climatic limitations and potential exceptions is critical to a holistic understanding of the species and for shaping future conservation goals.

Many authors cite the need for increased high-resolution, fine-scale studies to understand more fully how pikas interact with a changing climate (Beever et al. 2010; Jeffress et al. 2013; Schwalm et al. 2016, Varner and Dearing 2014a). Large scale studies must be complimented by studies at smaller scales. Large scales may mask certain impacts climate change has on individual survival in local populations (Jeffress et al. 2013); additionally, large scale studies may not be sufficient to make predictive models that accurately match pika’s local responses (Varner and Dearing 2014a). Microclimates represent the fine scale necessary to make assessments of habitat suitability, as microclimates can differ drastically within a single habitat patch (Varner and Dearing 2014a). Although most recent research, as outlined above, has used sub-surface temperature loggers to obtain fine scale data, only one study has begun to relate individual pika survival to microclimate (Wilkening and Ray 2016). To date, published studies have not explained extirpations based on a comparison of microclimates within a single population’s habitat on the scale of individual territories.

Methods:

Study Site

This study was conducted in the Niwot Ridge Biosphere Reserve, situated within the Roosevelt National Forest in Colorado. The West Knoll (40.056934, -105.595627) sits along Niwot Ridge, and has a maximum elevation of 3620 meters. The West Knoll was selected for study based on its inclusion in recent studies of pika survival and foraging behavior in relation to
climate (Bhattacharyya and Ray 2015, Wilkening et al. 2015a, Wikening and Ray 2016), its accessibility, and the availability of historical data on available forage at this site (Dearing 1996; 1997). The central study area was surveyed previously by an undergraduate who classified territories according to a metric of how recently they appeared to be used (Fig. 1; Max Wasser, unpublished data). Haypile remnants disintegrate slowly, providing evidence of the apparent time since occupancy or frequency of haypile construction in each pika territory. Using the apparent volume of haypile remnants as a metric of time since occupancy (Max Wasser, unpublished data), pika territories on the West Knoll were classified by apparent time since most-recency occupancy (Fig. 1). Territories were classified as historically occupied (small volume of remnant hay, little sign of recent pika occupancy), intermediate (moderate amount of remnant hay and sign of recent occupancy), or very recently occupied (large volume of remnant hay, much sign of recent pika occupancy); territories are referred to by their remnant haypile size category, which indicates the amount of recent sign of pika occupancy. Territories are also referred to simply in terms of the apparent time since occupancy. A randomized subset of these previously surveyed territories, stratified by time since occupied, were selected using GPS coordinates and random number generation in the R language (R Core Team 2017). An initial sample of 3 territories per category and an oversample of 6 territories per category was selected; each potential site was given a number relative to its order in the sample (e.g., S1, M8, L3). Territories in this random sample were ground-truthed, or visited and observed, in the same order sampled to select 3 sites of each haypile size class. Territories that did not appear to correspond in size with their original classification as “small,” “intermediate,” or “large” (Chris Ray, personal communication), as well as territories located within 50 meters of the last accepted site of that type, were replaced by territories drawn (in sequence) from the oversample.
Data Collection

To characterize sub-surface temperatures within each of the nine study territories, temperature data loggers (HOBO Pendant Model UA-001-64, Onset Computer Corp.), accurate to ± 0.53°C from 0 to 50°C, were placed in pairs at each territory. Data loggers were programmed, and data were uploaded from loggers to a computer using Onset’s HOBOware Pro v. 3.7.4 software, through a coupler and optical base station. Each data logger was programmed to start recording temperatures at 1-hour intervals, for 24 recordings per day, beginning on June 19, 2017 at 14:00. All loggers had fresh batteries (100% charged) at the time of programming, and were attached to 1 meter of bright green plastic “weed-wacker” cord to facilitate rediscovery and removal. Loggers were placed as soon as snow was melted from all nine territories. At each territory, a data logger was buried at shallow (10-25 cm) and deep (50-100 cm) depths to characterize the potential for behavioral thermoregulation by pikas. Sensor pairs were buried as close to the original GPS point and haypile as possible; small location shifts (<3 m) were made to avoid disturbing existing hay piles, while ensuring loggers were placed in rocks characteristic of the entire territory. Rocks were carefully removed to place deep loggers as deep as possible. To maintain consistency, deep loggers were not placed on dirt; if bare earth was reached, the sensor was placed on a small number of replaced rocks, elevating it approximately 5 cm from the earth. The depth of the logger was recorded relative to the average surface level of surrounding rocks. Rocks were then replaced as close to their original positions as possible. Shallow loggers were placed when all but 10-25 cm of rocks had been replaced. The remaining 10-25 cm of surface rocks were replaced on top of the shallow sensor; the exact depth was dependent on the size of the surface rocks to ensure the logger was below the surface and completely covered. The depth of the shallow logger was recorded, and a two-stone rock cairn constructed nearby (within
½ m) to aid rediscovery. All loggers were put in place no later than 12 July 2017, and removed no sooner than 8 October 2017. Temperature data from July 12 through September 22 were used in analysis; data were censored (omitted) beginning on the date of first snowfall, September 23. This data range included the entire warm season of summer, excluding incomplete cold season data.

Each territory was surveyed for ground cover within a 7.5 m radius around the loggers; though pikas have larger territories, this design allowed characteristics to be paired with temperature on a fine scale. Vegetation surveys were adapted to the scale of this study from methods used by Wilkening et al. (2011). A pair of 15 m vegetation transects were set up, each centered on the logger pair, with the first transect along the fall line through the territory and the second transect perpendicular to the fall line. Point surveys were conducted for vegetation every 50 cm on each transect. All vegetation within 1 cm of the point were recorded and identified to the lowest classification possible (usually species or genus). For analysis, vegetation was classified as alpine avens (G. rossii), forb (other than G. rossii), graminoid, rock cover, or “other,” which included ground lichen, moss, and fungi.

To determine current pika occupancy, a 20 minute observation was conducted at each territory, followed by additional observations at territories where pikas were not observed. Detection probability of pika has been estimated at over 90% when all types of sign are used (Ray et al. 2016); detection probability in the present study are likely equal to or higher than that estimate because additional sampling providing opportunistic occupancy observations. Two 45-minute behavioral observations were conducted at each occupied territory; all surface activities exhibited by the territory owner were recorded in one-minute intervals. When multiple behaviors occurred within a single minute, all were recorded and included in analyses. Behavior types are
described in Table 1. Additional stimuli and an associated response, such as disturbances and other animals, were recorded during each observation; ambient weather conditions were also described. Observations took place in August, when most pikas were often seen on the surface haying (Table 1). Activity minutes were determined by summing the number of minutes in which each respective behavior was observed. For example, if a pika was observed feeding (Table 1) at any point during minutes 5 and 20 of an observation (but during no other minutes), 2 activity minutes of feeding behavior would be calculated for that observation. Because more than one behavior could be expressed by a pika in a single minute, the total number of activity minutes for any observation may be more than the number of minutes in the observation.

Table 1. Behaviors, associated codes, and descriptions observed in behavior surveys

<table>
<thead>
<tr>
<th>Behavior Type</th>
<th>Behavior Code</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moving</td>
<td>M</td>
<td>Locomotion across the surface</td>
</tr>
<tr>
<td>Scanning</td>
<td>S</td>
<td>Head up and moving laterally to look for other animals, or visual search in response to a disturbance</td>
</tr>
<tr>
<td>Resting</td>
<td>R</td>
<td>No movement, head neutral or down, sometimes sleeping</td>
</tr>
<tr>
<td>Feeding</td>
<td>F</td>
<td>Eating vegetation, not collecting for transport</td>
</tr>
<tr>
<td>Haying</td>
<td>H</td>
<td>Collecting vegetation, or transporting collected vegetation to a haypile</td>
</tr>
<tr>
<td>Short Call</td>
<td>SC</td>
<td>Short chirp sound</td>
</tr>
<tr>
<td>Preen</td>
<td>P</td>
<td>Self cleaning using mouth and forelimbs</td>
</tr>
<tr>
<td>Cheek Rub</td>
<td>CR</td>
<td>Rub cheek against rock to deposit oil from apocrine glands</td>
</tr>
<tr>
<td>Unseen</td>
<td>U</td>
<td>Pika not seen on surface, assumed to be below the surface</td>
</tr>
<tr>
<td>Long Call</td>
<td>LC</td>
<td>Distinguished from short calls (Smith and Weston 1990), but not heard in the present study</td>
</tr>
</tbody>
</table>

Data Analysis:

All data were analyzed in the R language (R Core Team 2017). Site types were ordered, meaning a large territory has more apparent signs of apparent recent occupancy than an
intermediate territory, and an intermediate territory has more apparent recent signs than a small territory. To account for ordering, the response variable was coded as interval data (1 = small/historical, 2 = intermediate and 3 = large/recent), under the assumption that the time elapsed between the occupancy of historical and intermediate territories was similar to the time elapsed between the occupancy of intermediate and recent territories. Alternatively, the response variable could have been coded as ordinal data, under the assumption that the amount of time elapsed between the occupancy of historical and intermediate territories was much different than between intermediate and recent territories. However, the West Knoll supported a much larger population of pikas as recently as the late 1990s, according to trapping data archived by the Niwot Ridge LTER (http://niwot.colorado.edu). Thus, not enough total time has elapsed since the first pika losses to allow for large differences in time elapsed between territory classes.

Hypothesis 1 (ground cover) was tested by modeling the interval response variable as a function of ground cover data collected in the vegetation survey. Ground cover variables considered as predictors were percent cover of alpine avens, percent cover of graminoids and percent cover of rock. Interaction effects were identified with a two-way ANOVA and a linear model was used to characterize specific effects of each ground cover class, as cover was approximately normally distributed. In order to compare the modeled effects of multiple ground cover classes on the same response variable, a Bonferroni correction was used. The five classes were compared with an alpha level of p = 0.01.

To test hypothesis 2 (summer temperature) and elements of hypothesis 3 (behavioral thermoregulation), daily temperature data from sub-surface loggers were first fitted with a smooth curve to estimate temperatures between hourly sensor readings. Lowess, loess, spline and cubic polynomial smoothing were compared with a generalized additive model fit to temperature
data from a single day to narrow the candidate models based on a visualization of fit. The
generalized additive model (GAM), cubic polynomial, and loess curves appeared to fit the
summer data well An information criterion (AIC) was used to compare support for different
models of daily temperature data, indicating which candidate best fit the data using the fewest
number of parameters. A difference of greater than two between the AIC values of different
models indicates that one model is more highly supported, and lower AIC values indicate higher
levels of support (Burnham and Anderson 2002). In cases where multiple models based on the
same response variable were compared, a Bonferroni correction was used to adjust the alpha
level for multiple comparisons.

Hypothesis 2 (summer temperature) analyses were adapted from methods used by Beever
et al. (2010). Acute summer heat stress was measured by shallow loggers as the number of days
above 20°C. This value is below the upper ambient temperature limit of 25.5-29.4°C identified
for pikas (MacArthur and Wang 1973, 1974; Smith 1974), but was reported as the temperature in
which pikas reduce surface activity in order to spend more time behaviorally thermoregulating
beneath the surface (MacArthur and Wang 1974); a temperature of 20°C measured by the
shallow logger indicates that parts of the territory may no longer be suitable for behavioral
thermoregulation. Chronic summer heat stress was measured by the mean daily and daily
maximum temperatures. The grand summer temperature mean was calculated from all
temperature data in the warm season, and mean temperatures for each month were calculated.
Daily maximum and minimum temperatures were derived from the GAM model; the interval
response variable described above was modeled as a function of both the daily maximum and
minimum temperatures as predicted by the GAM model. Cold stress was not analysed because
minimum temperatures recorded did not drop low enough to allow cold stress analyses (Ray et
al. 2012). It was not possible to measure over winter cold days within the duration of the study, and minimum temperatures experienced in the summer do not necessarily reflect potential winter minimum temperatures.

Hypothesis 3 (thermoregulation) was tested by modeling the interval response variable as a function of the thermoregulation potential of each territory, where the thermoregulation potential represents the range of temperatures available to a pika as refuge from surface conditions. The thermoregulation potential of each territory was found by calculating the area between the mean daily temperature curves derived from data recorded by the shallow and deep loggers, each fitted to the GAM model. To further validate this hypothesis, thermoregulation potential was modeled as a function of rock cover, under the assumption that larger talus areas are deeper and offer a wider variety of microclimates. Pika behaviors that should cause more thermal stress (such as moving on the surface) and unseen behaviors that are assumed to reflect sub-surface activity, were compared to the potential for behavioral thermoregulation at currently occupied territories. Specifically, the number of behavior minutes spent either moving on the surface or unseen was modeled as a function of thermoregulation potential using a binomial generalized linear mixed effects regression fitted via the glmer function in the lme4 package for R (Bates et al. 2014). A mixed effects model accounts for variation within individuals measured in multiple observations through the addition of a random effects variable, which is not possible in a traditional linear model. The response was characterized as a binomial because each behavior could either occur or not within each minute of observation, and this type of data does not fit a normal (Gaussian) distribution. A Bonferroni correction was used to adjust the alpha level to \( p = 0.125 \) for multiple comparisons of behavior types.
Results:

Pikas were found to occupy 8 out of 9 territories surveyed in the present study; the unoccupied site was “S6,” a historically occupied or small haypile site. Two out of the 8 putatively occupied territories were on the periphery of an occupied territory; pikas in territories “M3” and “S1” (intermediate and small) were seen visiting the sensor location, but apparently hayed only to an adjacent area.

Land Cover - Hypothesis 1

Differences in land cover across territory types is summarized in Figure 2. A significant interaction effect was detected between ground cover class and the amount of recent signs of pika occupancy (df = 4, f = 4.60, p = 0.00431). In the linear models for ground cover class, graminoid cover was found to have a significant negative correlation with recent signs of pika occupancy, while rock cover had a marginally significant positive relationship (Table 2). No significant difference was detected in rock, alpine aven total forb or other cover categories (Table 2).

Table 2. Ground cover relationships summary based on multiple linear models for five cover classes. Significant p-values are denoted with *, using an alpha level of p = 0.01.

<table>
<thead>
<tr>
<th>Cover Class</th>
<th>df</th>
<th>R²</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rock cover</td>
<td>7</td>
<td>0.469</td>
<td>2.84</td>
<td>0.025</td>
</tr>
<tr>
<td>Alpine avens</td>
<td>7</td>
<td>-0.0164</td>
<td>-0.933</td>
<td>0.382</td>
</tr>
<tr>
<td>Total forb</td>
<td>7</td>
<td>0.00361</td>
<td>-1.01</td>
<td>0.344</td>
</tr>
<tr>
<td>Graminoid</td>
<td>7</td>
<td>0.714</td>
<td>-4.58</td>
<td>0.00254 *</td>
</tr>
<tr>
<td>Other</td>
<td>7</td>
<td>-0.0135</td>
<td>-0.945</td>
<td>0.376</td>
</tr>
</tbody>
</table>
Vegetation type by apparent time since occupation

Figure 2: Mean percent cover of vegetation and rock classes by apparent time since pika occupancy as defined by remnant haypile size (small, intermediate, large). Error bars represent 1 standard error above and below the mean. Asterisks represent significant regressions of apparent time since occupied on percent cover of the class, using an alpha level of 0.01 to account for multiple comparisons.

Temperature - Hypothesis 2

Territories showed potential for thermoregulation and indicated pikas experience varying temperatures depending on depth, as temperatures recorded by deep loggers were found to be significantly different from shallow loggers (df = 16, $R^2 = 0.900$, $t = 12.4$, $p < 0.001$). However, temperatures did not differ among territory classes in any model. Site types showed no difference in acute heat stress as measured by the number of hot days (df = 7, $t = 0.323$, $p = 0.756$). There was no significant difference in grand means for shallow (df = 7, $t = -1.19$, $p = 0.274$) or deep loggers (df = 7, $t = 0.667$, $p = 0.526$). Among shallow loggers, no significant difference among territory classes was detected in the mean temperatures of any summer month, and the same lack of significant difference was also observed among deep loggers (Table 3).
Table 3. Monthly mean temperatures in °C for each logger position, in territories occupied historically (little sign of recent pika occupancy), recently (large amount of recent pika sign), or at an intermediate level. The response variable, amount of sign, was modeled by mean temperatures in a linear model, as reported below. For all models, df = 7.

<table>
<thead>
<tr>
<th>Month</th>
<th>Sensor Type</th>
<th>Historical Site (mean °C)</th>
<th>Intermediate Site (mean °C)</th>
<th>Recent Site (mean °C)</th>
<th>t-value</th>
<th>Standard Error</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>July (days 12-31)</td>
<td>Shallow</td>
<td>11.3</td>
<td>11.6</td>
<td>11.7</td>
<td>1.64</td>
<td>0.106</td>
<td>0.145</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>8.1</td>
<td>8.0</td>
<td>7.6</td>
<td>-1.11</td>
<td>0.197</td>
<td>0.305</td>
</tr>
<tr>
<td>August</td>
<td>Shallow</td>
<td>9.0</td>
<td>9.1</td>
<td>9.8</td>
<td>0.612</td>
<td>0.202</td>
<td>0.560</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>6.2</td>
<td>5.8</td>
<td>5.7</td>
<td>-1.03</td>
<td>0.209</td>
<td>0.336</td>
</tr>
<tr>
<td>September</td>
<td>Shallow</td>
<td>6.4</td>
<td>6.5</td>
<td>6.5</td>
<td>0.222</td>
<td>0.223</td>
<td>0.831</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>4.8</td>
<td>4.3</td>
<td>4.1</td>
<td>-1.29</td>
<td>0.258</td>
<td>0.239</td>
</tr>
<tr>
<td>October (days 1-8)</td>
<td>Shallow</td>
<td>-1.1</td>
<td>-1.0</td>
<td>-0.6</td>
<td>0.786</td>
<td>0.300</td>
<td>0.458</td>
</tr>
<tr>
<td></td>
<td>Deep</td>
<td>-0.4</td>
<td>-0.2</td>
<td>0.0</td>
<td>0.786</td>
<td>0.180</td>
<td>0.272</td>
</tr>
</tbody>
</table>

Among the candidate model set tested to fit daily temperature fluctuations, the generalized additive model (GAM) was more highly supported than the cubic polynomial (cubic polynomial AIC = 2812.22, GAM AIC = 2772.85); AIC could not be calculated for a loess curve (Figs. 3-4). The GAM model was applied to all territories to determine the timing of the warmest and coolest points in each day, as these times could vary across all sites (Fig. 5). All territories appear to follow a similar trend in the timing of the warmest and coolest points, as well as in maximum and minimum temperatures (Fig. 5).
Figure 3. Daily temperature variation over the 24-hour day from the shallow logger at territory L3, showing temperature variation by month from July 12-Oct 8. Snow arrival, and the end of summer, is indicated when temperatures stabilize in late September and October.

Figure 4. Smooth curves fit to hourly temperature data from July 12 (left panel) and September 1-22 (right panel) at territory L3 (a recently occupied site), shallow logger. A generalized additive model (GAM) was found to have the most parsimonious fit (lowest AIC), or best fit to the data with the fewest parameters.
Figure 5: Daily temperature fluctuations for shallow (red) and deep (blue) loggers, July-September. Each panel displays temperatures at one territory, named for the amount of remnant haypile used to determine apparent time since occupancy (L=large remnant haypile and recent occupancy, M=middle or intermediate occupancy, S=small remnant haypile and historical occupancy) and assigned an identifying number based on the random sample. Fitted lines represent GAM means (heavy lines) and 95% confidence intervals (thin lines).
The mean daily maximum and minimum temperatures, as predicted by the GAM, did not have significant relationships with the apparent time since pika occupation when using an alpha value of \( p = 0.125 \) to correct for multiple comparisons (shallow max: \( df = 7, t = 0.479, p = 0.647 \); deep max: \( df = 7, t = -2.01, p = 0.0851 \); shallow min: \( df = 7, t = 1.14, p = 0.291 \); deep min: \( df = 7, t = -0.296, p = 0.776 \)).

**Thermoregulation - Hypothesis 3**

Thermoregulation potential was graphed for each territory (Fig. 6), based on the generalized additive model (GAM) as described above. The red line shows the temperatures at the position of the shallow logger, while the blue line shows the temperatures of the deep logger; the dots represent the daily minimum and maximum temperatures corresponding with shallow (red) and deep (blue) positions. The lines intersect at the boundary between the coldest and warmest parts of the day; just before this intersection, temperatures at the deep logger position can be warmer than the temperatures experienced by the shallow logger (e.g., see panel L4 in Fig. 6). The shaded area between the red and blue lines represents the range of temperatures a pika could use to thermoregulate, and is defined here as the thermoregulation potential. The thermoregulation potentials were found have a significant positive relationship with the apparent time since pika occupation (\( df = 7, R^2 = 0.376, t = 2.41, p = 0.0468 \)), and higher thermoregulation potentials were associated with more recent pika occupancy (Fig. 7). Rock cover did not have a significant positive relationship with thermoregulation potential (\( df = 7, t = 1.523, p = 0.172 \)), but may reflect the study’s small sample size.

Behaviors observed at each occupied territory (n=8) and overall behaviors are summarized in Figure 8. Site S6 is excluded because no pika occupied the territory at the time of study. Behavior minutes of each type observed appear to vary greatly between all territories (Fig.
Neither minutes unseen, which are assumed to approximate below-surface activity, nor minutes spent moving on the surface (Fig. 8) showed a significant relationship with thermoregulation potential in the generalized linear mixed effects model (observations = 16, groups = 8; unseen $z = -1.45$, $p = 0.148$; moving $z = 1.28$, $p = 0.199$). However, both relationships were in the expected direction, unseen behaviors showing a negative relationship, while moving behaviors showed a positive relationship with thermoregulation.
Figure 6. Thermoregulation potential for each territory, where territories are named for the amount of remnant haypile that indicates apparent time since recent occupancy. Potentials are calculated as the difference between GAM curves for deep and shallow loggers (Fig. 5).
Figure 7. Mean thermoregulation potential across territories sharing the same apparent time since pika occupancy, as defined by remnant haypiles (small, intermediate, large). Error bars show one standard error on either side of the mean, and are significantly different.
Figure 8: Mean surface behavior minutes, or the number of minutes in which a behavior was observed within a 45-minute observation of territory occupants at each occupied territory (n=8). Site S6 (small remnant haypile indicating historic occupancy) is excluded because no pika was observed there. Sites M3 (intermediate occupancy) and S1 (small remnant haypile indicating historic occupancy) were putatively occupied, but the pika observed visiting the logger location hayed only to an adjacent area. Mean overall behavior minutes for all territories is also shown (lower right panel). No behaviors are significantly different across territories.
Discussion:

Land Cover Hypothesis

The negative correlation of graminoids with territory type is consistent with relationships found in other studies (Rodhouse et al. 2010; Wilkening et al. 2011; Jeffress et al. 2013), and may reflect differential water availability in the summer (a climatic variable). Graminoids tend to do better in dry environments, while pika occupancy often has a positive relationship with precipitation (Beever et al. 2011, Erb et al. 2011). The marginally positive correlation of rock cover with recent signs of pika occupancy suggests the ability of a site to provide refuge from climatic variables is important in explaining differences in occupancy. The ground cover result is in partial agreement with those found by Hall et al. (2016), in which pika occupancy was most strongly predicted by microrefugia, rather than habitat characters such as available forage. However, our power to detect relationships is limited by sample size, as discussed further below.

Temperature Hypothesis

Though the temperature results are limited by small sample size, as discussed further below, the lack of significance in summer temperatures may point to the conclusion that cold season temperatures or may be more appropriate to explain differences in this region, assuming temperature is an important climatic variable (Yandow et al. 2015). The region of the Rocky Mountains studied may align more with results from Wyoming ranges than Great Basin ranges (see literature review above). The hottest temperatures recorded on the West Knoll are lower than those experienced in other parts of the pika’s range, and did not exceed the upper lethal temperature identified for pikas (MacArthur and Wang 1973; 1974; Smith 1974). Additionally, precipitation amounts and timing may play an important role. Precipitation can impact species used for food, as well as snowpack necessary for winter thermoregulation. Cold season
temperatures and winter snowpack hypotheses could not be tested in the present study due to time constraints, but represent a direction for future research, as described below.

The lack of significance in the number of hot days likely reflects the close proximity of all territories. Studies that have found the number of hot days to be explanatory have compared sites over a much larger area than the single prominence of the West Knoll. Many of the territories were separated by only a few hundred meters, across which scale ambient temperatures are unlikely to vary. However, because temperatures were not significantly different among territories, other factors can assume modeled correlations are not confounded by temperature variation in their ability to explain apparent site differences.

**Thermoregulation Hypothesis**

Thermoregulation potential was shown to have a significant positive relationship with the apparent time since pika occupancy. A greater thermoregulation potential would provide more opportunities for pikas to find an appropriate refuge temperature; pikas would be able to continuously occupy high thermoregulation territories, while they may struggle to survive more often at territories with lower potentials for thermoregulation. A calculation of thermoregulation potential has not been done before, but this result is similar to that found in a study performed by Hall et al. (2016). The authors found pika occurrence to be higher in areas where subsurface temperatures were buffered from surface temperatures (Hall et al. 2016). Further studies are needed to more fully represent the relationship between thermoregulation and the history of occupation in a given territory, as described below.

The lack of significance in the positive relationship between rock cover and thermoregulation potential suggests that additional physical factors may influence the
thermoregulation at a given site; it is possible that the size of rocks or the available space between rocks in a talus patch could play a significant role.

Behavioral observations and analyses were possible because the total population of pikas on the West Knoll appeared to be greater in 2017 than in 2015, when all territories were surveyed for apparent time since occupancy (Chris Ray and Max Wasser, personal observations). Current occupancy represents territories recently colonized by juveniles dispersing in the early summer, and does not necessarily indicate where individuals will persist over multiple years; historically occupied territories appear to have low consistent occupancy, while recent territories appear to have very consistent occupancy. Since this study was designed to examine the apparent range shift on the West Knoll and not just occupation in 2017, the comparison of behavior across site types is appropriate. This population allowed observations across historically occupied, intermediate, and recently occupied territories, facilitating the examination of behavioral plasticity.

Neither of the behaviors analyzed showed significant relationships with thermoregulation potential, but the directions of the relationships are also consistent with pika’s need to behaviorally thermoregulate (MacArthur and Wang, 1974; Smith and Weston, 1990); pikas would be able to spend more time on the surface in areas with a greater potential for behavioral thermoregulation, or a greater range of potential temperatures available under the talus, and conversely would need to spend more time under the rocks in territories with a lesser potential for thermoregulation. Though the results are insignificant, the suggested trend is consistent with expectations for behavioral plasticity in the face of apparent site differences (Varner and Dearing 2014b; Beever et al. 2017).
The results were limited by the sample size of behavioral data, which included two observations for each of the eight occupied territories. It is possible that this number of observations could not adequately account for daily fluctuations in behavior due to weather conditions, time of day, or other species present, masking any significant differences. It is likely that additional behavioral data across a greater number of territories would add clarity to the relationships between behavior and thermoregulation potential, as further discussed below. Future research should examine the potential relationship between temperature dependent behaviors and a territory’s thermoregulation potential with more behavioral observations at a greater number of sites.

Overall Findings

The results of this study indicate that climatic variables are an important factor in the apparent range contraction on the West Knoll, but leave opportunities for future research to more fully explore some variables, as described below. An importance of climate is indicated by the significant relationships between the explanatory variables graminoid cover and thermoregulation potential, with the predictor variable of apparent time since occupancy. However, the image painted by those results is complicated because other variables, such as temperature and rock cover, did not have significant or consistent relationships with the apparent time since pika occupancy.

None of the temperature metrics or models showed significant relationships with the apparent time since pika occupancy. This may indicate that the climatic variables measured in the summer season could be less explanatory than other climatic variables, such as winter temperatures that other studies have found to be explanatory (Beever 2011; Ray et al. 2012; Yandow et al. 2015). However, because the territories were subject to similar temperatures,
differences in thermoregulation potentials are likely more meaningful in explaining the apparent range contraction. Thermoregulation potential models were not confounded by varying surface temperatures, and thus represent the ability of a territory to provide refuge for pikas. As all territories experience increases in stress due to changing climate conditions that are observed around the globe (Brodie et al. 2012), territories that provide a greater opportunity for buffering in the form of thermoregulation potential will likely have more persistent occupancy than those with a poor buffer from stressful ambient conditions.

While rock cover had a marginally significant positive relationship with how recently a territory appeared to be occupied, rock cover had an insignificant positive relationship with behavioral thermoregulation. The direction of relationships in both models is consistent with what would be expected based on a pika’s need to use the substrate to as refugia (Hall et al. 2016), but represents an opportunity for further research to more fully understand how rock cover may impact the refuge available in a territory.

**Limitations and Future Directions**

This study has a number of limitations that affected the results and significance of the findings. The greatest limitation comes from the sample size; with only nine territories total, and three from each historical size category, the data does not have the predictive power to see all possible relationships. A small sample size is less representative of all possible microclimates in each category than a larger sample size would be; sites selected through random selection may not best represent the true variation or mean of all sites. The sample size in the present study was limited by the cost of sensors and time available to collect data. If funding and time allow, future studies should include additional territories from each category to increase the ability to see trends and results that may not have been significant with a small sample size. A power analysis
should be conducted to understand the number of territories needed for a high predictive power. Future studies could also include additional data sets collected by others in previous or future years.

Future studies could make increasingly fine measurements of the range of temperatures available to pikas with more than two loggers per territory; thermoregulation potentials calculated for each territory would more accurately reflect what pikas actually experience, and would provide more insight into the effect different depths or locations within a territory have on thermoregulation potential. In addition, rock cover should be surveyed in greater detail. Substrate complexity has been hypothesised to have an effect on thermal stability in the past (Millar and Westfall 2010; Rodhouse et al. 2010), but has not been supported using subjective ranking scales and temperature (Rodhouse et al. 2017).

This study could be improved if historical territories were selected based on exclusion by site type polygons as seen in figure 1, where small sites would only be chosen from outside the intermediate polygon where there were no intermediate or large sites, and intermediate sites selected from outside the large-territory polygon where there were no large sites. This selection method would be better suited to explain the observed trend of retreat towards higher elevation territories. The present study design was able to test differences between territory types, but identified statistical trends would likely be stronger with this modified site selection.

This study was also limited by the amount of time available for data collection. Ideally, loggers would be left in the ground for at least one full year, allowing hypotheses about winter snowpack to be tested alongside summer heat hypotheses for the same system in the same year. An extended data set would likely allow understanding of the most important drivers of pika occupancy change on the West Knoll, which is not possible with data from a few months.
Future studies operating on a multi-year time scale should also track individual survival at each of the occupied territories. Only one study has begun to relate individual pika survival to microclimate (Wilkening and Ray 2016). By tracking individual survival, source and sink dynamics could be understood, and data based on historical hay pile sizes could become increasingly fine. Thermoregulation potentials could be compared in a more meaningful way if additional data were available to suggest their relationship to pika persistence on a fine scale. Tracking overwinter survival could help us infer the effects of winter climate conditions, as well as the importance of food cache quality based on summer climatic data. Historical occupancy and the apparent retreat could be more directly studied by comparing current occupancy and survival with unoccupied territories; the present study was limited from this type of comparison because it was not designed to survey current occupancy, and only had 1 unoccupied territory at the time of sampling.

This study did not consider the effects of ecological interactions with other animals, because the scale of the study site was believed to be too small for such interactions to have an effect. However, it is possible predators and disease vectors could change with climate, making animal interactions of interest in future studies, especially on a larger scale.

Conclusions

The present study was designed to explain any differences that exist between territories with varying levels of apparent time since pika occupancy based on summer vegetation, climatic, and behavioral data. The amount of ground covered by rocks and graminoids, as well as the thermoregulation potential were related with more recent apparent pika occupancy, indicating climatic variables are important in explaining apparent occupancy shifts. However, a lack of
significance in the relationship between summer temperature results and apparent time since pika occupancy suggests that other climatic variables, such as winter snowpack, may be more appropriate for the region. Additionally, the lack of temperature differences indicates that differences in variables such as thermoregulation potential are more important. Temperature dependent behaviors may show a relationship with a territory’s thermoregulation potential in future studies, though they were not significant in the present study due to limitations such as sample size. A holistic understanding of how pikas respond to a changing climate based on fine scale microclimate data is important in making future climate predictions, as other animals will be increasingly pushed towards their physiological limits and exhibit responses similar to those seen in American pikas today. An understanding of what makes some territories better than others will become important as reintroduction efforts begin to be discussed (Wilkening et al. 2015b). Reintroductions into habitats that do not have the thermoregulation potential necessary, or have negative relationships with time since occupancy, would be in vain and represent a potential conservation failure. Understanding microclimates in relation to the specific needs of a species can be translated to other organisms as climatic and anthropogenic stress increases.
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