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Microclimate and summer surface activity in the American pika (*Ochotona princeps*)

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ABSTRACT.—As regional climates continue to warm, climate-sensitive species might increasingly depend on microclimates to maintain normal activities. The American pika (*Ochotona princeps*) has been suggested as a sentinel of montane climate change, largely due to its sensitivity to warm temperatures and high exposure to changing climatic conditions. Pikas use talus to thermoregulate and have been shown to persist more often in talus slopes that create stable microclimates. However, many studies of pika behavior and persistence use metrics of climate measured above the talus surface, outside of the proposed microclimates that pikas can access. We paired fine-scale microclimate measurements with behavioral observations of uniquely tagged pikas in the Colorado Rocky Mountains to model how pikas might use talus subsurface habitat as a microrefuge. Our findings suggest that pikas spend more time on the surface of the talus when there is a stronger gradient in temperatures between “shallow” (0.1 m below the surface) and “deep” (1 m below the surface) regions of the talus, especially during the middle of the day when shallow temperatures are warmer. These results underscore the importance of pairing fine-scale data on microclimate with behavioral observations of tagged individuals to more accurately evaluate how animals might use climate refugia to persist in changing conditions.

RESUMEN.—A medida que los climas regionales se vuelven más cálidos, las especies susceptibles al clima dependen cada vez más de los microclimas para realizar sus actividades habituales. La pica americana (*Ochotona princeps*) ha sido considerada como un centinela del cambio climático en hábitats montañosos, en gran medida por su sensibilidad a las temperaturas cálidas y por su alta exposición a las condiciones climáticas cambiantes. Las picas usan los taludes para termoregularse y se ha demostrado que subsisten con mayor frecuencia en taludes que crean microclimas estables. Sin embargo, muchos estudios sobre el comportamiento y la subsistencia de la pica utilizan métricas de clima medidas sobre la superficie del talud, sin considerar los microclimas a los que las picas podrían acceder. En el presente estudio, combinamos mediciones de microclimas a pequeña escala con observaciones del comportamiento de picas marcadas en las Rocky Mountains de Colorado, para modelar la manera en que las picas podrían usar el hábitat del subsuelo del talud como microrefugio. Nuestros hallazgos indican que las picas pasan más tiempo en la superficie del talud cuando el gradiente térmico es mayor entre las regiones del talud “poco profundas” (0.1 m debajo de la superficie) y las “profundas” (1 m debajo de la superficie), especialmente durante el medio día cuando la temperatura en la superficie es más cálida. Estos resultados resaltan la importancia de combinar datos de microclima a pequeña escala con observaciones de comportamiento de individuos marcados para evaluar con mayor precisión cómo estos animales podrían usar refugios climáticos para subsistir en condiciones cambiantes.

The effects of climate change on species distribution, abundance, behavior, morphology, and phenology are now well documented across a wide range of taxa (Root et al. 2002, Walther et al. 2002, Parmesan 2006). Although

these impacts are widespread, some species will be more immediately vulnerable to climatic changes, depending on their sensitivity to climate (i.e., intrinsic factors such as physiological heat tolerance), adaptive capacity (i.e.,

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ability to adjust phenotypically or genetically to a changing environment), and exposure to changing conditions (Williams et al. 2008). Although there is generally a lack of agreement on how to assess vulnerability (Pacifi et al. 2015), limited elevational ranges have been implicated as a predictor of extinction likelihood, indicating that montane species are particularly vulnerable (Sekercioglu et al. 2008, La Sorte and Jetz 2010). Range shifts have been documented across continents, suggesting that species in warming areas are shifting their distributions toward higher latitudes and elevations (Chen et al. 2011). But montane populations may have limited latitudinal mobility due to deep valleys that create “montane islands” (McDonald and Brown 1992), and limited elevational mobility due to topographic constraints (e.g., little terrain at higher elevations to colonize; Elsen and Tingley 2015). As such, montane species might have fewer opportunities to limit their exposure to changing conditions by shifting distributions to cooler habitats (Dawson et al. 2011).

Recent studies have emphasized the importance of locating and managing climate refugia as areas that preserve biodiversity and protect populations from stressful environmental conditions during past and current climatic shifts (Keppel et al. 2012, Morelli et al. 2016). Microrefugia, or areas that preserve favorable local climates on a small scale, may be critical in buffering a species from changes in regional climate and allow populations to live outside their main species distributions (Ashcroft 2010, Dobrowski 2011). Historical evidence suggests that as global climate fluctuated during the glaciations of the Pleistocene, many species that restricted their range to refugial areas not only persisted until they could expand their range again but also showed higher genetic diversity within the refugia than at the expanding edge of their range (Hewitt 2000, reviewed in Sublette Mosblech et al. 2011). Although identifying microclimates and related refugia at small, ecologically relevant scales has proved challenging (Ashcroft et al. 2012, Potter et al. 2013), microrefugia are of particular interest for developing management plans in the context of modern climate change (Keppel and Wardell-Johnson 2012).

One type of terrain that demonstrates unique thermal buffering effects and may function as a climate refuge is talus, or areas where broken

rock has accumulated (Millar et al. 2014, Shi et al. 2014, Varner and Dearing 2014b). Depending on the depth of the talus, air temperatures below the talus surface (hereafter, subsurface) can differ significantly from air temperatures above the surface (Harris and Pederson 1998). This partial decoupling of subsurface microclimates from surface climates arises through various seasonal processes. During the warm season, cool subsurface conditions may be created by evaporative cooling, shading effects, cold-air drainage and the Balch effect (in which cold, dense air from the cold season persists deep within the talus throughout the early part of the warm season; Millar et al. 2014). During the cold season, warm subsurface conditions are largely maintained by insulating snow-cover, which limits air flow and heat exchange between the subsurface interstitial spaces and the external surface air (Millar et al. 2014). The resulting microclimate is buffered from both extreme hot and cold temperatures, potentially providing a more thermally favorable microclimate for species that can access this habitat (Shi et al. 2014). However, talus depth and structure are highly heterogeneous within and among habitats (Fig. 1), suggesting that fine-scale microclimate measurements are essential to assess how species could use these microclimates as refuges to limit exposure to climate change (Varner and Dearing 2014b).

The American pika (*Ochotona princeps*; hereafter, pika) is a temperature-sensitive habitat specialist known for its use of talus as a thermal refuge (MacArthur and Wang 1974, Smith 1974, Hafner 1994, Millar and Westfall 2010, Varner and Dearing 2014b, Ray et al. 2016, Rodhouse et al. 2017). The pika has been proposed as a sentinel species for climate change in alpine and montane regions (McDonald and Brown 1992, Hafner 1993, Ray et al. 2012), largely due to its exposure to the rapid changes in climate affecting montane habitats, as well as its potential for low adaptive capacity as a species with low dispersal ability and low fecundity (Smith 1978, Smith and Ivins 1983, Beever et al. 2016a), and its high sensitivity to temperature. As a cold-adapted species (Smith 1974) with many morphological and physiological adaptations to cold environments (e.g., insulating fur, little exposed skin, high metabolic rate, low thermal conductance), the pika has limited capacity to tolerate high



Fig. 1. Talus heterogeneity at 2 sites in the Indian Peaks Wilderness Area, Colorado, USA. **A**, Talus characterized by small and medium rocks at the alpine West Knoll site. **B**, Talus characterized by large and medium rocks at the montane Long Lake site.

temperatures without behavioral thermoregulation (MacArthur and Wang 1973, 1974, Moyer-Horner et al. 2015). Behavioral thermoregulation is an adaptive strategy often used by endotherms to lower the metabolic costs of maintaining an ideal body temperature (Mason et al. 2017) and has long been documented in pikas (MacArthur and Wang 1974, Smith 1974, Moyer-Horner et al. 2015, Smith et al. 2016). Although a pika can succumb to hyperthermia when held at temperatures above 28 °C for as little as 2 h (MacArthur and Wang 1973, Smith 1974), pikas in the wild appear to avoid such temperatures by spending more time within the talus subsurface when temperatures are high, presumably using the cooler subsurface microclimate to shed heat and avoid warm conditions (MacArthur and Wang 1974, Smith 1974, Moyer-Horner et al. 2015, Varner et al. 2016, Smith et al. 2016).

Pika extirpations have been linked to climate-related factors such as mean summer air temperature, acute cold (number of days below –5 °C), acute heat (days above 28 °C), and a suggested interaction between climate and precipitation (Beever et al. 2010, 2016b, Wilkenning et al. 2011, Jeffress et al. 2013). However, the relationship between pika persistence and temperature is anything but clear. In 2010, the United States Fish and Wildlife Service determined that pikas did not meet criteria for protection under the Endangered Species Act because they were not vulnerable to climate change in the entirety of their range, had sufficient habitat to retreat to, and were likely to persist (USFWS 2010). Extant populations have increasingly been noted in relatively warm areas at low elevations considered unusual for pikas, such as the Columbia River Gorge (Varner and Dearing 2014b, Varner et al. 2016), Mono Craters (Smith et al. 2016), Lava Beds

National Monument (Ray et al. 2016), and various sites in the northwest Great Basin (Jeffress et al. 2017). There is evidence that behavioral plasticity may play a role in persistence at low-elevation sites, where pikas can shift surface activity to cooler times of day, such as dawn, dusk, or even night (Smith 1974, Smith et al. 2016). Dietary plasticity, such as consumption of mosses that are available year-round, may lessen dependence on food-caching activities that require considerable surface activity during the warm season (Dearing 1997, Varner and Dearing 2014a). Pika persistence and occurrence at such unusual sites has also been largely attributed to the accessibility of cool microclimates and thermal stability within talus refugia (Hall et al. 2016, Rodhouse et al. 2017), where cooler temperatures can be maintained by unique air dynamics (Smith et al. 2016) and vegetative cover (Varner et al. 2016).

Yet Wright and Stewart (2018) argued that subsurface temperatures may not predict pika persistence well, reporting extirpations at sites with suitably moderate subsurface temperatures in the northern Sierra Nevada. Wright and Stewart (2018) instead suggested that above-talus temperatures might be more important through negative effects on foraging and dispersal. Pikas experiencing warm surface temperatures have been shown to spend less time foraging (Hall et al. 2016), which could limit a pika's ability to cache food for winter and have negative effects on pika persistence (Dearing 1997, Morrison et al. 2009, Bhattacharya and Ray 2015). Dispersing juveniles may be more affected by temperature-related foraging constraints because juveniles must disperse during the warmest time of year (late summer; Smith and Ivins 1983), must allocate time to dispersing instead of foraging (Smith 1974), might be impeded from dispersing during cooler parts of the day by territorial interactions with nearby adults (Smith and Ivins 1983), and might be forced to settle in the warmest areas in the talus, where competition for territories is less fierce (Millar et al. 2016). But there is also doubt as to what extent such above-talus temperatures can predict pika distributions, as Millar et al. (2018) found substantial overlap among above-talus climates at sites in the Great Basin where pikas were "extant" versus "extirpated" or where only "old" pika sign was found. To address this lack of consensus, we studied how individual pikas respond

to subsurface thermal profiles. Our study paired detailed behavioral observations of pikas in the wild with fine-scale microclimate data to determine whether pika surface activity can be predicted by subsurface temperature profiles.

Apparent controls of temperature on species distributions can result from a variety of direct and indirect effects (Walther et al. 2002, Buisson et al. 2008, Moritz et al. 2008, McQuillan and Rice 2015). Pika distribution and occupancy have been linked to temperature repeatedly (e.g., Beever et al. 2011, Wilkening et al. 2011, Schwalm et al. 2016, Mathewson et al. 2017, Millar et al. 2018), but fewer attempts have been made to elucidate direct effects of temperature on pika behavior (Moyer-Horner et al. 2015, Smith et al. 2016, Varner et al. 2016). Notably, Smith et al. (2016) found significant buffering effects of talus at a low-elevation site with hot summers, even when talus surface temperatures were consistently well outside what is typically considered thermally tolerable for pikas. Although pikas were less active during midday when summer surface temperatures were high, their activity did not cease completely, suggesting they were able to shed heat even during these times (Smith et al. 2016). If the degree of coupling between surface and subsurface temperatures mediates pika persistence directly, then each individual pika should respond to its local subsurface temperature profile.

A gradient in subsurface temperature, formed by a difference between shallow subsurface temperature (measured about 0.1 m below the talus surface) and deep subsurface temperature (measured about 1 m below the talus surface), could arise in 1 of 3 ways: shallow temperatures could increase, deep temperatures could decrease, or both. When such differences result from increasing shallow subsurface temperatures, such as at low elevations in the Sierra Nevada (Smith et al. 2016), the need for pikas to thermoregulate may also increase because temperatures on the surface and in the shallow subsurface may become too hot. When differences in temperature result from decreasing deep subsurface temperatures, pikas might not experience temperatures above their thermotolerance, and hence may not need to cool off. Finally, when differences in temperature result from both increasing shallow and decreasing deep subsurface temperatures, pikas could have both the need to thermoregulate

and a cooler microclimate in which to shed heat. All 3 processes should provide a thermal refuge for pikas, but the cooler microclimate created by lower deep temperatures could help pikas shed heat faster and resume surface activities more quickly. Thus, we hypothesize that a stronger gradient between shallow and deep subsurface temperatures should allow pikas to increase their surface activity, especially when shallow temperatures are high at the warmest period of the diurnal cycle. Our hypothesis assumes that there are costs to spending too much time in the deeper strata of the talus, such as reduced opportunities for surface activities like foraging, territorial defense, and antipredator vigilance. Such costs might explain recent patterns of pika loss reported in a growing body of literature which suggests that relatively cool and stable talus microclimates are associated with greater pika occupancy (Varner and Dearing 2014b, Hall et al. 2016, Rodhouse et al. 2017). Therefore, investigation into how pikas adjust their behavior to fine-scale variation in subsurface temperatures could illuminate how the American pika will respond to rising temperatures, helping to guide targeted conservation strategies and future vulnerability assessments.

METHODS

Study Area

Behavioral observations (193 total) were conducted at 3 sites in the Colorado Rocky Mountains, USA: West Knoll (WK; 61.1% of observations) at the Niwot Ridge Long-Term Ecological Research site (NWT; 40°3' N, 105°36' W), Long Lake (LL; 23.3%) in the Indian Peaks Wilderness Area (IPWA; 39°9' N, 105°6' W), and Mitchell Lake (ML; 15.5%) also in the IPWA (40°5' N, 105°35' W). Data were collected on wild individuals over 6 years (2012–2017). Sites ranged in elevation from approximately 3200 to 3700 m. WK is characterized by alpine tundra with north- and south-facing slopes. LL and ML are forested subalpine areas located on a north- and south-facing slope, respectively. All sites contained multiple patches of talus occupied by pikas under study for demographic patterns (Wilkenning and Ray 2016).

Behavioral Observations

Pikas were observed opportunistically from June to September 2012–2017, using a focal

animal approach (Altmann 1974) and standardized observation procedure. Pikas were identified by unique colored ear tags assigned during annual summer live-trapping efforts (Wilkenning and Ray 2016). To minimize influencing the focal pika's behavior, the observer was positioned approximately 20–50 m from the core of the focal pika's territory, estimated by the presence of a relatively high density of pika sign (Jeffress et al. 2013), including scat and urine stations (whitewash) and/or freshly cached plant material (haypiles). Observations were 45 min long to allow pikas time to adjust to the observer (Ivins and Smith 1983, Roach et al. 2001, Hayes and Huntly 2005). Behaviors of the focal pika—food-caching (haying), feeding, moving, scanning/resting, calling, chasing, escaping, and preening—were recorded in 1-min intervals. If the focal pika was not seen during a 1-min interval, it was recorded as unseen. For the purpose of this study, surface activity refers to the total number of minutes in which an animal was seen or heard calling above the surface during an observation. Surface activity was also averaged per focal pika for the first, middle, and last 15 min of each 45-min observation. The actual time at which the midpoint of the observation took place (*time*) was defined in minutes from midnight. Observations that began between 08:30 and 17:30 were categorized as *midday* observations and those that began before 08:30 or after 17:30 (ca. dawn and dusk) were *non-midday*, creating a binary category. All observations began after sunrise (ca. 06:00) and ended before sunset (ca. 20:30). The seasonal period during which the observation was conducted (*period*) was categorized as either early summer (June and July) or late summer (August and September) in order to correspond with the late-summer onset of food-caching behavior reported for a pika population at a similar site in Colorado (Dearing 1997). Wind strength (*wind*) and amount of cloud cover (*skies*) were estimated by averaging qualitative assessments made at the beginning and end of each behavioral observation (Table 1).

Temperature Measurements

Before the start of each focal observation, 2 HOBO® temperature data loggers (accuracy ±0.2 °C; Onset Computer Corp.) were placed near the edge of the focal pika's core territory. Loggers were placed several meters away from

TABLE 1. Candidate predictor variable definitions.

Predictor name	Definition
<i>shallow</i>	Shallow subsurface temperature, scaled (here and below) as $x_i = (x_i - \mu_x)/\sigma_x$
<i>deep</i>	Deep subsurface temperature
<i>temp difference</i>	The difference between subsurface temperatures, <i>shallow</i> minus <i>deep</i> , scaled
<i>deep residuals</i>	Residual of <i>deep</i> regressed on <i>shallow</i> , scaled and log transformed
<i>time</i>	Actual time (minutes from midnight) at midpoint of the observation, scaled
<i>midday</i>	Binary classification, daily time period in which an observation began: 1 = midday (08:30 to 17:30), 0 = non-midday (before 08:30 or after 17:30, generally close to dawn or dusk)
<i>wind</i>	Qualitative assessment of average wind strength during observation: 1 = low (bends only grasses), 2 = low-moderate, 3 = moderate (bends tree branches), 4 = moderate-high, 5 = high (bends whole trees)
<i>skies</i>	Qualitative assessment of average cloud cover during an observation: 1 = sunny, 2 = partly cloudy, 3 = moderately cloudy/overcast, 4 = mostly cloudy/overcast, 5 = fully overcast, 6 = light precipitation
<i>period</i>	Early summer (June and July) or late summer (August and September)
<i>aspect</i>	North or south
<i>site</i>	West Knoll (WK), Long Lake (LL), or Mitchell Lake (ML)
<i>year</i>	2012–2017 (categorical)
<i>observer</i>	One of 10 observers who contributed to the data set
<i>pika</i>	Each unique pika observed ($n = 97$)
<i>pika_{year}</i>	Pika-year: data from a pika in one year was treated as independent of data from the same pika in another year ($n = 103$)
<i>pika_{obs}</i>	Pika-observer: when pikas were nested within observers to account for random effects, data from a pika observed by one observer were treated as independent of data from the same pika observed by another observer ($n = 108$)
<i>seen</i>	total time a pika was observed during a given 45-min observation

any haypiles to avoid direct interference with pika activities. One logger was placed within the top strata of talus (ca. 0.1 m below the surface) to measure shallow subsurface temperature (*shallow*), and the second was placed nearby (about 1 m below the surface) to measure deep subsurface temperature (*deep*; Fig. 2). All loggers were positioned in full shade to avoid direct sun exposure. Each logger was programmed to record temperature every 5 min. We averaged the middle 3 temperature records (from minutes 20 to 30) to characterize the mean temperature during each observation. Temperatures recorded during the first 15 min were discarded to avoid remnant influence of surface temperature on the data logger. Records from the last 15 min were also discarded, because discarding only the first 15 min of temperature records would bias the mean temperature estimate if temperature truly trended during a 45-min observation (a common occurrence).

We characterized the difference between *shallow* and *deep* temperatures (*temp difference*) at each point in a day using a post hoc analysis of temperature data from paired shallow and deep temperature data loggers placed at 9 focal pika locations on the West Knoll. Each

logger pair recorded temperatures every hour from 12 July to 8 October 2018. An average daily temperature profile for each month was estimated by fitting a curve to the hourly data from each logger. Specifically, we employed a generalized additive model (GAM) to generate each curve and fit the daily peak and trough in temperature using a cyclic cubic spline as a basis for the smooth term in each GAM. GAMs were fit using function *gam* in package *mgcv* (Wood et al. 2016) of the R language for statistical analysis (version 3.3.1, R Core Team 2016). To characterize *temp difference* associated with our behavioral observations, the average daily time progression of *shallow* and *deep* temperatures was estimated using mean *shallow* and *deep* temperatures from each observation. We fit similar curves to the mean *shallow* and *deep* temperatures and could then use the difference between curves as an estimate of the expected difference between *shallow* and *deep* temperatures for any arbitrary time of day.

Modeling Surface Activity

To study the relationship between surface activity and microclimate, we fit generalized linear mixed effects models using the R package

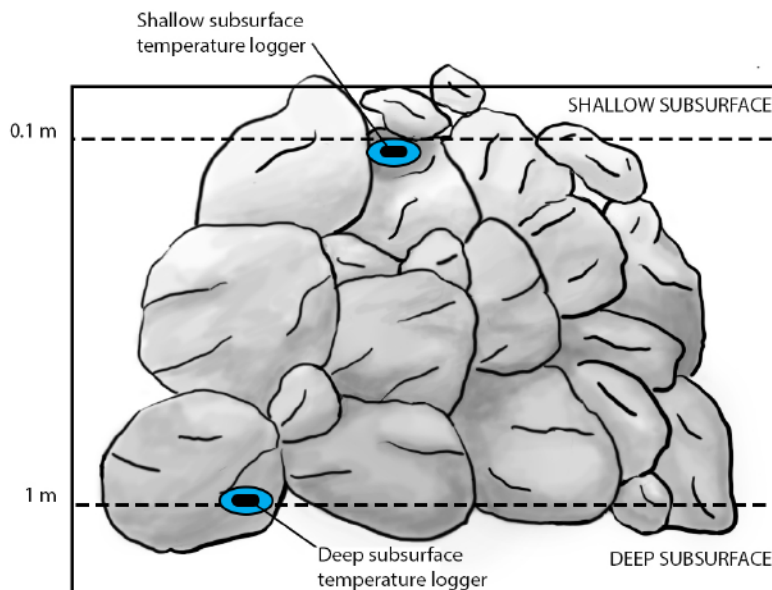


Fig 2. Placement of shallow and deep subsurface temperature data loggers in the talus. Cross section of a typical talus slope, consisting of boulders and smaller rocks, with data loggers (blue) placed in shallow and deep subsurface positions.

lme4 (Bates et al. 2015). The independent variable, focal pika surface activity (y = minutes seen), was treated as a binary independent variable modeled with a logit link. Minutes seen and unseen summed to 45 for each standard observation. Candidate predictor variables were selected based on the extensive pika literature and relevancy to summer surface activity (Table 1). Prior to regression analysis, all numeric variables were scaled and two (*wind*, *skies*) were log-transformed to reduce heteroscedasticity. The Akaike information criterion with correction for small sample size (AICc; Burnham and Anderson 2002) was used to determine the support for each model. To avoid multicollinearity, predictor variables that were highly correlated (Pearson's rho [ρ] or Kendall's tau [τ] > 0.5; Fig. 3) were not included in the same model. However, in the case of *deep* and *shallow* temperatures (ρ = 0.68), we included effects of both predictors in the same model, following the method of Graham (2003), by replacing *deep* with the residual of its linear regression on *shallow*. This residual (*deep residual* in Table 1) represents the components of *deep* that are not correlated with *shallow*.

Our null model included a fixed effect of *site* (WK, LL, or ML) and nested random effects of *observer* (n = 10) and *pika_{obs}* (n = 108). In

general, each observer conducted research in a separate year, so *observer* explained much of the variance that might otherwise have been explained by *year*. *Pika* identity was also somewhat confounded with *year*. Of 97 unique pikas observed, only 8 were observed by multiple observers, and these 8 were mostly observed by different observers in different years. Thus, we accounted for repeated observations of each *pika* by each *observer*, but we treated as independent each pika-observer combination (*pika_{obs}*).

We did not test for every possible interaction effect between predictor variables. Instead we considered only those interaction effects that we hypothesized would have a strong effect on pika surface activity. For example, interaction effects between *wind* and *skies* were well supported by initial models but were eventually excluded from model analysis because observations were not conducted when both metrics were relatively high (e.g., during afternoon thunderstorms).

Ethical Note

Research protocols were approved in 2008 and renewed annually by the IACUC at the University of Colorado at Boulder. Permits were issued by the Colorado Division of Wildlife (2008–2017). Wire mesh live traps

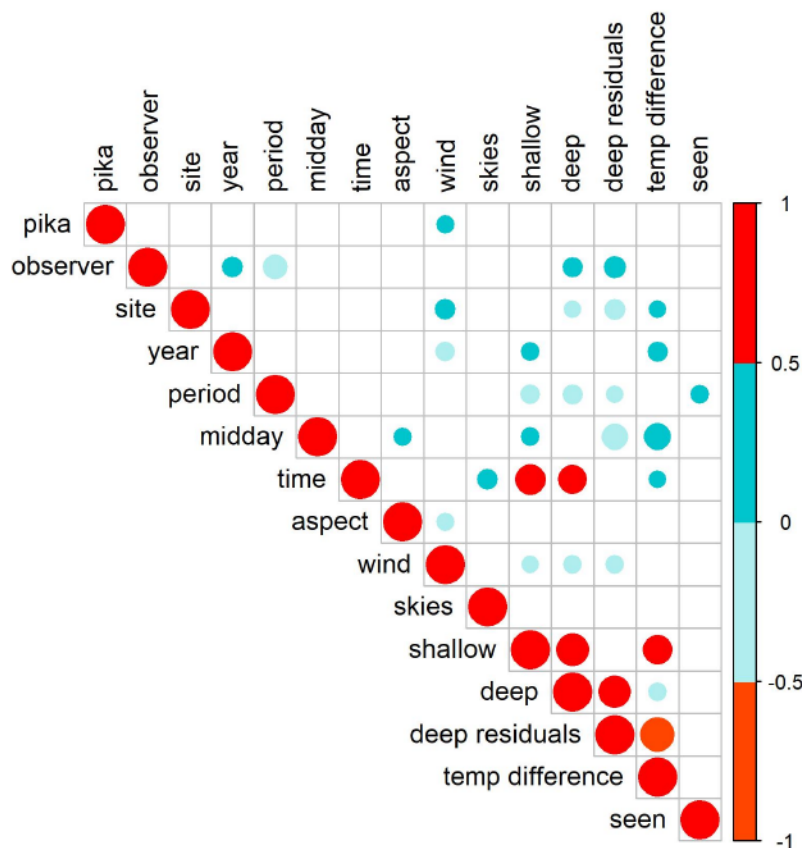


Fig. 3. Correlation plot for candidate predictor variables (see Table 1 for definitions).

were provisioned with vegetation and were covered and surrounded closely by rocks to protect trapped pikas from exposure to sun, rain, and predators. Trapped pikas were self-transferred to an anesthetizing (drop) chamber for light anesthesia using vaporized isoflurane diluted in propylene glycol (Itah et al. 2004). Pika respiration was monitored continuously throughout a brief (20–30 min) handling process that included color coding each ear with a commercially available rabbit ear tag (National Band and Tag Co.) adapted for use on the smaller, shorter ears of a pika by removing excess material (weight) from the tag. Tagged pikas were released immediately at the point of capture and were not subject to behavioral observations for at least 24 h.

RESULTS

The final data set included 193 observations of 97 unique focal pikas, of which only

3 were observed in multiple years. A 2-way ANOVA without replication indicated that mean surface activity was not significantly different between the first, middle, and last 15-min periods of the 45-min behavioral observations ($F_{1,95} = 0.390$, $P = 0.534$), suggesting that the initial arrival and continued presence of the observer did not substantially influence how frequently a pika was seen during an observation. Thus, surface activity was analyzed for the full 45-min observation.

Mixed Effects Models

Midday, *temp difference*, and *wind* emerged as the predictor variables most consistently present and significant in the top models (Table 2). Pikas were less surface active at midday, as wind strength increased and as the difference between shallow and deep subsurface temperatures increased. Effect sizes for these 3 predictors were small across all models, but

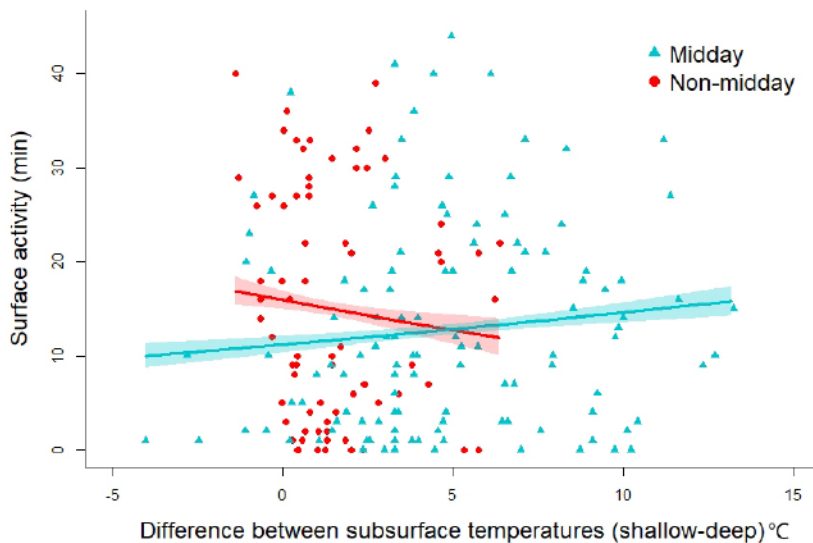


Fig. 4. Surface activity by time of day versus difference between subsurface temperatures. Relationships between surface activity and the difference between shallow and deep subsurface temperatures differ between midday observations (light-blue triangles) and non-midday observations from dawn and dusk (red circles), as illustrated here using a pair of simple linear regressions (lines) and 95% confidence intervals (shaded areas) for each set of observations.

TABLE 2. Models with highest support. Each model included a fixed effect of site and a random effect of $pika_{obs}$ nested within observer, abbreviated here as SOP. The effect of site was consistent for each model (positive for Mitchell Lake [ML] and West Knoll [WK]). A colon (":") indicates terms included in an interaction. Sign (+ or -) indicates the sign value of the regression coefficient. Sample size: 193 observations. Bold text indicates the top-performing model.

Model rank	Model	AICc	$\Delta AICc$
1	-midday*** -temp difference*** -wind*** +midday:temp difference*** + SOP	1898.55	0.00
2	-midday*** -temp difference*** +skies** +midday:temp difference*** + SOP	1904.42	5.87
3	-midday*** -temp difference*** -wind*** -temp difference: wind* + SOP	1909.42	10.87
4	-midday*** -temp difference*** +midday:temp difference*** + SOP	1911.47	12.92
5	-midday*** -wind*** -temp difference*** + SOP	1913.28	14.73
6	-time*** +time2*** +deep*** -wind*** + SOP	1919.46	20.91
—	SOP (null model): site + (1 observer/ $pika_{obs}$)	2037.19	138.60

*Significant at the 0.05 probability level

**Significant at the 0.01 probability level

***Significant at the 0.001 probability level

P values generated by the package *lme4* for these predictors were <0.05 for all of the top models (Table 2). Models that included other temperature metrics (i.e., *shallow*, *deep*, *deep residuals*) were less supported: the most supported model with *deep* as a predictor was ranked sixth ($\Delta AICc = 20.91$). The most supported model included a positive interaction between *temp difference* and *midday*, indicating that pika surface activity increased with the difference in subsurface temperatures at midday but declined with the difference in subsurface temperatures near dawn and dusk (Fig. 4). Pikas were more likely to be active at

dawn and dusk and less active during the middle of the day when the difference between *shallow* and *deep* temperatures was smallest. Removing the random intercept term for focal pika significantly reduced support for all models, suggesting the importance of individual variation. Models based on *midday*, our binary metric of time of day, were more explanatory than models based on *time*, our continuous metric of time (Table 2).

Daily Subsurface Temperature Fluctuations

Our post hoc analysis of temperature data from paired shallow and deep loggers placed

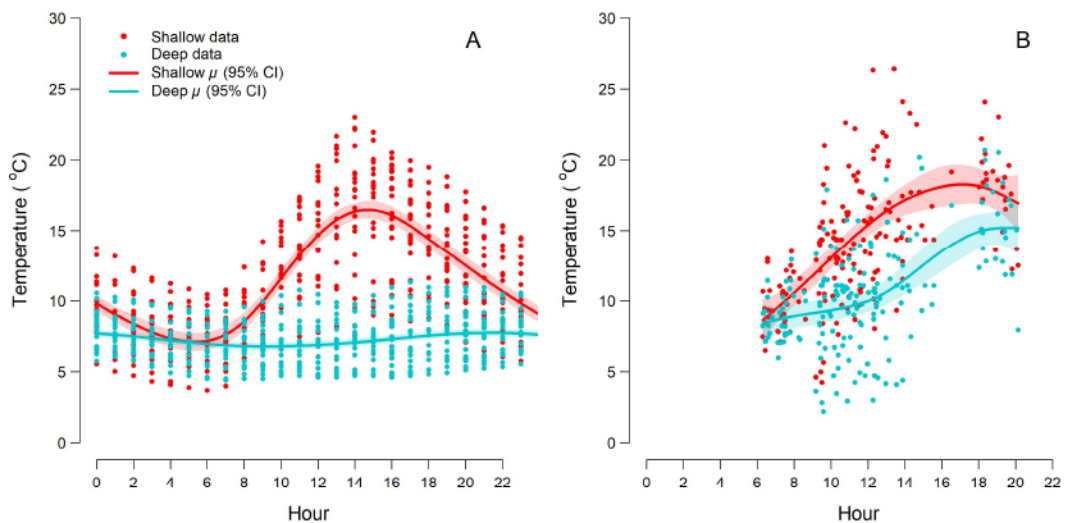


Fig. 5. Shallow (red) and deep (light blue) hourly subsurface temperature variation observed (points) and fitted (lines) using a generalized additive model (GAM). Bold lines indicate the GAM fit, while shaded bands indicate 95% confidence intervals. **A**, July (2017) temperatures recorded by a pair of temperature data loggers on the north face of the West Knoll. **B**, Mean temperatures recorded by paired loggers during all behavioral observations (2012–2017).

at 9 focal pika territories on the West Knoll suggests that shallow temperatures fluctuated much more than deep temperatures (Fig. 5A). Shallow temperatures were lowest just after dawn and peaked in the early afternoon, when the difference between shallow and deep temperatures was greatest. There was a difference between shallow and deep subsurface temperatures throughout each day, and this difference was largest when shallow subsurface temperatures were highest (ca. early afternoon). Similarly, GAM fits to subsurface temperature data from all behavioral observations (Fig. 5B) also showed an increasing difference between shallow and deep temperatures due to increasing shallow temperatures.

DISCUSSION

In this study, we found that pikas at these high-elevation Colorado sites were less surface active in high winds and less surface active when the difference between shallow and deep subsurface temperatures was greater. The difference between shallow and deep subsurface temperatures explained pika surface activity better than either shallow or deep temperature considered individually, particularly during midday observations. These findings supported our hypothesis that pika sur-

face activity will be higher where there is a stronger gradient in subsurface temperatures to facilitate behavioral thermoregulation. However, the difference between shallow and deep temperatures appeared to increase mainly as a result of rising shallow temperatures at our sites, with deep temperatures remaining more consistent during this study. Thus, our ability to discriminate among predictions of how pikas react to different processes forming the subsurface temperature profile was limited. To better evaluate how pikas respond to microclimate, future studies should compare surface activity among sites that differ by the process affecting the subsurface temperature profile.

Reduced surface activity during high winds has previously been documented in pikas and could be a result of increased risk of predation during conditions that reduce alarm call transmission (Hayes and Huntly 2005). Alternatively, reduced activity in the wind could represent behavior to limit increased heat loss (Tregear 1965). Hayes and Huntly (2005) argue that the heat-loss hypothesis is unlikely during summer months, considering the many cold-weather adaptations documented in pikas. However, in our study areas, high winds were typically correlated with moderate to severe thunderstorms during summer. While observations were not conducted during severe conditions (active

lightning or rain), high winds might have been associated with cold downdrafts as well as incipient rain that pikas would likely avoid. These explanations remain speculative in the absence of more detailed data on how wind, temperature, and precipitation interact in this area.

Biophysical models (Moyer-Horner et al. 2015, Rodhouse et al. 2017) and at least one comprehensive behavioral study (Smith et al. 2016) have suggested that subsurface spaces serve as places for pikas to shed heat while temperatures above the talus are hot. Moyer-Horner et al. (2015) demonstrated that pika surface activity decreased when surface temperatures above the talus were high, but they did not find shallow subsurface (10–15 cm) temperature to be a significant predictor of activity. Smith et al. (2016) found that pikas were less active when both surface and subsurface (0.5–1 m) temperatures were high at a warm low-elevation site, but not at nearby high-elevation sites more comparable to elevations in our study system. We also found no effect of shallow subsurface temperature on surface activity until we considered the potential for an effect of the difference between shallow and deep temperatures on pika thermoregulation.

Why would pika surface activity respond to the subsurface temperature profile only during midday? Although we lack data on specific subsurface behaviors, we offer 2 hypotheses given the results: (1) the difference in subsurface temperatures was typically larger at midday, suggesting that a larger difference in temperatures may have been more effective for pikas to shed heat and resume surface activities more quickly; and (2) surface temperatures might be low enough near dawn and dusk that pikas do not need to rely heavily on behavioral thermoregulation (Smith 1974, Moyer-Horner et al. 2015, Rodhouse et al. 2017). Smith (1974) found that pikas were significantly less active during midday and when air temperatures were high at lower elevations (approximately 2300–2550 m) in the Sierra Nevada. But at nearby higher elevations (approximately 3350–3400 m), which had far fewer days with temperatures over 20 °C, pikas were active throughout the day (Smith 1974). There might be a similar threshold for subsurface temperatures, above which the talus subsurface is no longer effective as a micro-refuge or below which pikas do not need to use subsurface temperatures to thermoregu-

late. We are not suggesting 20 °C as such a threshold; indeed, we found a significant relationship between surface activity and the difference between shallow and deep temperatures when shallow temperatures were commonly below 20 °C. Yet pika behavior below the talus surface is still poorly studied, and reduced surface activity could be due to thermoregulation, predator avoidance, resting behavior, interactions with young (e.g., nursing), or activities related to food-caching (e.g., cache rearrangement), among others. These ideas suggest potential complexity in factors controlling surface activity and warrant further studies of pika activity in relation to the microclimate.

In summary, we showed that the surface activity of one small mammal can be predicted by subsurface temperature profiles using fine-scale temperature data. Our results do not resolve the lack of consensus concerning pika vulnerability to temperature and climate change; however, we provide further evidence for understanding how pikas respond to microclimates. Smith et al. (2019) found that intraspecific variation in pika responses to climate primarily varied by ecoregion, not genetic affinity. Their findings underlie the importance of understanding local drivers of behavior, rather than comparing results across the entire range. We additionally suggest that pairing fine-scale measurements of microclimate with behavioral observations of tagged individuals may allow more accurate evaluation of how animals might use climate refugia to persist in changing conditions, and could have implications for assessing species persistence and habitat use. While our results provide a more nuanced view of how pikas may respond to microclimates, our scope of inference is limited because data were collected at a cluster of Colorado sites that represent only a small portion of the pika's range. Additional studies replicating these results in other locations, especially at low-elevation sites, might further illustrate how pika surface activity may be affected by the difference in temperature between shallow and deep strata of the talus subsurface.

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